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Evolutionary thanatology: impacts of the dead on the living in humans and other animals

Theme issue compiled and edited by James R. Anderson, Paul Pettitt and Dora Biro

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Evolutionary thanatology

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Introduction

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Societies, including those of humans, have evolved multiple ways of dealing with death across changing circumstances and pressures. Despite many studies focusing on specialized topics, for example necrophoresis in eusocial insects, mortuary activities in early human societies, or grief and mourning in bereavement, there has been little attempt to consider these disparate research endeavours from a broader evolutionary perspective. Evolutionary thanatology does this by adopting an explicit evolutionary stance for studies of death and dying within the sociological, psychological and biological disciplines. The collection of papers in this themed issue demonstrates the value of this approach by describing what is known about how various nonhuman species detect and respond to death in conspecifics, how problems of disposing of the dead have evolved in human societies across evolutionary time and also within much shorter time frames, how human adults' understanding of death develops, and how it is ultimately reflected in death-related language. The psychological significance and impact of death is clearly seen in some species' grief-like reactions to the loss of attachment figures, and perhaps uniquely in humans, the existence of certain psychological processes that may lead to suicide. Several research questions are proposed as starting points for building a more comprehensive picture of the ontogeny and phylogeny of how organisms deal with death.

This article is part of the theme issue 'Evolutionary thanatology: impacts of the dead on the living in humans and other animals'.

Death could not be more profound a subject for the biological sciences. The treatment of the corpse, and the effect of an organism's death on its surviving conspecifics, are core research topics for biological and social scientists, clinical practitioners, and philosophers, for myriad reasons including death's universality, inevitability, irreversibility, and its social and behavioural consequences. Many of us fear death—or at least dying in pain—and as we shall see, even our languages reveal how deep-rooted our concern with it is; the moral standing of the dead can be profound and exert considerable agency among the living, and self-induced death remains a considerably controversial moral and social issue. Despite this, however, as several of the contributors to this themed issue note, social and cultural trends over the last century have distanced most of us from the direct experience of death, and have often fostered a concern to shield children from exposure to it. The result has been the replacement of direct experience and explicit reference by a complex system of culturally varied euphemisms that are usually aimed at masking death or denying its terminal effects [1].

Studying the antecedents, causes and sequelae of death in the animal kingdom and over the long term should, we suggest, form one of the most profound scientific endeavours. Many disciplines have contributed specific perspectives on these, in species ranging from bacteria to insects, birds to aquatic and terrestrial mammals, and anthropoid primates including humans. The literature in these disparate fields, comprising observational, experimental, clinical and sociological studies, is already voluminous; however, thanatology—the academic study of death and dying—has largely lacked a broad evolutionary perspective that could draw these fields together.

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We formally propose here the field of *evolutionary thanatology*. We believe that now is a highly appropriate time to do so, developing a more explicit evolutionary consideration of all aspects of studies of death and dying across the biological and sociological fields. Many volumes have been published that are devoted to bereavement, grief, and to the development of 'funerary' activities in both early and modern humans (e.g. [2–5]), but little attention has been paid to the evolutionary roots and development of many of the death-related activities that have been observed in ancient, recent and modern human societies, and to their psychological foundations and significance. Major changes in human funerary activities can be traced not only over thousands of years [6], but also within much shorter time frames [1]; examples include an increasing distance from the experience of death and funerary treatment of the corpse, by way, for example, of the increasing outsourcing of funeral services, smaller funeral gatherings, and new ways of disposing of corpses as a result of increasing urbanization and industrialization [7]. The use of online social media has played an increasing role in the dissemination of death notices and expressions of condolences and commemoration, essentially a digitalization of funerary activity, and in the USA some drive-through funeral parlours are even tailored to allow mourners to pay their respects without leaving their car. Funerals and memorial events for dead nonhuman animals (not only pets) are becoming increasingly popular in various countries [8], and in Japan this extends to defunct ('dead') robotic dogs, whose parts ('organs') may be removed and donated to other defective robots [9] (figure 1). Clearly, such rapid and profound changes in how we treat the dead, and indeed even in what our concept of 'dead' might mean, reflect cultural developments that fall within the scope—if at one extreme—of evolutionary thanatology.

But where to start? As we shall see, the recognition of death, and responses to the corpse, can have chemical, emotional, rational and cultural bases. The evolutionary perspective we advocate requires a comparative approach, not just within but also across biological taxa. Our aims should be ambitious. What, then, do observations of insects, birds and nonhuman mammals contribute to modern human thanatology? Is it justifiable to seek links between complex modern beliefs and practices and the chemically determined responses of insects or emotionally variable responses of mammals? Can one distinguish discrete packages of responses, perhaps correlated with distinct animal classes, orders, families, and genera? If so, are certain categories or 'levels' of thanatological behaviour predictable under given biological and social circumstances? Under what circumstances do taxa come under selection for evolution of their treatment of the dead? How do the dead impact on the living in various species, and how important is this to the expression of behaviour towards the corpse? A coherent collection of papers that address such issues will be an important first step on the road to setting out an agenda for the emerging field of evolutionary thanatology, and we outline a more specific set of research questions at the end of this paper.

Figure 1. A funerary ceremony for robots, Chiba Prefecture, Japan, April 2018. Photo credit: Kei Oumawatari/28Lab.

Currently, most thanatology-related reports comprise isolated publications in specialist journals (e.g. in archaeology, primatology, zoology, psychology, sociology or human thanatology). Although it is increasingly rich and nuanced, and despite some broader accounts aimed at a general audience (e.g. [10]), this literature provides us with mostly unconnected glimpses of 'crow funerals', 'elephant graveyards' and 'Neanderthal burials', with no rigorous investigation of their intra- or interspecific significance or examination of the evolutionary connections between them. Although, as we shall see from several contributions, current thanatological understanding is for most taxa incomplete and even poor, the available literature does provide a valuable set of studies on which to base preliminary hypotheses for an explicit evolutionary thanatological perspective with which to address these lacunae. From our own research on responses to dead individuals in chimpanzees and early humans [6,11,12] the three of us have become increasingly aware that a cross-field fertilization is critical for this new thanatology. Hence, to provide comprehensive and balanced coverage, this themed issue presents a broad survey of nonhuman responses to the dead, including corpse avoidance and disposal mechanisms in social insects, exploratory interactions with deceased companions in corvids, and caretaking responses to dying and dead individuals in mammals including cetaceans and primates. Contributions also address the evolution of funerary activities in ancestral humans, cultural variations in funerary practices in prehistoric to modern humans, and related phenomena including suicide, infanticide, 'cannibalism', developments in the treatment of grief, cognition, and linguistic and philosophical underpinnings of humans' perception of and activities towards the dead, which take us from the chemical to the cultural realm.

An obvious point of departure is the mechanisms by which animals detect that death has occurred, and at what stage they are cognizant of it. Drawing on evolutionary thanatology's broad taxonomic comparison of non-human animals' responses to death and the deceased, Goncalves & Biro [13] explore the cognitive and sensory bases for detecting life and death in others across invertebrate and vertebrate taxa, seeking phylogenetically ancient as well as more derived mechanisms behind the responses exhibited. When vertebrate taxa encounter dead conspecifics they are confronted by conflicting data; the brain's imperfect agency system will retain notions of the animacy of the deceased, albeit in the absence of any signs of animacy. The authors suggest that the resulting 'animacy detection malfunction' is the mechanism that unites the drivers of responses to the dead in the vertebrate taxa examined. They argue for the integration of approaches from a variety of disciplines—including those as diverse as cognitive science and robotics—as a way of advancing the field of evolutionary thanatology.

The eusocial insects present a remarkable array of ways in which the living deal actively and efficiently with corpses. Sun *et al.* [14] emphasize the risks of disease from dead individuals in densely populated, enclosed colonies of ants, termites and bees; and describe the often sophisticated and complex ways in which these risks are managed, largely based on olfactory cues. It is apparent from their review that variable causes of death will affect the specific ways in which the corpse is treated, introducing a number of behaviours that must, therefore, have deep evolutionary roots, notably necrophobia (avoiding the corpse), necrophoresis (removal of the corpse from the colony), intraspecific necrophagy (cannibalism) and entombment (burial, elsewhere referred to as necroclaustralisation). In an evolutionary sense the eusocial insects, therefore, provide a remarkably variable core set of basic responses to the dead, from which further elaboration is possible over a number of trajectories.

Swift & Marzluff [15] study the drivers of tactile and other interactions with the dead, through controlled experiments with wild American crows. By presenting live crows with taxidermy-prepared specimens in various postures, they find that tactile contacts are rare and typically take the form of aggressive or sexual interactions, while the more frequent alarm calling response suggests correct identification of the specimens as being dead. The extreme manifestations of aggressive and sexual responses to the corpse, which in the case of crows may derive from an inability to mediate between conflicting stimuli, can also be traced among primates and early humans, perhaps providing an evolutionary basis for expression of the common conflicting emotions of anger and sorrow as human responses to death.

These interactions with the corpse are not restricted to the terrestrial realm. Reggente and colleagues [16] provide a compendium of more than 100 reported cases of responses to conspecific death events among aquatic mammals—most of which comprise behaviour towards deceased young—and perform a comprehensive quantitative treatment to seek individual and social variables that predict the type of response exhibited. Cetaceans and non-cetaceans both react to death, but in distinct ways; whereas the latter protect their dead from attack, cetaceans carry the corpse, a difference that may relate to the relative maternity investment (short in non-cetaceans), and is reminiscent of the effects of the parent–offspring bond on corpse management observable among primates. Reggente *et al.* identify characteristics such as levels of alloparental care and calf dependence as variables that shape behaviour towards the dead in different species, for example by increasing the length and intensity of caretaking directed at deceased young.

The parent–offspring bond takes centre stage again in Watson & Matsuzawa's [17] discussion of the phylogeny of maternal responses towards dead infants among non-human primates. In their review they identify varied responses among apes and monkeys including grooming, protection of the corpse, and filial cannibalism. As in crows, the wide range of these responses is notable. They argue that to elucidate proximate and ultimate drivers of these varied responses the detailed reporting of data from a diverse range of species will be needed. To facilitate the development of evolutionary thanatology they propose explanatory hypotheses for these behaviours, and provide a systematic framework for testing alternative hypotheses through the quantitative coding of post-mortem behaviour.

Anderson [18] focuses specifically on chimpanzees, reviewing the literature and describing the various ways in which they can learn about death in conspecifics and other species. As in Sun *et al.*'s analysis of eusocial insects, his review of causes of death raises the question of to what extent cause is reflected in the behaviour towards the corpse. Based on chimpanzees' known cognitive and empathic abilities, Anderson notes that they are likely to be aware that death is characterized by a cessation of function, and that it is irreversible, traits that, as we shall see, modern human children possess by the age of 10. Anderson suggests that with sufficient personal experience of dangerous situations, and through witnessing injurious or fatal events in others, these great apes may construct a concept of death that shares several of the components of adult humans' death concept, a notion picked up by Pettitt (see below). As with other contributors, Anderson notes a desire for researchers to pay more attention to cultural (i.e. inter-group) variations in practice.

Several contributors take us into the complexities of the modern world. Shimane [7] is interested in how modernization over the last century has impacted on funerary practices. His quantitative analysis of contemporary practices in five east and southeast Asian countries reveals that in the context of relentless population migration and rise of average age at death, death-related services have become increasingly commoditized and outsourced over a very short period of time, alongside a growing disengagement of local communities from their own funerary ceremonies. Thus, he documents how the evolution of human funerary practices, which began with simple necrophoresis, is undergoing rapid and significant change in the industrialized world.

This rapid pace of change in modern, industrialized societies has altered children's exposure to death, with changes in multiple direct and indirect factors variably affecting their acquisition of death concepts. In their discussion of the changing weight of these factors, Longbottom & Slaughter [19] highlight the importance of direct experience (including the deaths of animals), parental communication, and media portrayals in children's developing concept of death. They conclude with recommendations for enhancing children's understanding and readiness to cope with bereavement. Harris [20] takes a developmental psychologist's perspective on children's concepts of death. By the age of 10 children know that it is inevitable for all living creatures, and irreversible. Harris argues in particular that children adopt two parallel concepts of death: one from a biological viewpoint in which the dead are corpses, and another in which they are thought of as continuing in another existence, despite being deceased in this one. Such continuing ties to the dead manifest, among other things, in burials. Given their proximity to the living, he argues, these may ratchet up the accumulation of memories about the dead, and hence deepen awareness of antecedent generations.

In an agenda for how Palaeolithic archaeology may contribute to wider evolutionary thanatology, Pettitt [21] shares the interest in the origins of burial, reading the earliest burials of Neanderthals and *Homo sapiens* in the context of a developing sense of persistent social space. Picking up from observations such as Anderson's, he argues that a core set of mortuary activities occurring face-to-face—similar to those documented for modern primates in this volume—began to extend into the landscape as early human group size and social complexity grew to the extent that peripersonal mortuary behaviours were no longer sustainable. He sets out a number of research questions for Palaeolithic thanatology. Chronologically, Orschiedt [22] follows on, reviewing the burial practices of the European Final Upper Palaeolithic and Mesolithic, the stable but diverse practices of Europe's last prehistoric hunter-gatherers. He observes geographical variation in whether burial was practised or not, and differences in extreme states of corpse processing (disarticulation, as opposed to burial). Most importantly, he identifies the appearance of 'cemetery-like' clusters of relatively large numbers of burials, a pattern that one can also see in North Africa and the Near East. He sees considerable continuity between the first cemeteries of the last few thousand years of the Pleistocene and the Mesolithic communities of early and mid-Holocene Europe, while recognizing an increasing diversity of practice among the latter. Matsumoto [23] takes us even further into the cultural evolution of burials, reviewing the relationship between the living and the dead in Japanese prehistory. The dead seem to have continued to play a central role in the social systems of the living among Jomon hunter-gatherers, evidenced, she argues, by funerary practices that changed significantly alongside major demographic thresholds. With the first population increase in the Middle Jomon period, the first cemeteries were created, as a response to increased sedentism. Following a population disruption, subsequent practices focused on burials placed centrally in circular planned settlements; after these, in turn, collective secondary burials were emplaced in newly established settlements. All of these are clear examples of the centrality of the dead to kinship systems, and the effects of population movement and disruption on the latter.

Not just our actions but also the ways we speak about death can inform us about how we think about it. In a powerful linguistic analysis, Husband [24] examines death-related verbs, which are remarkably prevalent in *any* language, to argue that death has a special significance in human cognition. Death-verbs are shown to exhibit different grammatical constraints compared to other verbs, and to do so consistently across different languages, suggesting that language surrounding death can reveal aspects of the evolution of mental representations of thanatological phenomena in humans. Perhaps the most profound indication that most societies believe—if unconsciously—in some kind of continued agency of the dead, is their persistence in the moral systems of the living. Luper [25] provides a philosophical treatment of the moral issues surrounding our treatment of the dead, asking if the dead have moral standing. By demonstrating that events that happen after an individual's death can indeed be good or bad for them (despite the fact that they are dead)—and thus by affecting their prudential interests it is possible for us to benefit or harm them posthumously—the dead can be argued to have moral standing.

Given that death constitutes the mental and physical cessation of an individual in the world, and as at some point in evolution individuals have come to know that they can choose when to end their existence within it, death has come to be imbued with considerable moral responsibility. Two papers focus on suicide. Noting that suicide constitutes a remarkable 1.4% of deaths worldwide—it is the leading cause of violent death—Humphrey [26] explores some of the psychological particularities of humans that might make the purposeful killing of oneself a uniquely human phenomenon. He contrasts 'altruistic' and 'egoistic' suicide, and explores how these puzzling behaviours have evolved. The suicide meme is highly infectious, and most suicides are egoistic—deriving from a desire to remove one's own mind from the world, a concern with personal escape, often with no concern for its effects on others. But how could this be adaptive, and how might attempts to deter it create cultural beliefs about death? O'Connor & Kirtley [27] note that, despite some 800 000 suicides globally per year, we are still unable to predict its imminence; it is a major public health concern. Commencing from the heuristic that suicide is a *behaviour*, built on precedents of ideation and intention, they present the 'integrated motivational-volitional model' of suicide, to explain how suicidal ideation can progress to completion of the act. The model focuses on interactions between negative feelings such as defeat or entrapment and other personal and environmental factors such as impulsivity, access to means, and exposure to suicide, with implications for preventive intervention.

Grief—and its emotional precursors—forms a central concern of thanatology, and although humans experience it as a natural response to bereavement, in many cases it may become pathological: it can persist, with little sign of the sufferer returning to normal functioning. Nakajima [28] provides a study of extreme cases of grief, through examples of persisting grief with high levels of acute symptoms. She traces developments in the understanding of normal and 'complicated grief', the latter of which can have profound mental health implications and act as one stimulus for suicide. Agreement on criteria for the identification of complicated grief is still lacking, hence research is required for its diagnosis and treatment.

The contributions to this themed issue understandably present a disparate set of behaviours, although there are surprisingly repeated themes that are shared by most and they provide fruitful opportunities for cross-disciplinary research. Studies across modern animal taxa will provide the spatial perspective; the long-term perspectives offered by archaeology will provide the time; and perspectives on the modern urban and industrial world will provide the extreme complexity. What do these disparate studies reveal? Certainly a surprising variability of responses to death and to the corpse in both terrestrial and aquatic realms, whereby responses vary with the relationship of the deceased to the living, the cause of death and condition of the corpse, and involving chemical, visual and tactile information gathering. We outlined some broad aims for evolutionary thanatology above; now, some more specific research questions for evolutionary thanatology emerge:

- Is it feasible to construct a phylogeny of responses to death; what traits are phylogenetically ancient, and what ones derived?
- Does the evolutionary diversification of responses to death/the corpse always follow an elaboration from chemical through emotional to cultural stimuli?
- To what extent do cues in various sensory modalities elicit thanatological responses (including motoric and affective or emotional) in different taxa?
- How variable can behaviours such as necrophobia, necrophoresis, necrophagy and necroclaustralisation be within a specific taxon? Are they applied to all of the deceased? If not, under what conditions are they applied?

- — Exactly how does social structure of the living—and the position of the deceased within this—determine the specific responses to death/the corpse? At what classificatory level/s can one identify this?
- — Can specific responses to death/corpses in a particular taxon be related to the specific nature of the death event? At what biological classificatory level/s can one identify this?
- — How are mechanisms for detecting, dealing with or denying the effects of death determined by evolving social environments?
- — As Humphrey eloquently puts it, how has natural selection got to grips with *not being*? At what point in evolution can one identify a specifically moral concern with suicide (and, we would add, murder)?

These questions are merely a sample; others, along with new ideas and methods for advancing knowledge of the evolution of responses to death will emerge from both ontogenetic and phylogenetic perspectives. Field workers have often been reluctant to report single case studies of death-related responses in animal societies given the perceived problem that they may be unique and hence unrepresentative of any 'norms'. Why not? We must start somewhere, and uniqueness in a thanatological sense may be as important to document as norms. The accumulation and critical assimilation of such accounts, along with results of experimental studies such as those conducted in social insects and birds, will be of immense importance for organizing and assessing a holistic picture of the impacts of the dead on the living across evolutionary history. It is our hope that this volume will provide a valuable starting point in this endeavour, and we thank all contributors for taking this in the spirit intended.

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Comparative thanatology, an integrative approach: exploring sensory/cognitive aspects of death recognition in vertebrates and invertebrates

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Review

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Evolutionary thanatology benefits from broad taxonomic comparisons of non-human animals' responses to death. Furthermore, exploring the sensory and cognitive bases of these responses promises to allow classification of the underlying mechanisms on a spectrum from phylogenetically ancient to more derived traits. We draw on studies of perception and cognition in invertebrate and vertebrate taxa (with a focus on arthropods, corvids, proboscids, cetaceans and primates) to explore the cues that these animals use to detect life and death in others, and discuss proximate and ultimate drivers behind their capacities to do so. Parallels in thanatological behaviour exhibited by the last four taxa suggest similar sensory–cognitive processing rules for dealing with corpses, the evolution of which may have been driven by complex social environments. Uniting these responses is a phenomenon we term 'animacy detection malfunction', whereupon the corpse, having both animate and inanimate attributes, creates states of fear/curiosity manifested as approach/avoidance behaviours in observers. We suggest that integrating diverse lines of evidence (including the 'uncanny valley' effect originating from the field of robotics) provides a promising way to advance the field, and conclude by proposing avenues for future research.

This article is part of the theme issue 'Evolutionary thanatology: impacts of the dead on the living in humans and other animals'.

1. Introduction

> It is often difficult to judge whether animals have any feeling towards others' sufferings. Who can say what cows feel, when they surround and stare intently on a dying or dead companion?
>
> —Darwin [1, p. 73]

> [Researchers] state without qualification that man is the only animal that can be aware of his own future death. But I suggest that we pause and ask just how anyone knows this. What sort of evidence is available either pro or con?. (. . .) The available negative evidence supports at most an agnostic position.
>
> —Griffin [2, pp. 104–105]

Awareness of death has been regarded as one of the defining traits of *Homo sapiens* by distinct schools of thought, including philosophy [3], psychology [4], anthropology [5] and biology [6]. However, at least since Charles Darwin, the possibility of a psychological continuity between humans and other animals has been entertained. While Darwin himself expressed doubts regarding the extent to which non-human animals (hereafter: 'animals') could comprehend the death of a conspecific, his question was of a different nature from that of Griffin (see quotes above): he asked not if animals have an awareness of their own mortality, but, more modestly, to what extent they recognize death in others and how they 'felt' in response.

These questions are at the centre of the field of comparative thanatology [7], which is concerned with how animals respond to their dead. Recent scientific

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interest notwithstanding, so-called funerary activities among animals have been reported since ancient times. Most notably, stories of elephants and ants burying their dead or dolphins assisting dead companions to the surface are recounted by Pliny the Elder (AD 29–79) and Aelian (AD 175–235) [8,9]. Already in the eighteenth and nineteenth centuries, first-hand reports and anecdotes accumulated on the interactions of animals with dead conspecifics. These included protection of the corpse, transport, vigils and emotional distress, with allusions to grief in non-human primates [10,11], corvids [12,13], proboscids [14,15], cetaceans [16], ungulates [17], carnivores [18,19] and sirenians [20]. Observations similar to these have been confirmed more recently by researchers studying many of the same species [21–27].

In the present paper, our aim is to bring together hitherto partially disparate lines of research, which, in combination, can provide new perspectives on how, and to what extent, non-human animals detect death in others. We draw on empirical case reports as well as current research on animal perception and cognition relevant to elucidating some of their enigmatic responses towards their dead, compare these responses across taxa and discuss how they may have emerged in the course of evolution. We begin by exploring how animals detect life, then through what cues they might detect death, and which aspects of cognition might contribute to processing such sensory information as ‘death awareness’. We conclude by proposing avenues for future research.

2. Detecting life

Within their natural surroundings, animals are constantly confronted with dynamic (moving) visual signals. Interpreting these correctly is a significant factor in evolutionary fitness, as such signals can come from both living (self-propelled motion patterns) and non-living (objects moved by external forces) entities [28]. The ability to distinguish biological from non-biological movement was presumably part of an ancient mechanism that evolved for modulating interactions with other organisms, be they heterospecific predators or prey, or conspecific kin, mates or competitors.

Movement through self-propelled motion was present in the first living organisms during the Pre-Cambrian some 3000 Mya. These organisms moved around with the help of cilia and flagella [29]. Predation was already a strong selective force and one that likely gave rise to the first eukaryotes [30] around 1600–2500 Mya [31]. By the Ediacaran Period (635–540 Mya), a division between chordates, molluscs and arthropods appeared, as indicated by genetic and fossil evidence [32]. These organisms were essentially relegated to a two-dimensional world confined by bio-mat grazing [33] where, possessing photo-receptors, they navigated discerning between light and darkness. Later yet, during the Cambrian Period, in an increasingly three-dimensional world [34], innovations in many animals emerged that have continued until now: the presence of brains and nervous systems [35], fully formed eyes [36], attention [37], associative learning [38], embodied cognition [39] and even the beginnings of primary consciousness [40].

(a) Biological motion

It was in the field of biological motion perception [41] that researchers found evidence for a perceptual life detector likely common to all land vertebrates [42]. Humans [43,44] and newly hatched chicks [45] were presented with stimuli consisting of moving light point displays against a dark background, one set of stimuli depicting a moving being (human or other) and the other a moving but scrambled or inverted version of the first. Despite light points being severely impoverished percepts, the visual system decodes them in a straightforward manner when their movement corresponds to biological motion, but not non-biological motion; both studies found quick detection by humans and an inherent attraction in the chicks towards biological as opposed to non-biological motion. Further evidence for an ancient neural mechanism common for the detection of animacy came from additional studies with chicks [46] and with human newborns, who also attend preferentially to biological motion stimuli [47,48].

Recent work confirms the biological motion effect in adults of species such as Medaka fish [49], pigeons [50], rats [51], cats [52], dolphins [53] and non-human primates including common marmosets [54], rhesus monkeys [55], baboons [56] and chimpanzees [57]. But to date, no newborn non-human primate has been tested; hence, the issue of innateness is unresolved outside humans. The ability to detect biological movement paired with an inversion effect has some commonalities with other fields in perception such as face recognition in humans [58] and non-human primates [59], a capacity that appears to be innate in many species including primates [60]. The perception of biological motion is likely only one of many components of a larger perceptual system for animacy detection comprising ‘detectors’ of biological cues such as faces, eyes, texture, odour and particular shapes, all fundamentally tied with agency attribution. In humans, self-propelled motion by itself is not a sufficient cue to trigger detection of intentional agency [61,62].

(b) The animate/inanimate distinction

In a recent review of the development of the animate–inanimate distinction in human infants, in addition to biological motion and self-propelled movement, Opfer & Gelman [63] list goal-directed movement (the directness with which an agent moves towards its perceived goal) and contingency of behaviour (the timing between an agent’s actions and specific events) as cues. In studies of human infants’ capacity to decode an agent’s intentions, infants seeing a human hand reaching for an object react to changes in its goals, whereas no such response is observed when a mechanical rod or claw replaces the hand [64–68]. Similar results have been found in capuchin monkeys (*Cebus apella*) [69], while the use of a monkey-like robot but not a moving box induces goal-direction ascription in common marmosets (*Callithrix jacchus*) [70]. During later development, these components of animacy attribution underlie various aspects of human infants’ social cognition [71]. Importantly, the developing refinement of understanding and attribution errors are informative in terms of infants’ categorization of ‘alive’ versus ‘dead’ (including discrete components of full death-awareness: universality, irreversibility, causation and non-functionality [72]; see also Anderson [73] this issue).

The animate and inanimate conceptual categories may relate to distinct neural circuits representing domain-specific knowledge systems that are evolutionarily adaptive [74,75]. Support for this theory includes discovery of a close match between humans and rhesus macaques (*Macaca mulatta*) in inferior temporal cortical object representations, both categorical and continuous [76,77].

3. Detecting death

(a) Scent cues

In the animal kingdom, responses to dead conspecifics include necrophobia (avoidance), necrophagia (feeding) and necrophoresis (transport), and in many cases, these are elicited primarily by chemical signals. Aversion to 'death scents' (fatty acid necronomes or cadaverine/putrescine) may be a highly conserved response that is either innate or acquired easily due to a predisposition. Unlike freezing [78] or thanatosis (death-feigning) [79], which are visual in character, energetically non-costly and have evolved to transmit a specific message from sender to receiver, scent associated with decomposition is an unambiguous cue that receivers can reliably exploit. Necrophobic responses are adaptive in terms of predator evasion or pathogen avoidance. Below we explore in more detail specifically scent-triggered responses to dead conspecifics across different taxa.

In eusocial insects (numerous species of ants, termites and bees), two major, non-mutually exclusive scent-based hypotheses have been proposed to explain the typical burial or corpse removal responses to dead colony members (reviewed in [25] and [41]; see also Sun *et al*. [80] this issue). These hypotheses relate to the presence of specific chemical death-cues (necromones) and to the absence of chemical signatures of life (chemical vital signs), respectively. For example, while some ant species apparently respond to the decomposition-driven accumulation of fatty acids in corpses [81,82], others, such as the Argentine ant (*Linepithema humile*), engage in undertaking activities following the rapid disappearance upon death of cuticular chemicals secreted by live individuals [83]. As the latter mechanism potentially allows for a faster response, it is likely favoured in situations where the removal of dead bodies is time-sensitive, for example, in densely populated colonies where the risk of contamination from pathogens is high. Interestingly, sensitivity to these cues appears to vary in some species according to caste—e.g. soldiers of *Atta mexicana* do not respond to oleic acid, the most common death cue in many social insects [84]—consistent with the observation that undertaking and corpse removal responses are often performed by a subset of colony members only, in a division of labour. Outside of eusocial insects, several genera of Isopoda as well as social caterpillars are known to be sensitive to oleic and linoleic acid extracts (and to avoid these chemical cues), suggesting an ancient origin stretching back to at least the Crustacea–Hexapoda common ancestor 420 Ma for the involvement of necromones in arthropod corpse removal behaviour [85].

By contrast, among vertebrates, death cues such as cadaverine and putrescine, alongside other decay- and putrefaction-related substances, typically elicit aversion responses. Zebrafish avoid cadaverine [86] and show elevated stress levels upon encounter [87], and sea lampreys [88] and sharks [89] avoid odours emanating from decaying conspecific tissue. Rodents, including various species of mice, voles, shrews and chipmunks, also avoid areas where deceased rodents—even heterospecifics—are present, presumably at least partly informed by olfactory cues associated with decaying flesh [90]. California sea lions reportedly avoided a pool used for cooling after the carcass of a dead pup fell into it, moving away after apparently sniffing at it [91]. In humans, a range of interesting emotional and conscious, and unconscious responses to putrescine have been documented, including increased vigilance, active and planned retreat, and hostility towards out-group members [92]. However, not all vertebrates show avoidance: in rats, cadaverine and putrescine elicit the burying of dead conspecifics [93], and in goldfish, the same chemicals enhance feeding activity [94].

(b) Beyond scent: visual, tactile, multi-modal cues

Many animal species exhibit complex responses towards their dead that are not necessarily triggered by scent; furthermore, these often rely on a combination of several sensory modalities. Already among the arthropod examples described above, scent cues may combine with tactile cues to modulate responses to dead conspecifics (e.g. in the termite *Reticulitermes virginicus*; [95]), although the latter alone are insufficient to trigger a response. Here, we explore non-olfactory and multi-modal cue use in corvids, proboscids, cetaceans and primates, with a focus on observational and experimental field studies. The species comprising these taxa display many complex behaviours across both the physical and social domains, and have been argued to possess episodic-like memory. Many live in hierarchy-based social structures in which they cross-modally recognize individuals and act based on their past interactions [96–102]. Moreover, some individuals in these taxa are able to recognize themselves in the mirror, suggesting self-awareness [103–106]. It has been suggested that such species might be capable of an understanding of death [107]; however, there appears to be no qualitative difference between species that fail and those that pass the mirror test of self-recognition in regard to thanatological behaviour (i.e. dead infant carrying, exploratory behaviours towards the corpse, vigils, visitations, etc.) [108].

(i) Corvids

The family Corvidae includes crows, ravens, rooks, magpies, jays and jackdaws. These species generally live in bonded pairs, possess the largest relative brain size of any avian group and show rates of behavioural innovation and complexity unparalleled in other bird species [109].

Observations of thanatological behaviours have been made in several corvid species. Several reports describe a 'ceremonial gathering': an assembly of living individuals near a deceased conspecific. The participants utter alarm calls but seldom touch the corpse or show aggression, in comparison to their predator mobbing or scavenging the corpse of another species [110–114]. Also, compared to the amount of time spent by cetaceans, elephants and primates near corpses (see below), these gatherings tend to be relatively short-lived. There are two reports of objects (feathers, sticks/grass) being placed near the corpse [111,112]. Survivors subsequently tend to avoid the place where a dead conspecific is found [115], so much so that effigies have been found useful for pest control [116,117].

In many bird species, a dead conspecific generates cautious inspection and/or mobbing behaviours (reviewed in [118]). Lorenz [119] reported his tame jackdaws (*Corvus monedula*) attacking him when he carried his black swimming shorts in his hand, and suggested that the likeness of the trunks to a dead jackdaw triggered this mobbing behaviour. Barash [120] paired a predator model—a great horned owl (*Bubo* *virginiatus*)—with either a black cloth or a crow model and obtained similar results: live crows (*Corvus brachyrhynchus*) mobbed these significantly more than the owl model alone. Feathers resembling those of a conspecific may also trigger alarm responses in several crow species [121–123].

The primary mode of recognition, therefore, is likely visual: corpses not exhibiting visual cues such as coloured feathers will not elicit responses from live conspecifics. For instance, Heinrich [110] described how a dead crow he attempted to feed to live ravens (*Corvus corax*) was promptly rejected; it was only accepted as food after removal of the feathers, head, wings and feet. Similarly, Lorenz [119] found that adult jackdaws did not mob him if he was holding a young jackdaw before it acquired black feathers, but they did after those feathers grew. In what has been termed the information-gathering hypothesis [7], assemblages around a dead conspecific might serve to acquire information surrounding the death and to assess a potentially dangerous situation. Additionally, assembling corvids might be appraising new social changes in the group [111,113,115,118,124]. Three experiments formally tested these hypotheses [115,124,125]. In scrub-jays (*Aphelocoma californica*), corpses of conspecifics and similar-sized heterospecifics elicit aggregations and site avoidance [125]. A corpse in prone posture elicits cacophonous aggregations, whereas an upright one elicits mobbing behaviour [124] (see also Swift & Marzluff [126] this issue). Moreover, unlike dead conspecifics, corpses of pigeons (*Columba livia*) elicit little reaction in crows. Interestingly, pigeons are similarly low-responsive to dead pigeons, suggesting that this species processes and evaluates the situation differently from crows [115]. Earlier research on wood pigeons (*Columba palumbus*) used models and showed that pigeons tend to avoid corpses of conspecifics as a default response [127,128], which contrasts with corvids' initial curiosity.

Studies on crows have not yet explored how the social relationship with the dead affects the interactions of the living, particularly in the case of pair-bonding corvids, although this has been alluded to in single-case reports [111,114] (see also §5). In addition, compared to the taxa discussed next, corvids show limited prosocial tendencies [129], including little regard for conspecifics beyond kin or mate; this may explain their shorter-duration and more frequently agonistic responses to corpses compared to non-human primates, proboscids and cetaceans.

(ii) Non-human primates

Currently, more is known about thanatological behaviours in non-human primates than any other vertebrate taxon, and these include mobbing/alarm calling, aggression, dead infant carrying, vigils and visitations of the corpse. Physical interactions with the corpse include grooming, gentle touching, poking, attempted sexual mounting, dragging, rough touching, hair-plucking, beating and even cannibalism (reviewed in [108]; see also Anderson [73] and Watson & Matsuzawa [130] this issue).

Dead infant carrying is a prevalent behaviour throughout Old and New World anthropoid primates, and can last from a few hours to a few months. Reports of extended carrying behaviour exist for great apes [131–134] and Old World monkeys [135–138], with the largest study, on Japanese macaques, documenting 157 cases over a 24-year period [139]. Several hypotheses have been proposed to explain such behaviour, not necessarily mutually exclusive: infants live or dead are perceptually attractive to females: maternal hormones involved in mother–infant bonding likely reinforce carrying behaviour, and some behaviours (such as removal of larvae by grooming) and climatic factors (such as high altitude or low humidity) can contribute to preserving the corpse for extended carrying (reviewed in [108]). Contrary to the mother, other adult group members show little interest in the dead infant, engaging much more with live ones [136,140–143], although periodic inspections and attempts to play with and carry a mummified corpse (e.g. [144]) have been reported. Instances of guarding the infant corpse or its mother against approaches by other group members have also been witnessed [143,145–148].

To what extent primates' (or indeed any taxon's) responses to the dead are shaped by learning is an intriguing question. Witnessing death events can allow information-gathering about various sets of cues associated with the phenomenon that can be retrieved on similar subsequent encounters; active information seeking in such situations has been suggested, for example, in chimpanzees [149]. With respect to the extended carrying of dead infants, the eventual abandonment of the corpse by a mother may reflect her acquisition of some component of death-awareness, through a combination of visual, olfactory and behavioural cues—or their lack of correspondence with those emitted by live infants. Social learning may also shape some thanatological responses: it has been suggested that witnessing dead-infant carrying by others may promote the behaviour in mothers experiencing their own infant's death [144].

Experimental studies of thanatological responses in wild primates are largely lacking in comparison with corvids. Allen & Hauser [150] proposed an experiment using playback calls (as done with vervet monkeys (*Chlorocebus aethiops*)) with recently dead infants, to study concept attribution (e.g. cognizance of death) in non-human primates. Females, they argued, when presented with the playback would (i) orient towards the speaker and act as if the infant were alive, (ii) respond in a distressed manner and search for the infant, or (iii) not react at all and continue engaging in ongoing activities. To our knowledge, this experiment has never been implemented, possibly due to ethical concerns. However, a variation was conducted in a study of the strength of male–female relationships in free-ranging chacma baboons (*Papio ursinus*) [151]. The authors found that males responded to a female's call if there had been a close association (friendship) between them, but not if the female's infant had recently died. Their interpretation was that females, primarily responsible for maintaining these close associations, ended friendships with males upon their infant's death, either because they no longer needed a male to protect their infants or because they themselves no longer benefited from protection by the male. However, an alternative interpretation is that the males themselves chose not to respond on the basis of knowing that the infant had died (including, perhaps, knowledge of the event's irreversibility). We further discuss potential experimental approaches for studying death-related psychological states in non-humans in the final section.

(iii) Proboscids

The order Proboscidea comprises three extant species, the Asian elephant and the African bush and forest elephants. Wild elephants live in complex fission–fusion societies with female matrilineal kin forming a family unit with close, lifetime bonds. The encephalization quotient of elephants rivals that of primates, and they possess as many cortical neurons as humans do, albeit less densely packed than in primate brains (reviewed in [99,152]).

Like non-human primates, elephants have been observed to surround a dead conspecific, interact directly with it, touch it with their feet or trunks, at times attempt to lift it with either foot or tusks, and vocalize in apparent distress. They may also guard the body against predators or other conspecifics and revisit the corpse in the following days [153–156]. Adult females have also been observed carrying dead infants weeks after death [157–159].

Unlike non-human primates observed to date (but see [160]), elephants occasionally cover dead conspecifics with branches, leaves or soil, and may attempt to patch wounds on the dead with dirt or put food in their mouth [21,22,153,158,161]. It is important to consider these behaviours in the context of the elephant's social repertoire with live conspecifics and heterospecifics. Elephants have reportedly buried humans and dead animals [162,163].

Contact behaviours with the corpse include using the trunk to inspect the head and body; even the torso may be used for such inspections. Pulling and stepping over the corpse have been observed, as have scent-related behaviours such as sniffing the corpse with the tip of the trunk and displaying the flehmen response (touching the tip of the trunk to the openings of the vomeronasal organ). Elephants may also put the trunk in their mouths to assess gustatory information about the corpse [156,164]. Elephants show striking responses to the bones of other elephants, particularly skulls and tusks, carefully inspecting them [21,22,165]. McComb *et al.* [166] showed experimentally that African elephants are primarily attracted to tusks in comparison to skulls, pay more attention to conspecific skulls than other objects and show no evidence of recognizing skulls of familiar conspecifics. The attraction to tusks might be because they represent an externally visible cue to identity that is consistent across life and death.

Playback of calls of dead elephants to live group members has also been attempted [167]. When vocalizations of a female were broadcast to her family unit 3 and 23 months after she had died, group members responded with contact calls each time, even approaching the speaker (but did not do so in control trials involving the vocalizations of unfamiliar individuals), suggesting long-term memory and recognition. As it was not specified whether the group members had directly observed the death or seen the female's corpse, it is unknown whether responses to playback calls would differ depending on such knowledge.

(iv) Cetaceans

Thanatological behaviour among cetaceans (whales, dolphins and porpoises) is also becoming increasingly well documented and shows many parallels with primate and proboscid data. The vast majority of reports (compiled in Reggente *et al.* [168], see also [27] for a recent review) concern interactions with dead calves or juveniles; carrying their carcasses has been documented in various dolphin and whale species. Indeed, the behaviour has been observed worldwide and in a range of environments including open oceans, bays and inlets, and rivers [169]. Although carrying can be for extended periods, due to the nature of the aquatic environment rapid decomposition limits carrying duration in comparison to, for example, primates in dry habitats. Carrying typically involves holding the calf on the dorsal fin, against the melon or in the mouth. Along with transport, potentially breathing-related behaviours such as lifting the corpse to the surface of the water and pushing it down have been observed (e.g. [170,171]).

Aside from transport, several other categories of behaviours have been documented, including striking the corpse, non-contact attendance such as stationing next to the corpse, and sexual arousal and copulation (towards adults only; e.g. [172]). Unrelated individuals also occasionally interact with corpses, and carriers of an infant corpse are frequently seen surrounded by other pod members swimming in cohesive, possibly protective formations [169].

Like proboscids, cetaceans possess a keen sense of hearing that likely plays an important role in navigating their physical and social environments [173]; however, most cetaceans do not possess a sense of smell or taste [174]. This is likely to impact both the sensory drivers and the nature of their interactions with the dead. Visual cues (presence of wounds, lack of autonomous movement) and lack of auditory cues (vocalizations) are the most probable sources of information about a deceased conspecific's state.

(v) Vertebrate species in context

Outside of the taxa discussed above, various mammalian species including giraffes [175–178], otters [179], dingoes [180], seals and sea lions [114,181–183] and manatees [184] have been observed stationing around, manipulating, or carrying their dead infants for extended periods of time. Phylogenetically ancient maternal caretaking mechanisms continue to operate even after the offspring has died in both mammalian and avian taxa. On a proximate level, the mother may perceive the infant's condition as ambiguous, or she may anticipate that the infant will yet recover, whereupon she continues her caregiving. On an ultimate level, her actions likely represent behavioural error because of the cost of too readily abandoning a potentially temporarily unresponsive infant. A transitional phase ensues that can vary widely (days, weeks or months), during which the mother will carry or stay in close proximity and interact with the corpse (e.g. inspecting, grooming, licking); these responses will decrease over time, culminating in abandonment or occasional consumption of the corpse (see below).

Nonetheless, corvids, primates, proboscids and cetaceans appear to exhibit the greatest similarities in thanatological behaviours, a trend we predict to occur in other behaviourally/socially complex taxa (see e.g. [185]). This is surprising as they do not share a recent evolutionary past and occupy different ecological niches. What they do have in common, however, are complex societies, extended parental care and large brains. Hence, the parallels among these taxa in thanatological responses may be the result of similar perceptual–cognitive processing rules that evolved in the context of increasingly complex social environments. Responses to adult conspecific corpses are both stronger and longer than in other taxa, in which the most common response is avoidance (e.g. rodents [90]). Alternatively, the fewer occurrences of thanatological behaviours reported in other vertebrate species could be due to observation bias (see §5 for further discussion).

4. The 'uncanny' corpse

What are the perceptual–cognitive processing rules that give rise to complex thanatological responses? Here, we draw on several aspects of visually oriented animals' detection of dead conspecifics to propose a novel synthesis of underlying cognitive mechanisms. Species with larger brains and more advanced cognitive processing, causal reasoning, and information-gathering abilities appear to have comparable responses, suggesting an overlapping phenomenon that is shared across them.

(a) Threat assessment mechanisms

Brains coupled to nervous systems evolved as a means to process ecologically relevant information, and to orchestrate adaptive interactions with the surrounding world. They emerged to deal with the challenges that arise from the physical and social environments, and as these became increasingly complex, so did organisms and their brains [40,186,187]. Detecting cues to the presence of life-threatening risks remains critical for animals, and natural selection has equipped organisms with and without large brains to do this. However, with associative learning, animals no longer adapted only through evolutionary time, but also within their lifetimes via experience-based behavioural adjustments. Thus, cognition and memory, capacities shaped by natural selection, are critical in regulating expectation, detecting discrepancies and anticipating events.

The corpse, a highly salient object, represents a conceptual novelty (any familiar object displayed in unfamiliar configurations or unfamiliar settings) (*sensu* [188]). Comparative neuroimaging research has revealed that novel stimuli are encoded by the hippocampus [189] and the amygdala [190], and damage to these areas diminishes fear and vigilance to threat (reviewed in [191]).

Cross *et al*. [192] used positron emission tomography scans to examine cerebral circuitry involved in integrating visual cues into behavioural responses in crows. Crows possess brain regions analogous to the hippocampus and amygdala in mammals that are activated during potentially dangerous situations. The sight of a novel person holding a dead crow activated visual pathways and the hippocampus, while the amygdala was significantly activated by a predator stimulus (a hawk). These patterns of activity were explained as distinct processing activities when gathering novel threat information (person holding a dead crow) versus retrieving past fear information (mounted hawk).

(b) The uncanny valley

Corpses, as passive entities, defy expectations, provoke emotions and generate various behaviours in the living. Notably, they present a conflicting mixture of presence (odour, wounds, vermin) and absence of cues (movement, sound, body heat). This contradiction is illustrated by the dual approach/avoidance and exploratory/fearful reactions when encountering a dead body. Paying attention towards dead conspecifics is, as previously discussed, evolutionarily relevant, because the corpse might provide information about potential predation events or a pathogen hazard. Furthermore, taking a proximate approach, the living may be responding to novelty in the form of something 'uncanny'.

The uncanny valley phenomenon was originally proposed by roboticist Mori [193,194] to describe the eerie feeling humans experience upon encountering a human replica, and we suggest that it also applies to thanatological responses in non-human animals. Mori used examples such as hand replicas and dead bodies to describe the drop in emotional valence the closer something resembles living specimens of our own species, movement being a key factor in the intensification of eeriness. Cognitive hypotheses posit that an uncanny eliciting stimulus remains in a category boundary or provokes a perceptual mismatch, two explanations that are not necessarily mutually exclusive [195] and not necessarily related to cadavers. An interesting example of this is Goodall's description of chimpanzees' fearful and aggressive responses towards physically deformed conspecifics affected by poliomyelitis who moved in unusual ways [196]. At the ultimate level, an adaptive pathogen-avoidance mechanism could be at play, whereby abruptly acquired physical abnormalities in conspecifics trigger a disgust response in other group members (*sensu* [197,198]).

Steckenfinger & Ghazanfar [199] attempted to test the uncanny valley effect in rhesus macaques and found that both humans and macaques display the same aversion to realistic reconstructions of conspecific faces, particularly, as predicted by Mori, if these were moving (also see [144] for an example of aversion to a 'moving'—i.e. dragged—corpse among wild chimpanzees). This suggests that the mechanism causing uncanny-valley-like responses was present already in the common ancestor of Old World monkeys and *H. sapiens*. Experimental work with human infants suggests that the uncanny valley phenomenon emerges in the first year of life, likely due to perceptual narrowing and learning/differentiation processes [200]. Regarding the quality of dynamic cues, research suggests that the more natural movement is (see §2a), the more likely it is to be accepted by human subjects (suggesting less of an uncanny effect) [201]. Some types of stimuli such as androids or corpses likely fail sensory/cognitive scrutiny based on these learning processes, thus triggering an aversive response.

(c) Animacy detection malfunction

In primates, life detection is part of a series of core knowledge systems [202], in this case, the core system of agency (C.S.A.). The core knowledge theory proposes that hard-wired cognitive skills shape mental representations about the world. It remains unclear how many subsystems contribute to agency representation and how they are inter-related; however, some have been unveiled by developmental and comparative cognitive scientists [202–204]. The animate/inanimate distinction level likely operates through dual core knowledge systems specialized for dealing with animate and inanimate entities: the aforementioned C.S.A. and the core system of object (C.S.O.), respectively. Contrary to agents, objects are predictable. They are inert, moving only when external force is applied to them, and as such, they exhibit no contingency or any of the other traits associated with agency: they neither act nor react, but are acted upon by the living agents.

We suggest 'animacy detection malfunction' as a cognitive term for the conflicting responses exhibited by vertebrate taxa upon encountering dead conspecifics. The agency system is not perfect but prone to error; however, in terms of its primary purpose (agent detection), it normally functions well. Inspired by earlier views [194,205,206], animacy detection malfunction is defined as the conflicting cognitive process upon seeing a corpse brought about by perceptual mismatch ultimately causing a violation of expectation. The mismatch stems from the absence of dynamic cues to animacy with the presence of static cues to animacy and is intensified by individual recognition of the dead conspecific. The corpse then has both animate and inanimate attributes, triggering a conflict between the core knowledge system of agency and the core knowledge system of object.

(d) Death detection mechanism

Humans have long dealt with conflicting stimuli from corpses through cultural mortuary practices that are rooted in the deep hominid past [207]. Barrett & Behne [208] argued for the existence of a death detection mechanism, evolved through the course of human evolution, contending that reliable visual cues indicating death, such as fatal disruptions of the body envelope (e.g. decapitation, severe mutilation), were important in the recategorization from 'living' to 'dead' in humans. This can be illustrated with reference to predator detection accuracy, where failure results in death. The ability to discriminate a live predator (snake, leopard, crocodile) from a dead one allows for the activation of different behavioural decision-making outcomes with implications for survival [208].

In a study of grief after the loss of a companion animal, White *et al*. [209] found that humans viewing a corpse that exhibited reliable cues for death (i.e. grievous injuries, disruption of the body envelope) displayed less vigilant behaviour than when the corpse was intact. What they termed 'false recognitions' (incorrect attributions of sight and sound to the deceased) were also more frequent when the corpse was intact. Adopting and expanding on Barrett & Behne's [208] death detection mechanism, these authors suggest that natural selection shaped the increase in vigilance behaviour whenever a valuable partner was missing, and that attending to reliable cues of death was selected for throughout human evolutionary history.

Earlier applications of these assumptions (i.e. uncanniness, bodily disruptions) feature in experiments on fear performed by Hebb. He revealed concealed objects in a box to captive chimpanzees. Among the stimuli were what he called 'primate objects', which included a plaster taken from the death mask of an adult female chimpanzee, adult and infant chimpanzee replicas, an adult human head replica, a juvenile chimpanzee skull with a movable jaw, the mounted skin of a spider monkey with movable head and shoulders, the curated hide of a juvenile chimpanzee and the corpse of an infant chimpanzee. Some of the objects elicited intense fear or panic (in decreasing order: movable chimpanzee skull, snake cast, movable spider monkey skin, chimpanzee death mask), which Hebb interpreted as fears due to conflict; he suggested that the sight of mutilated bodies aroused an incompatibility at both the perceptual and at the cognitive level [205].

Butler [210] tested rhesus macaques in a test-box where they could see through an opening into another box. This other box contained live snakes, a live conspecific, an anaesthetized conspecific or a dead conspecific with its head on its outstretched hands. Butler predicted that the more frightful the stimulus, the more suppressed the viewing behaviour would be. However, this was not the case, and Butler explained the monkeys' reactions as a possible result of a psychological barrier between the subjects and the objects because no physical contact was possible. The decapitated monkey did elicit more looks than the live one, even though mean looking times were higher for the latter. This result might reflect a configural incongruity in the corpse eliciting a greater number of viewings but decreased overall looking time due to aversion (*sensu* the uncanny valley phenomenon).

How do these considerations help us advance our understanding of death awareness in non-humans in their natural environment? Boesch [160] has suggested that wild chimpanzees have a capacity for the 'causation' subcomponent of a full-blown awareness of death. Chimpanzees of the Taï Forest (Ivory Coast) face higher predation risks than many other chimpanzee communities [147]; they exhibit more fearful responses to individuals that died of disease (10 cases) than those that show wounds due to leopard predation (5 cases). Furthermore, Taï chimpanzees lick the wounds of injured group members, but not the dead. If the reason for these differences lies in an understanding of reliable cues for death (grievous wounds, severe disruptions of the body envelope), then chimpanzees may have an implicit awareness of death, not only distinguishing between dead and alive, but also between different manners of death, potentially providing evidence for the subcomponent of causation.

5. Conclusion and future work

Our review has brought together observations of living individuals' responses to dead conspecifics in invertebrates and vertebrates, evidence regarding the sensory bases of detecting life and death in others, and potential cognitive underpinnings for animals' awareness of death. We suggest that phylogenetically ancient responses relating to death that are present in many animals exist not only for specific predator detection but also form part of a generalized threat detection mechanism. Presumably in corvids, cetaceans, proboscids and non-human primates, these mechanisms run in parallel with living–dead discrimination processes based on associative concepts. We also argue that analogical reasoning is a *sine qua non* condition for human-like death awareness with all of its main subcomponents (universality, irreversibility, cessation and causation).

Many authors have called for more and better data on animals' responses to the dead (including a number of contributors to the present issue—e.g. Watson & Matsuzawa [130]; Reggente *et al*. [168]; Anderson [73]) to advance comparative thanatology—greater taxonomic breadth, more quantitative descriptions and more systematic phylogenetic comparisons. While fully supporting these calls, we also advocate controlled experiments to probe the sensory and cognitive bases of the detection of death and its associated psychological states. For example, presenting taxidermy specimens of dead individuals of various species and in various poses might elucidate what cues trigger responses to the dead, and what adaptive explanations might lie behind animals' interest in the dead [115,124,125]. In addition, further manipulation of stimuli—such as the computer-generated images used by Steckenfinger & Ghazanfar [199] to probe the uncanny valley effect in monkeys—could permit analysis of underlying cognition. What cognitive processes are tapped into when detecting life and death in others? How are cues that conflict within or between modalities (e.g. a decapitated but moving individual, or a moving individual smelling of necromones) resolved in different taxa, and can cross-species comparisons of cue hierarchy inform our reconstruction of phylogenetically ancient versus derived mechanisms for death detection? How do parameters such as state of decomposition, visible cues indicating cause of death, social/kin relationship of corpse and observer, observers' previous experiences with death, etc., influence responses in different taxa? Of course, such experiments need careful ethical consideration to minimize distress to subjects.

In addition, playback experiments like those proposed by Allen & Hauser [150] could probe how living individuals conceptualize dead conspecifics, stress assessment (such as analysis of glucocorticoid levels [211]) can reveal physiological reactions to the loss of conspecifics with close or distant social or kin bonds, and non-invasive neuroimaging studies [192] might demonstrate how animals process corpses on the animate–inanimate spectrum. While both technically and ethically challenging, such a research programme may go a long way towards elucidating the proximate and ultimate drivers of thanatological responses across taxa.

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Review

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Managing the risks and rewards of death in eusocial insects

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Eusocial insects frequently face death of colony members as a consequence of living in large groups where the success of the colony is not dependent on the fate of the individual. Whereas death of conspecifics commonly triggers aversion in many group-living species due to risk of pathogens, eusocial insects perform cooperative corpse management. The causes and social context of the death, as well as feeding and nesting ecology of the species, influence the way that corpses are treated. The corpse itself releases cues that dictate the colony's response. As a result, social insects exhibit behavioural responses that promote disease resistance, colony defence and nutrient recycling. Corpse management represents a unique adaption that enhances colony success, and is another factor that has enabled eusocial insects to be so successful. In this review, we summarize the causes of death, the sensory detection of death and corpse management strategies of social insects. In addition, we provide insights into the evolution of behavioural response to the dead and the ecological relevance of corpse management.

This article is part of the theme issue 'Evolutionary thanatology: impacts of the dead on the living in humans and other animals'.

1. Introduction

The shift from solitary life to eusociality is one of the major transitions in evolution [1]. Eusociality is rare in the animal kingdom, but the eusocial bees, wasps, ants and termites have achieved extraordinary ecological success and dominate many terrestrial habitats [2]. Eusocial insects typically live in highly complex colonies, which are comparable to human societies on many aspects. They live in densely populated colonies, conduct tasks through division of labour, build complex nesting architectures and engage in extensive social communications [3,4]. One of their intriguing social behaviours is the disposal of dead colony members through removal, burial or cannibalism. This behaviour has fascinated many naturalists and biologists with descriptions of 'cemeteries' in early documents, and social insects were once considered the only animals that exhibit this practice other than humans [5–7]. Corpse management has been found both in eusocial hymenopterans (bees, wasps and ants) and in isopterans (termites), and represents a convergent evolution.

Although corpse management in social insects shares similarities with humans in many regards, the underlying mechanisms and the evolutionary significance are different. Social colonies are conceptually analogous to the multicellular organisms and can be considered 'superorganisms' [4]. Unlike social practices in human societies where centralized laws and orders are often required and followed, insect societies operate under environmental inputs in a decentralized manner. Tasks are accomplished by individuals through responding to local cues, and social organization emerges via interactions among colony members [8]. In social insects, recognition of death is achieved

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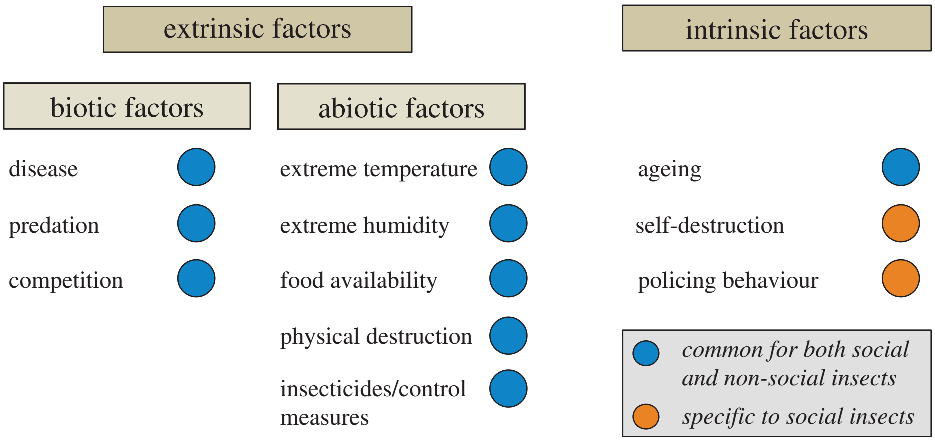

Figure 1. Causes of death in social and non-social insects. In all insects, death commonly results from a variety of extrinsic causes, including both biotic and abiotic factors. In addition, natural ageing eventually leads to death of the individual. In eusocial species, however, two other intrinsic factors contribute exclusively to death, namely self-destruction and policing behaviour.

primarily though olfactory cues, i.e. the post-mortem change of chemical signatures. In humans, the smell of death also triggers threat management responses [9]. The behavioural response in social insects, however, benefits the colony rather than individuals.

Eusociality is characterized by reproductive division of labour with non-reproductive workers, cooperative brood care and overlapping adult generations [3]. This social organization provides many benefits, such as improved foraging efficiency, enhanced defence against predators and increased reproductive success [10]. On the other hand, group living has drawbacks, and one of the major fitness costs is an increased risk of disease. The close genetic relatedness between colony members makes them vulnerable to the same pathogens, and their extensive interactions facilitate the spread of contagious disease [11–14]. Death of the sterile workers or soldiers frequently occurs in insect societies owing to their high density in social colonies. In addition, their lifespans are relatively short compared with the lifespan of the colony, and a high turnover rate of sterile individuals is expected. This is analogous to the high rate of somatic cell turnover throughout the life of an organism [15]. Death not only terminates an individual's contribution to the colony, but also leaves the corpse as a pathogenic risk. Management of corpses is often a prophylactic mechanism to enhance social immunity and represents an essential adaption to social life [12–14].

In 1958, Wilson *et al.* [16] carried out a pioneering study on corpse removal in ants and revealed that decomposition products, fatty acids, are the major death cues. Since then, many studies have been conducted to elucidate the pattern and regulation of this stereotypic behaviour. With a growing interest, researchers have recently discovered novel death cues [17,18], new behavioural patterns and functions [18–21] as well as underlying molecular mechanisms governing death recognition [22,23]. Dead individuals in eusocial colonies, however, represent rewards rather than risks under certain circumstances. Corpse management, which was previously considered as stereotypic, is sophisticated and complex. Social insects often show plastic responses depending on the trade-offs between costs and benefits associated with the nature of corpses, the behavioural strategy employed and the ecology of the species. We start this review by summarizing the causes of death in social insects (§2) and then update current knowledge on the chemical and molecular mechanisms of social response to the dead (§§3 and 4). We also provide an overview of corpse management strategies in eusocial insects compared with non-eusocial species, discuss the costs and benefits of each behaviour, and subsequently introduce behavioural plasticity (§§5 and 6). We hope that this review offers a comprehensive understanding of corpse management in social insects from ecological and evolutionary perspectives, and provides directions for future research.

2. Causes of death

In nature, the death of insects can result from a variety of causes. Ageing as a natural process is the main cause of death for reproductive individuals, which leads to the death of a colony in many species. Death of sterile individuals (i.e. workers and soldiers), by contrast, can be attributed to other biotic and abiotic factors in addition to ageing (figure 1). Workers are considered as the 'somatic' support in the 'superorganisms' [24]. Death of workers is a frequent event as they have shorter lifespans [25], and face higher mortality due to taxing and risky tasks such as foraging, colony defence and hygienic activities [26].

Disease is a common cause of death, as the group-living lifestyle and low genetic diversity make social colonies easy targets for pathogenic attacks [11–14]. A wide range of pathogens and parasites (e.g. fungi, bacteria, virus, protozoans and helminths) can infect and kill individuals and spread in the colony. Recent progress in social immunity, the colony-level protection against infectious disease, has revealed the underlying mechanisms and behavioural responses towards infected corpses and dying individuals (reviewed in [13,14]). Moreover, workers and soldiers often die in their defence against predators and competitors. In addition to direct antagonistic interactions, mortality of social insects can also be induced indirectly by the mere presence of predator or competitor cues [27,28]. Common abiotic factors contributing to the death of social insects, as with other insects, include extreme temperature (e.g. freezing and heat), water availability (e.g. desiccation and drowning), lack of food (e.g. starvation) and physical damage to nests by vertebrates or natural disasters. A variety of synthetic

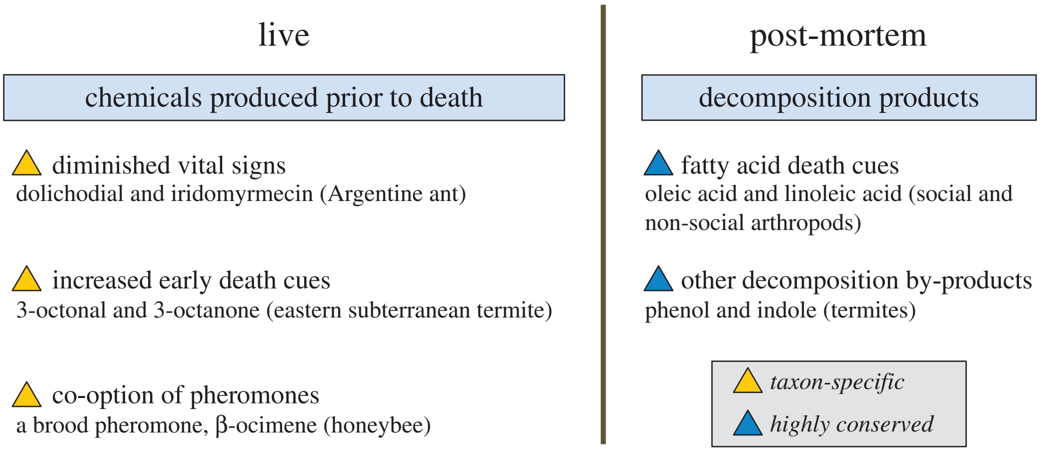

Figure 2. The classification of death cues based on the timing of chemical production. In eusocial species, certain chemicals are produced prior to death but change in quantity or function and, consequently, facilitate early death recognition and elicit corpse management. Examples include dolichodial and iridomyrmecin, which diminish rapidly after death in the Argentine ant, 3-octonal and 3-octanone, which increase immediately upon death in the eastern subterranean termite, and a brood pheromone (β-ocimene), which recruits workers for brood removal in the honeybee. These chemicals are probably taxon-specific and represent evolutionary novelties in eusocial insects. Decomposition products are produced post-mortem. Fatty acids are highly conserved death recognition cues both for social and for non-social arthropods. Phenol and indole are probably conserved volatile death cues in termites.

pesticides are used in the control of social insects of economic importance, and the behavioural response of colonies to insecticide-killed individuals has been the focus of some applied research [29]. These causes of death, which are associated with different types or levels of risks under natural settings, are expected to influence chemical signatures of dead individuals and elicit different behavioural responses in the living.

While the above-mentioned biotic and abiotic factors can contribute to death in almost all insects, there are two causes of death that occur exclusively in eusocial species, namely self-destructive behaviour in colony defence [30] and policing behaviour to resolve colony conflicts [31] (figure 1). Examples of altruistic self-destruction include the suicidal sting of honeybee workers in their defence against vertebrate intruders [32], old workers of the termite *Neocapritermes taracua* releasing defensive secretions through body rupture [33], workers of the Brazilian ant *Forelius pusillus* sacrificing themselves by routinely closing their nest from the outside to avoid nocturnal predators [34], and sick and dying workers of the ant *Temnothorax unifasciatus* leaving the nest before death to prevent infection of other colony members [35]. While altruism is the foundation of cooperation in eusocial insects, conflicts need to be resolved to maintain colony function. Policing behaviour refers to coercive action that reduces direct reproduction by other individuals. It has been observed widely in social insects in diverse forms, including consuming worker-laid eggs, immobilization, biting and stinging that could eventually lead to the death of focal individuals [36–38]. Self-destruction reflects social strategies to ease risks from natural enemies, and policing behaviour enhances colony efficiency through the regulation of reproductive division of labour.

3. Death cues: the novel and conserved chemical signatures

Individuals that die within a colony must be recognized by colony members for efficient and timely management. Recognition of dead individuals and elicitation of corpse management are primarily achieved by olfactory cues. Death cues, here, refer to post-mortem changes of surface chemicals that mediate behavioural responses in live insects. Depending on the timing of chemical production (before or after death), we classify them into two categories, ‘chemicals produced prior to death’ and ‘chemicals produced post-mortem’, i.e. ‘decomposition by-products’ (figure 2).

The first category includes chemicals actively synthesized in live insects, which change in quantity or function after death. For instance, in the Argentine ant *Linepithema humile*, dolichodial and iridomyrmecin are produced in the pygidial gland and present on the cuticle of live workers to mask the corpse removal stimuli, triglycerides. The rapid decline of the two compounds after death (within 40 min) allows workers to recognize death and remove the corpses before substantial decomposition occurs [17]. In the eastern subterranean termite, *Reticulitermes flavipes*, workers release two volatiles, 3-octonal and 3-octanone, synchronously with death, stimulating nest-mates to detect and locate the corpses [18]. These two volatiles are not released, although presumably produced and stored, in live workers. After death, they rapidly peak in quantity to recruit undertakers in a timely manner and then gradually decrease. In the honeybee *Apis mellifera*, a volatile brood pheromone, β-ocimene, which signals food begging, continues to emit after death and recruits workers to uncap and remove dead larvae [23]. The above-mentioned examples represent three distinct patterns of using chemicals produced prior to death for the timely detection of death: diminished vital signs, increased early death cues and co-option of pheromones, respectively.

The second category of death cues, decomposition by-products, refers to chemicals produced after death. In a pioneering study of chemical stimuli for corpse disposal, Wilson *et al.* [16] found that oleic acid was the most effective stimulus eliciting corpse removal in two ant species, *Pogonomyrmex badius* and *Solenopsis saevissima*. Since then, ‘fatty acid death cues’ have been found in many other social species, including the archaic ant *Myrmecia vindex* [39], the red ant *Myrmica rubra* [20], the fire ant *Solenopsis invicta* [40], a fungus-growing termite *Pseudacanthotermes spiniger* [41], two subterranean termites *Reticulitermes virginicus* [42] and

R. flavipes [18], as well as the honeybee *A. mellifera* [23]. Oleic acid and linoleic acid are the most common stimuli for corpse disposal in those species; the two compounds have low volatilities and require direct contact or short distance detection. Phenol and indole, which are decomposition products of proteins, are additional volatile death cues involved in corpse burial in the termites *P. spiniger* and *R. flavipes* [18,41]. While volatile death cues facilitate the orientation of insects from a distance, low-volatility cues, such as fatty acids, allow workers to pinpoint the specific location of the dead individual that requires disposal [43]. Fatty acids accumulate in dead individuals as a result of autolytic catabolism or bacterial hydrolysis of triglycerides [44]. The 'fatty acid death cues' represent a group of conserved post-mortem chemical signatures that trigger avoidance in gregarious species in both Crustacea and Hexapoda, including amphipods (Amphipoda) [45], woodlice and pill bugs (Isopoda) [46], springtails (Collembola) [47,48], crickets (Orthoptera) [49], cockroaches (Blattodea) [46,50], booklice (Psocoptera) [51] and social caterpillars (Lepidoptera) [46]. These compounds are comparable to cadaverine and putrescine in vertebrates, which are emitted from decaying flesh and stimulate burial in rats [52] and aversion in fish [53].

While decomposition products usually require longer post-mortem time to accumulate and affect behaviour, chemicals produced prior to death facilitate early detection and timely prophylactic corpse management. These early death cues, although emanating from dead individuals, function similarly to 'pheromones'. By contrast to the decomposition by-products, which are taxonomically conserved death cues, the chemicals produced prior to death are probably specific to species or closely related lineages (e.g. genus). We propose that the use of chemicals produced prior to death represents evolutionary novelties and that it occurs widely in social species, where early detection and disposal of corpses enhances colony fitness.

In contrast to olfactory cues, no evidence supports a role for visual, auditory or thermal cues for death recognition in social species examined so far. However, possible roles for such cues cannot be excluded, owing to the limited number of species investigated, available toolsets and the predominant focus on chemical cues in most studies. Tactile cues (e.g. glass beads carrying candidate chemicals) were found to synergize the effect of oleic acid on burial behaviour in a termite *R. virginicus* [42], suggesting potential non-olfactory contributions to corpse management. In most studies focused on death cues, freezing has been used as a standard protocol to induce death. A few chemical cues from diseased (and dying) brood that trigger hygienic behaviour have been identified in honeybees [54,55]. In the ant *Lasius neglectus*, fungal infection alters the cuticular hydrocarbon profile of pupae, which triggers workers to kill both infected individuals and the pathogen (i.e. destructive disinfection) [43]. Although a variety of other factors can contribute to the death of social insects, olfactory cues associated with different causes of death are largely unknown.

4. Perception of death cues and molecular basis of corpse management

Olfaction is the key sense for insects to detect their chemical environment [56]. In social insects, odorant-binding proteins (OBPs), odorant receptors and other chemosensory proteins are expected to be involved in the perception of diverse death cues. In the fire ant *S. invicta*, a chemosensory protein gene, *Si-CSP1*, was found to be responsible for detecting oleic acid and linoleic acid and thus mediating corpse removal [22]. In the honeybee *A. mellifera*, both oleic acid and β-ocimene are ligands for two OBPs (OBP16 and OBP18), which are associated with hygienic behaviour (removal of diseased brood) [23,57]. Receptors for either conserved fatty acid death cues or species/taxon-specific death cues remain unknown in insects. In addition to genes encoding proteins for death cue perception, others are expected to influence the behavioural response, as corpse management is a complex and sequential behaviour involving multiple steps and often dependent on the social context (see §§5 and 6).

Pheromones and other social stimuli can influence gene expression, which further affects behaviour or physiology of the recipients [58–61]. Comparison of gene expression patterns between individuals that specialize in corpse management and that do not, and before and after exposure to death cues, can be informative to determine the genetic underpinnings of corpse management. This approach has been applied to analyse gene expression associated with hygienic behaviour in the honeybee [62–64]. Gene expression in the brain of undertaker bees, which are temporarily specialized in corpse removal, is similar to that of guards but slightly different from comb builders [65]. Our recent transcriptome analysis in the eastern subterranean termite *R. flavipes* found that death cues cause changes in gene expression in workers within 30 min, and different sets of genes are associated with corpse cannibalism versus burial (unpublished data). Although our understanding of corpse management at the molecular level is in its infancy, the advent of genomics and functional genomics technologies, including the next-generation sequencing, RNAi and genome editing, will facilitate our efforts in the near future.

Remarkable progress has been made in the field of sociogenomics, unveiling the molecular basis of sociality from altruistic behaviour to division of labour [66–68]. One emerging theme is that genes involved in simple, non-social behaviour can be used for complex social behaviour. For example, the *foraging* (*for*) gene, encoding a highly conserved cGMP-dependent protein kinase, can cause a sitter to display rover-like behaviour in *Drosophila* [69] and facilitate the transition of gregarious desert locusts, *Schistocerca gregaria*, into solitary ones [70]. In eusocial insects, *for* functions as a positive regulator for foraging behaviour in the honeybee, *A. mellifera* [71], and a negative regulator in the bumblebee, *Bombus ignites* [72], the common wasp, *Vespula vulgaris* [73], the harvester ant, *Pogonomyrmex barbatus* [74,75], and the termite, *R. flavipes* (unpublished data). The detection and recognition of fatty acids as death cues is prevalent in arthropods, suggesting conserved genes/gene networks in the receiving end (perception) of these compounds. With readily available genomes, the molecular dissection of oleic acid perception and the downstream signalling pathway in the social hymenopterans might be the most logical initial steps in investigating corpse management at the mechanistic level. In the meantime, an array of taxa should be analysed to understand how corpse management has evolved from a simple ancestral trait of death recognition to a complex sequential behavioural response.

5. Behavioural responses: a comparison between social and non-social species

The behavioural response to corpses, also called 'undertaking behaviour', has evolved into diverse forms in eusocial insects, including corpse removal, cannibalism and burial. The strategies of undertaking behaviour depend on the feeding and nesting ecology of the species. Even within the same species, undertaking response to the dead can vary because of the risks and rewards associated with the corpses. The behavioural strategies employed in different groups of social insects and detailed behavioural responses have been previously reviewed [7,76]. In this review, we compare similar behaviours in non-eusocial species with corpse management in eusocial species, and discuss the potential costs and benefits of each behavioural strategy, as well as the ecological relevance of corpse management (table 1).

(a) Avoidance

Avoiding the dead, also known as necrophobic behaviour, is considered a behavioural mechanism to manage threats such as predation and disease. Avoidance of dead individuals or smells associated with death is common in animals ranging from arthropods to fishes, birds and mammals, including primates [46,53,124–127]. Among arthropods, avoiding dead conspecifics has been found in a wide range of non-eusocial but gregarious species [45–51]. While staying away from the dead is an effective solution to manage risks in these species, it is not commonly observed in eusocial species that live in permanent nests. Avoiding dead individuals in the nest means eventually abandoning the nest. Relocating or reconstructing the nest requires labour input from the entire colony and may pose increased risk of predation to the brood and reproductive individuals. Social insects only employ this strategy when the level of risk from not doing so is not manageable. For example, the fire ant *S. invicta* opts to relocate the nest only when it is heavily infected with nematodes or fungal pathogens [77,78]. In species that live in simple nests or frequently relocate, such as the rock ant, *Temnothorax albipennis*, workers avoid new nest sites containing conspecifics' corpses [79] (but see also contrary behaviour in the pharaoh ant, *Monomorium pharaonis* [128]). In subterranean termites, the nest is a complex structure composed of dynamic foraging galleries and chambers expanding to thousands of square metres. The colony size can reach millions of individuals [129]; therefore, the costs of relocating the entire colony are prohibitive. Workers avoid dead individuals infected with pathogens or killed by insecticides by sealing off (i.e. burying) the area where corpses are located [29,82,83]. In other words, subterranean termites simply modify the nesting structure locally, rather than relocating, indicating that avoidance in termites is less energetically costly than in other species. Avoidance of corpses often occurs following burial or construction to prevent contagion, but avoidance without burial activity is also observed in a higher termite *Globitermes sulphureus* under laboratory conditions [84].

(b) Corpse removal

Corpse removal, also called necrophoresis, was coined initially by Wilson *et al*. [16] to describe social insects carrying dead colony members away from the nest. Although behavioural processes are similar, corpse removal is a derived social behaviour distinguishable from waste disposal, in that corpses are removed in a timely manner and dropped further away from the nest [16,17,88]. Management of waste materials, such as faeces and food remains, is a sanitation practice in eusocial insects [130–132], as well as many subsocial species including spiders [91], spider mites [92], webspinners [93], crickets and grasshoppers [94,95], cockroaches [96], bark and ambrosia beetles [97]. In the eusocial gall-forming aphids, *Pemphigus spyrothecae*, soldiers dispose of corpses in the same manner as nest wastes [90], suggesting that they may not distinguish death cues from other aversive odours, or that dead nest-mates and other wastes both pose pathogenic risk. Based on current knowledge, we predict that corpse removal has evolved from waste removal. This hypothesis can be tested by examining the olfactory and behavioural response towards corpses and other wastes in eusocial and closely related non-eusocial species within the same lineage.

Corpse removal is the most common management strategy in ants and bees [16,17,20,39,40,86–89] (and see summaries in reviews [7,76]). One worker can carry one corpse at a time; therefore, it is not a labour-intensive behaviour, and it is expected to be an efficient solution when the number of corpses is low. This behaviour provides fitness benefits to the colony through keeping the nest a sanitary environment [133]. Workers that perform this behaviour, however, may expose themselves to risks of infection or predation if the corpse is carried outside the nest.

Stereotypic corpse removal has been found only in eusocial insects, not subsocial or communal species, implying that it is a consequence of the evolution of eusociality. Their highly complex social living leads to increased frequency of death inside the nest and increased risks of pathogen transmission from the dead, and corpse removal is a behaviour performed primarily by workers [12,13]. Besides sociality, nesting ecology is the other important factor in shaping the behaviour. Removal of dead individuals is not expected in species living in open nests where dying inside the colony is less likely, such as paper wasps. However, removal of dead or diseased brood (i.e. hygienic behaviour) is common in both wasps and bees, because the immature stages are reared in confined cells [85,134]. In addition to hygienic benefits, removal of dead or dying brood also allows the colony to re-use the nest space. In an extreme case, when removing individual brood is not sufficient to eliminate infestation of phorid flies, the queen of the social wasp, *Mischocyttarus labiatus*, cuts off the entire comb to remove all brood, and constructs a new comb with the help of her workers [85], representing a highly costly behaviour similar to avoidance to negate high risk.

It is interesting that some ants leave the nest when they are dying owing to certain pathogen infections [35,135]. Self-removal has been explained as parasitic manipulation of host behaviour [136,137], but non-manipulating generalist fungi, such as *Metarhizium brunneum*, can also elicit this behaviour. A recent study in *M. rubra* found that dying workers, infected with *Metarhizium brunneum*, left the nest due to impaired olfactory function [138]. However, this behaviour also represents a form of altruism, because non-infected individuals are also found to withdraw from the nest when they are moribund, such as in *T. unifasciatus* [35].

Table 1. Corpse management in eusocial insects. NA, not available, which indicates that the behaviour is absent or not reported in the given eusocial group.

behavioural strategy	description	terminology	nesting and feeding habits	costs	benefits	eusocial insects	non-eusocial arthropods[a]
avoidance	intentionally staying away from the dead or where corpses are located	necrophobia	non-permanent nest, or flexible nest structure	losing at least partially the nest; increased labour and energy input in nest reconstruction or relocation; risk of predation during relocation	preventing disease transmission in colony	wasps (NA), ants [77–79], bees [80,81], termites [29,82–84]	amphipods [45], woodlice and pill bugs [46], springtails [47,48], crickets [49], cockroaches [46,50], booklice [51], caterpillars [46]
corpse removal	carrying the dead out of nest, to refuse piles or specialized chambers; leaving the nest before death (self-removal)	necrophoresis	enclosed nest	risk of contagion at individual level; risk of predation at individual level; reducing individual lifespan in the case of self-removal	preventing/reducing disease transmission in colony; saving nest space	wasps [85], ants [7,16,17,20,39,40,76,86,87], bees [7,88,89], termites (NA), aphids [90]	*waste removal*: spiders [91], spider mites [92], webspinners [93], crickets and grasshoppers [94,95], cockroaches [96], bark and ambrosia beetles [97]
cannibalism	consuming dead, dying or injured conspecific individuals	intraspecific necrophagy	nutrition-imbalanced food or seasonal food shortage	risk of contagion at individual level	preventing/reducing disease transmission in colony; recycling nutrients and potentially symbionts	wasps (NA), ants [86,98–103], bees (NA), termites [7,18,76,84,104–106]	*cannibalism of live individuals*: shrimps [107], spiders [108], mantids [109], crickets [110], cockroaches [111], assassin bugs [112], fruit fly larvae [113], lady beetles [114], moths [115]
burial	covering dead individuals or blocking the areas where corpses are present with soil and/or other materials	entombment	enclosed nest	risk of contagion at individual level; labour and energy intensive	preventing/reducing disease transmission in colony; colony defence against predators or competitors	wasps (NA), ants [19,39,116], bees [117–119], termites [18,41,83,84,106,120,121]	*burying dead brood*: ambrosia beetles [122]; *burying carrion as food source*: burying beetles [123]

[a]Similar behaviours in non-eusocial arthropods are summarized.

Dying away from the colony can limit disease transmission through a less costly approach because it requires no additional input from the colony, but the lifespan of the worker that performs the behaviour is reduced [35]. Self-removed corpses are scattered outside the nest and can be re-encountered by other ants, and, as a result, transmit disease to their nest-mates. We predict that self-removal evolves only in species with small colonies or small nesting ranges, whereas in ants that live in large colonies or range across large areas, carrying corpses to refuse piles is more effective to reduce re-encountering pathogen sources.

(c) Cannibalism

Cannibalism describes the consumption of conspecifics; it is not specific to eusocial insects. Cannibalism of live individuals is widespread in animals, including predatory cannibalism [110,113], sexual cannibalism [108,109] and brood cannibalism [112]; it rewards the cannibals with nutrients and energy [109,110]. Eusocial insects also cannibalize live brood or other colony members under stressful conditions such as starvation, to regulate resources [139,140], or consume worker-laid eggs to resolve reproductive conflict [141]. Here, cannibalism that qualifies as corpse management practices is also called intraspecific necrophagy, which refers to the consumption of dead, dying or injured conspecifics. Cannibalism provides nutritional benefits as in other species, and in social species it also benefits the colony by eliminating the potential source of pathogens. However, cannibalism has also been considered to increase the risk of pathogen uptake by the cannibals [142,143].

Cannibalizing the dead is rare in ants (but see [86,98–102]), but can happen during seasonal food shortages, indicating that dead conspecifics can be used as a food supply [103]. Consumption of dead nest-mates has not yet been reported in wasps or bees. In termites, however, corpse cannibalism has been documented in diverse species [18,84,104–106] (see also summaries in previously published reviews [7,76]). Termites primarily feed on wood, which is rich in carbon but poor in nitrogen, and cannibalism of corpses is an important mechanism for nitrogen recycling [144]. In two higher termite species, *Microcerotermes crassus* and *G. sulphureus*, which feed on highly decomposed plant materials with higher nitrogen content, cannibalism of the dead rarely occurs, supporting the role of feeding habit in corpse management [84]. Termites rely on a variety of gut symbionts to digest lignocellulose, and these symbionts are transferred among nest-mates through proctodeal trophallaxis and coprophagy [145]. Cannibalism of newly dead individuals potentially allows termites to acquire symbionts [146], but the hypothesis of symbiont recycling requires further testing. Cannibalism in termites is restricted to freshly dead and dying individuals [18,84,147], thus reducing the loss of nutrients (and possibly symbionts) and minimizing the risk of disease transmission due to pathogen development during decomposition. The risk of infection by cannibalism can be mitigated through antimicrobial properties in termite saliva and guts [148–150].

(d) Burial

Although burying the dead with soil or other materials is not common in non-eusocial species, it can be found in ambrosia beetles, in which females bury the dead and weak brood [122]. Burying beetles are known to bury small vertebrate carrion as a food source for their larvae; this is a parental care behaviour that serves a different function from corpse management [123].

Ants generally prefer corpse removal, and corpse burial is an uncommon behaviour with only a few cases reported. For example, *M. vindex* buries objects treated with oleic acid [39], *Temnothorax lichtensteini* tends to bury freshly dead corpses of a foreign species [19] and *S. invicta* covers fungus-infected corpses with soil in artificial nests, which reduces transmission of the disease [116]. In the black garden ant, *Lasius niger*, co-founding queens bite and bury dead co-foundresses in closed nests where removal is impossible, and such undertaking behaviours improve their survivorship [151]. Although honeybee workers rarely practice burial behaviour, they use propolis (plant-produced resins used in the hive) to entomb dead mice or large insects that are not removable [117–119], and to encapsulate nest intruders such as parasitic beetles [152]. In termites, although cannibalism brings nutritional benefits, burial is more efficient when corpses are in large number, as cannibalism takes a longer time and requires more workers [106]. Termites also bury corpses that are highly decomposed [18,84], highly infected [106,120], killed by insecticides [29,83] or from competitor species [121,153].

Taken together, these observations suggest that burial behaviour is preferred when corpses pose higher risks or other behavioural strategies are impractical. Infected corpses indicate direct risk of pathogenic attack, and those that are highly decomposed or in large quantity also suggest increased pathogenic risks. Corpses from a foreign species imply predatory or competitive risks, or risks of unknown pathogens that other disease defensive mechanisms in the focal species may not cope with [19,121]. Compared with corpse removal, burial behaviour is costly. Burial is a collective behaviour that requires more labour force and energy than removal [18], and it often involves utilization of antimicrobial compounds secreted in saliva or excreted in faeces [154]. However, burial seems to be the most effective behaviour to suppress disease transmission in the nest, as it prevents any further contact and decreases the decomposition process through physical isolation [155]. In addition, burial functions as a defensive mechanism against potential intruders, as it blocks the entrance where more intruders may be present, thus preventing further aggression [153].

6. Behavioural plasticity to manage risks and rewards

Corpses pose different types or levels of risks and rewards according to their nature, such as post-mortem time, cause of death, origin and quantity. These characters can be recognized via different death cues, and they elicit differential responses in social insects. Furthermore, the social context and other environmental conditions provide additional information, which social insects integrate with death cues to evaluate the risks and rewards, and make the management decision.

(a) Differential response influenced by the nature of corpses

Corpses decompose over time, and surface chemicals change with post-mortem time. Honeybees and ants can distinguish dead nest-mates with different decomposition status, and remove those that have decomposed for longer more rapidly [20,88]. In *M. rubra*, this process is dictated by the level of fatty acids that accumulate after death [20]. In termites, dead and injured individuals offer nutritional rewards, but the nutritional value drops and the risk of pathogenic attack increases as the corpse decomposes. The trade-off between nutritional rewards and pathogenic risks leads to a behavioural shift from cannibalism to burial in *R. flavipes*, *R. speratus* and *Coptotermes formosanus* [18,84]. In *R. flavipes*, this behavioural plasticity is regulated by the dynamic change of death cues over time, which include an early death cue composed of two volatiles that recruit workers to locate and consume the dead and late death cues composed of mainly fatty acids that trigger burial [18]. The behavioural regulation of risks and rewards associated with corpses is comparable to the care–kill dichotomy in social immunity, which refers to the differential behaviour towards diseased colony members according to whether the individual can be cured or poses a threat to colony fitness [14,43,147].

Corpses that die from disease pose a direct risk of epidemic outbreak in the colony; therefore, rapid behavioural response or more effective strategies are expected. For instance, in the fire ant *S. invicta*, dead pupae infected with a fungal pathogen *Metarhizium anisopliae* are removed to the refuse pile more promptly than non-infected pupae [40]. When the same fungal pathogen kills individuals in the subterranean termite *R. virginicus*, workers bury the diseased corpses whereas they cannibalize pathogen-free corpses [105].

Social insects distinguish nest-mates from non-nest-mates and recognize castes within a colony through cuticular hydrocarbons (CHCs) [156], which remain on the surface of the individual after death for a period of time [20]. CHCs, therefore, can provide information about the identity of corpses and influence behavioural response. Non-nest-mate corpses, representing additional threats such as competition, predation and foreign pathogens, elicit complex behaviour different from nest-mate corpses. For example, in *R. flavipes*, freshly dead individuals from a competitor species, *R. virginicus*, trigger intensive burial behaviour in workers while soldiers are recruited to guard the burial site and attack the dead [121]. Similarly, in the ant *T. lichtensteini*, workers bury and bite newly dead alien corpses, whereas they normally remove dead nest-mates [19]. And in *M. rubra*, freshly dead alien corpses are removed more frequently and elicit more aggression than nest-mate corpses [20]. Interestingly, in *Formica cinerea*, corpses from a territorial competitor and a slave-maker species provoke aggression and are quickly carried inside the nest rather than outside, which is presumably a behavioural mechanism to avoid further detection by live intruders [21]. Developmental stages of corpses also influence the behavioural response. In a bumblebee, *Bombus terrestris*, workers remove larval corpses faster than adult corpses [157], while in the ant, *S. invicta*, dead pupae are removed more slowly than dead workers [40].

(b) Differential response influenced by social context

Social insects often display differential behaviour in a context-dependent manner, even towards the same stimuli. For example, in the ant *Temnothorax rugatulus*, alarm pheromone repels or attracts nest-mates depending on whether it is released in an unfamiliar site or in the vicinity of the nest [158]. In the dampwood termite, *Hodotermopsis sjostedti*, workers show increased aggression towards intruders in the presence of reproductive caste, but reduce aggressive activities when soldiers are present [159]. Social context provides important information regarding risks and rewards, and social insects are remarkably flexible in their behavioural response. This is also true in corpse management practices. For example, bees and ants may encounter dead conspecifics during foraging, but only those that die inside or near the nest present risks to the colony and trigger corpse disposal. Bumblebees and honeybees are known to remove corpses from the nest, but they show avoidance when foraging on flowers with death cues of conspecifics [80,81]. This suggests that the context of ‘nest’, presumably recognized by chemical cues or physical properties, is associated with risks or rewards at colony level and thus a prerequisite for corpse management. Fatty acids are common death cues initiating corpse management; however, they also appear on food sources such as dead insects or seeds that many ants feed on [160]. Although synergistic chemical cues possibly allow social insects to discriminate food from dead colony members, social context plays a role in their response. In the ant *Pogonomyrmex badius*, oleic acid elicits necrophoresis when most of the ants are engaging in nest maintenance or cleaning, but induces foraging behaviour if the colony is actively feeding or convening [161]. Another example concerns behavioural plasticity in the reproductive caste. Queens do not perform non-reproductive activities in mature colonies, but in newly founded colonies where worker helpers are not available, they engage in tasks of corpse disposal. This has been documented in a fungus-growing termite, *P. spiniger*, and an ant, *L. niger* [41,151]. In *L. niger*, biting and burying dead co-foundresses by queens when removal from closed nests is restricted [151] illustrates how nest structure and environmental conditions can play a role in behavioural plasticity. When disposing of corpses outside is restricted due to factors such as nest blockage, flooding or freezing, alternative behaviours such as burial or cannibalism are expected. In addition, colony size influences the behavioural response in the management of infection. When challenged with objects bearing fungus spores, *M. rubra* workers living in large colonies removed the infected items fast, whereas workers in small colonies relocated themselves and larvae first, and returned to the nest after waste items were removed by a few individuals [162].

7. Conclusion

Death in social colonies occurs due to various factors, which in turn present different risks and rewards to the colony. Death cues differ according to the nature of the corpses and change over time. To manage death properly, social insects must discriminate between the dead and the alive, distinguish corpses of nest-mates from non-nest-mates, and locate and assess the status of corpses. With all the information integrated, they perform a specific behaviour, such as corpse removal, cannibalism, burial or avoidance. All of these behavioural mechanisms serve the function of disease resistance, as one of the major threats posed by dead individuals is pathogen transmission. However, corpse management is not only a hygienic behaviour, but also benefits the colony through nutrient recycling and promoting defence against intruders. In addition, the nesting structure and feeding habits of a given species are important factors in evaluating the risks and rewards associated with corpse management strategies.

Most studies have focused on behavioural analyses and the chemical bases of death cues. The causes of death at individual and colony levels, which provide critical information for understanding the chemical cues and behavioural responses, have not been thoroughly investigated. Few species have been investigated, with a bias towards social insects of economic importance, such as invasive ants (e.g. fire ant and Argentine ant), honeybees and subterranean termites. Corpse management in wasps, ants that live in smaller and simpler societies, and primitive species of termites (such as drywood and dampwood termites) remain mostly unexplored. Many analogous behavioural responses can be found in non-eusocial species, which can be helpful in determining how specific behavioural responses were shaped during the evolution of eusociality. In addition, evaluation of the benefits of corpse management at colony level, which provides proxies for fitness advantages, has so far been studied in only one species [133]. To better understand how corpse management has evolved in different social groups, we look forward to studies on comparative analyses of costs and benefits between behavioural strategies, direct measurement of fitness value associated with corpse management, and phylogenetic analyses of eusocial and non-eusocial species exhibiting similar behaviour with consideration of their nest and feeding ecology.

Data accessibility. This article has no additional data.

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Occurrence and variability of tactile interactions between wild American crows and dead conspecifics

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Observations of some mammals and birds touching their dead provoke questions about the motivation and adaptive value of this potentially risky behaviour. Here, we use controlled experiments to determine if tactile interactions are characteristic of wild American crow responses to dead crows, and what the prevalence and nature of tactile interactions suggests about their motivations. In Experiment 1, we test if food or information acquisition motivates contact by presenting crows with taxidermy-prepared dead crows, and two species crows are known to scavenge: dead pigeons and dead squirrels. In Experiment 2, we test if territoriality motivates tactile interactions by presenting crows with taxidermy crows prepared to look either dead or upright and life-like. In Experiment 1, we find that crows are significantly less likely to make contact but more likely to alarm call and recruit other birds in response to dead crows than to dead pigeons and squirrels. In addition, we find that aggressive and sexual encounters with dead crows are seasonally biased. These findings are inconsistent with feeding or information acquisition-based motivation. In Experiment 2, we find that crows rarely dive-bomb and more often alarm call and recruit other crows to dead than to life-like crows, behaviours inconsistent with responses given to live intruders. Consistent with a danger response hypothesis, our results show that alarm calling and neighbour recruitment occur more frequently in response to dead crows than other stimuli, and that touching dead crows is atypical. Occasional contacts, which take a variety of aggressive and sexual forms, may result from an inability to mediate conflicting stimuli.

This article is part of the theme issue 'Evolutionary thanatology: impacts of the dead on the living in humans and other animals'.

> *Thereupon Allah sent forth a raven who began to scratch the earth to show him how he might cover the corpse of his brother. So seeing, he cried: 'Woe unto me! Was I unable even to be like this raven and find a way to cover the corpse of my brother'? Then he became full of remorse at his doing.*
>
> Qur'an Sura 5.31

1. Introduction

Within the field of comparative thanatology, observations of prolonged transport of dead infants, and affiliative, sexual or aggressive contact with dead adults call into question the understanding and motivations behind animal responses to conspecific (members of the same species) death [1,2]. Tactile interactions with conspecific corpses have been widely observed among dolphins, elephants and non-human primates, though whether tactile interactions are a characteristic response of these species is unknown [3–5]. Prolonged contact may even continue over the course of days or weeks in cases involving dead infants [6,7]. Among these mammals, tactile interactions may manifest as affiliative behaviours such as grooming and gentle touching, aggressive interactions and sexual behaviours [8]. Touching or remaining close to dead conspecifics may expose animals to disease or increase the risk of attack from dangerous scavengers, such as stinging insects or larger predators [9–12]. Therefore, what purpose, if any, these interactions serve remains unclear.

Tactile interactions may aid the assessment of an individual's state or identity, or allow animals to acquire other important information such as cause of death [8,13]. Alternatively, they may be a by-product of adaptive behaviours such as territory defence, mating or caretaking [4]. To date, motivations behind mammalian contact with dead conspecifics remain largely untested. In contrast to large or marine mammals, systematic studies of death responses among birds are more feasible due to the fact that carcasses are smaller and easier to obtain and transport, and limited olfactory abilities enable realistic experiments using taxidermy specimens. Among birds, some corvids demonstrate consistent responses to dead conspecifics, though it remains unknown if they engage in tactile interactions.

Humans have long noted the attendance of corvids near their dead, even incorporating them into their parables, as is evident in the epigraph we chose to start this paper. When confronting a dead conspecific, wild American crows (*Corvus brachyrhynchos*), common ravens (*Corvus corax*) and California scrub-jays (*Aphelocoma californica*) alarm call and recruit other birds to the area [14–16]. Following these events, jays and crows avoid or show wariness in areas associated with conspecific death, and crows harass people they observed handling dead crows [14,15]. These findings suggest that crows and some other corvids recognize dead conspecifics as cues of danger and use such information to inform future actions and learn novel threats. During studies with California scrub-jays, dead jays were presented in the absence of predators that might otherwise keep observers away, but no episodes of contact akin to those described in some mammals were reported [14]. Studies done on crows and ravens, however, have largely prevented such opportunities for contact due to the manner in which birds were presented (as hanging effigies or paired with predators, [15,16]).

Given the similarities between crows and the mammals for which contact has been repeatedly observed, crows make a viable model for exploring tactile interactions between wild animals and their dead. Like dolphins, elephants and primates, crows share a large relative brain size and a complex social system [17–19]. If interactions with dead conspecifics serve to provide key information to the investigating animal, it is possible that crows would seek the same kinds of information as these mammals. Among crows, interactions may also be simply extensions of typical scavenging behaviours that include interest in dead animals. Alternatively, given that crows defend territory boundaries and female mates, particularly during the period of peak female sexual receptiveness between March and April, it is possible that contact with dead crows is the result of attempts to evict intruders [20,21]. Through two controlled experiments, we seek to determine if tactile interactions between wild crows and dead conspecifics are a defining feature of crows' response repertoire, and if food, information acquisition or territoriality are motivating factors.

To meet our objectives, we present wild crows four stimuli: a dead adult crow, a dead juvenile crow, a dead feral pigeon and a dead eastern grey squirrel (Experiment 1). Although, in our area, scavenging accounts for a minority of a crow's diet, crows are known to scavenge both pigeons and squirrels ([22]; K.S. personal observation). By contrast, crows are not known to regularly scavenge conspecifics [23]. Given that taxidermy-prepared animals are of no real food value, we expect contact with heterospecifics to lack alarm calling and neighbour recruitment, be exploratory and aggressive in nature, and only last for brief periods until crows determine they are of no value. If interactions with dead crows mirror those with squirrels and pigeons in these ways, it is likely that contact is food motivated. Alternately, efforts to glean information such as the individual's state, identity or signs of depredation may be responsible for observed contact. If such information acquisition motivates tactile interactions, we expect that interactions will be coupled with alarm calling and recruitment, be primarily non-aggressive in nature and occur frequently and uniformly across the study period. Finally, previous studies have suggested that danger learning and avoidance motivate crows' attraction to dead conspecifics [16]. If crows exhibit a danger response, we expect higher rates of alarm calling and recruitment coupled with lower rates of contact in contrast to heterospecifics.

We then determine what role stimulus posture has on the occurrence of interactions (Experiment 2). In contrast to food or information, crows may regularly contact dead crows because they fail to recognize their deceased state and mistake them for an intruder, provoking territoriality and mate guarding. To test this, we present wild crows with a dead adult crow or a life-like upright mounted crow. We expect that the life-like crow will result in scolding and dive-bombing, but infrequent recruitment, and that contact will be primarily aggressive. If crows fail to correctly assess the state of the dead crow, then we expect to see similar behaviours between life-like and dead crows. Lastly, because our initial crow stimulus resembles female copulation posture (wings outstretched with tail exposed), we wondered if any observed sexual responses in Experiment 1 were mediated by stimulus posture. To test this, in addition to evaluating if crows attempt to copulate with the life-like crow, we present crows with a dead adult crow with wings prepared close to the body ('tucked' crow in dead posture). If sexual behaviour is released by stimulus posture, we expect that neither the tucked crow, nor the life-like crow will elicit copulation attempts.

2. Material and methods

(a) General information

We conducted experiments at sites in Washington, USA in the cities of Seattle, Bellevue, Issaquah, Renton and Kent. For these experiments, we selected individual trial sites based on the presence of a territorial adult pair. We identified pairs based on seasonally relevant breeding activity including nest building, nestling provisioning or the presence of a fledgling. In our area, helping behaviour occurs infrequently, so we assumed that no more than two adults occupied a single territory [24]. Each pair only received one stimulus during the course of the study. All trials were spaced at least 300 m apart in an attempt to prevent carry over effects and increase independence.

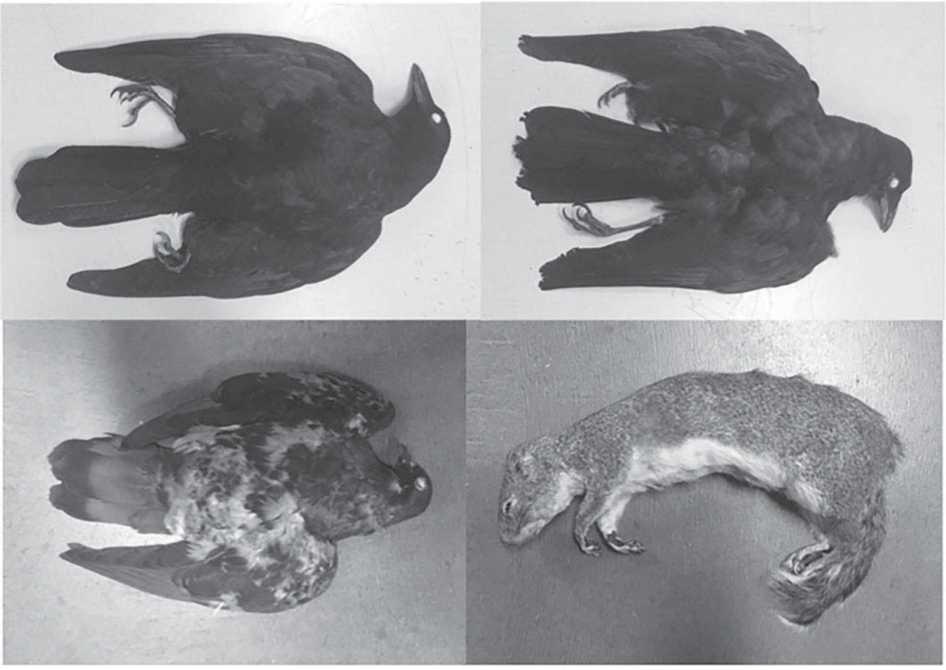

Figure 1. Stimuli used in *Experiment 1*. Clockwise from top left: adult American crow in standard dead posture, juvenile American crow in standard dead posture, feral pigeon in standard dead posture and Eastern grey squirrel in dead posture. (Online version in colour.)

During experimental trials, a single observer, K.S., placed the appropriate stimulus 35–45 m from the nest or fledgling in the absence of any adult birds. We attached all avian stimuli in dead posture to a lead weight via 1.5 m of transparent fishing line to prevent removal by crows. The squirrel was prepared with an internal lead weight and packed with sand. Stimuli were maintained in roughly the same condition and replaced by an identically prepared skin if irreparably damaged. All specimens were collected outside of the study area and presumed to be unfamiliar individuals to the observing crows.

Once the specimen was in place the observer stood and recorded data from 15 to 25 m away. The observer waited for up to 2 h for the first adult bird to come within 25 m of the stimulus and look in its direction (stimulus discovery). Once these criterion were met the observer recorded data for 30 min, after which the stimulus was removed. The distance from the nest, and 25 m radius, was determined using a TruePlus 200 Laser Rangefinder. We recorded all experiments with a tripod mounted JVC Everio camera.

(b) Experiment 1: tactile interaction with conspecifics and heterospecifics

During the breeding season of 2015 (March–August) and 2016 (March–April), we tested the response of wild American crows to the sight of either a taxidermy-prepared adult crow in dead posture ($N = 78$), a taxidermy-prepared fledgling crow in dead posture ($N = 78$), a taxidermy-prepared adult rock pigeon (*Columba livia*) in dead posture ($N = 77$) or a taxidermy-prepared adult Eastern grey squirrel (*Sciurus carolinensis*) in dead posture ($N = 76$; figure 1). We prepared avian skins with their heads turned to the side with wings slightly outstretched and placed ventral side down. The squirrel skin was prepared caudal side down and slightly curled.

Once the stimulus was discovered by the first adult bird, we recorded the number of birds within 2 and 25 m from the stimulus, the number of scolds emitted and whether dive-bombing or contact with the stimulus occurred. We defined scolding as harsh, unstructured calling. We defined mobbing as the presence of three or more adults engaging in scolding. We defined dive-bombing as u-shaped swoops directed at a specific target that may or may not result in brief physical contact. If tactile interactions occurred, we used the video recordings to count the number of such instances, determine the amount of time spent with one or both feet on the stimulus (stand time) and categorize the nature of each contact into one of the following five categories:

1. *Peck*. We defined a peck as forceful contact by the living bird with its beak delivered to any part of the stimulus.
2. *Touch*. We identified a touch as non-forceful contact made by the living bird with any part of its body (bill or foot) to any part of the stimulus.
3. *Drag*. We considered dragging to be the intentional movement of the stimulus by the living bird via its beak. Dragging could occur up to a metre and could include attempts to pick up and fly off with the stimulus.
4. *Tissue pull/dismember*. We considered tissue pulling any instances where the living bird removed fur or feathers from the stimulus by grabbing the material in its bill and yanking forcefully. Dismemberment included removal of limbs or cotton stuffing from the stimulus.
5. *Sexual behaviour*. We considered sexual behaviour to include: attempted copulation with the stimulus defined as the observation of the living bird mounting the stimulus and positioning the tail while attempting to, or successfully making, cloacal contact; copulation between mates occurring following the discovery of the stimulus and within 25 m of it; and sexual solicitation posturing occurring on or within 25 m of the stimulus, following stimulus discovery.

(c) Experiment 2: effect of stimulus posture on respondent behaviours

During the breeding season of 2016 (July–August) and 2017 (April–June), we tested the response of wild American crows to the sight of either a (i) taxidermy-prepared adult crow in dead posture with wings partially outstretched as in *Experiment 1* (‘standard’ crow in dead posture, $N = 52$), a (ii) taxidermy-prepared upright life-like crow mount ($N = 45$) or (iii) a taxidermy-prepared adult crow in dead position but with the

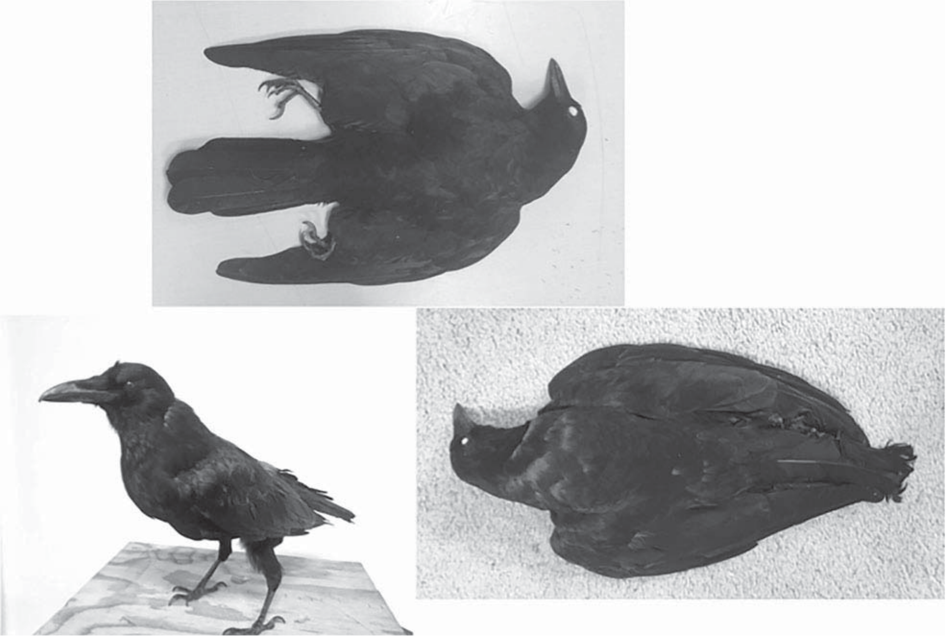

Figure 2. Stimuli used in Experiment 2. Clockwise from top: adult crow in 'standard' dead posture, upright, life-like adult crow and adult crow in 'tucked' dead posture. (Online version in colour.)

wings tucked close to the body ('tucked' crow in dead posture $N = 26$; figure 2). We presented the third stimulus only during March–May of 2017. We prepared the upright crow mount with glass eyes and assuming a standing posture typical of a live American crow. To aid with stability, we attached the specimen to a 36 × 36 cm piece of plywood via hidden screws in the feet. Site selection, stimulus presentation data collection and contact analysis procedures matched that of Experiment 1.

(d) Statistical analysis

We conducted tests in SPSS v.19 (IBM, Armonk, NY, USA) and RStudio 1.1.383 using the MASS package [25]. Apart from determining the likelihood of contact overall, all tests regarding contact omitted trials where no contact occurred, to control for zero-inflated data. In cases where there were only two stimuli such as heterospecifics and conspecific or life-like versus dead, we used Pearson's χ^2 tests to determine likelihood differences among binomial measurements such as scolding, mobbing or contact. To evaluate differences in binomial responses among three or more stimuli, we used negative binomial regression. In Experiment 1, we used logistic regression to determine if there were interaction effects between date and stimulus types. This test excluded data taken in 2016, because data collection in 2016 was limited to the months of March and April, and its inclusion may have biased the test's outcome. We used negative binomial regression to evaluate means among contact count data (ex: number of pecks) and one-way ANOVAs to compare all other means. In $n = 1$ case, a crow was able to remove the pigeon stimulus to a nearby rooftop. Because the bird was visible and audible for the duration of the trial, we included this point in binomial scolding, mobbing and contact tests, but not in tests of specific interaction types because the observer was unable to film them.

3. Results

(a) Experiment 1: tactile interaction with conspecifics and heterospecifics

The majority of trials (70%) resulted in no contact between wild birds and the stimulus. With respect to conspecifics, the most typical reaction by wild birds was scolding (94% of 156 trials) often followed by mobbing (54% of trials). Among heterospecifics, scolding occurred less often than in response to crows (41% of 153 trials; Pearson's $\chi^2_1 = 96.94$, $p < 0.001$) and mobbing was only observed in a small number of cases (7% of trials).

Crows only made contact with conspecifics in 24% of trials. Contact occurred more frequently with heterospecifics than with conspecifics (36% of heterospecific trials; Pearson's $\chi^2_1 = 4.93$, $p = 0.026$). Of the $n = 55$ that contacted heterospecifics, 82% ($n = 45$) engaged in pecking. During these encounters, birds would often target eyes or other weak spots including ventral areas.

The contacting crow was more likely to scold during contact with a conspecific than a heterospecific (Pearson's $\chi^2_1 = 38.97$, $p < 0.001$). This finding was not driven only by a lack of a scolding response towards the squirrel, because crows were still more likely to scold during contact with conspecifics than with pigeons (partial χ^2_1 conspecifics versus pigeons $= 14.33$, $p < 0.001$). Crows were no more likely to scold during contact episodes with adult versus juvenile crows (partial $\chi^2_1 = 0.89$, $p = 0.34$). In addition, among trials where contact occurred, mobs were significantly more likely to form in response to conspecifics (60% of $n = 38$ contact trials) than to heterospecifics (7% of $n = 55$ contact trials; Pearson's $\chi^2_1 = 30.93$, $p < 0.001$). Wild crows contacted adult crows in dead posture in 25% of the 79 trials, juvenile crows in dead posture in 23% of the 77 trials, pigeons in dead posture in 34% of 77 trials and squirrels in dead posture in 38% of 76 trials (table 1). We observed crows engaging in all five categories of interaction with each stimulus, with the exception of sexual behaviours following presentations of the squirrel, which were never observed. Among the touch, peck, drag and tissue pull categories, we observed no difference in responses between the four stimuli (touches: Wald $\chi^2_1 = 2.28$, $p = 0.52$; drags: Wald $\chi^2_1 = 4.50$, $p = 0.21$; tissue pulls: Wald $\chi^2_1 = 5.67$, $p = 0.13$). We found no interaction effect of date and stimulus type on the occurrence of contact (Wald $\chi^2_3 = 3.20$, $p = 0.36$).

Table 1. Occurrence of tactile responses during Experiment 1. With the exception of 'Occurrence of contact', all other percentages are representative of the occurrence of the contact category out of the total trials in which contact occurred for each stimulus.

			exploratory behaviours			
	total trials (N)	occurrence of contact	occurrence of touching	average touches ($\pm$s.d.)	occurrence of dragging	average drags ($\pm$s.d.)
adult crow	78	$n = 20$, 25%	$n = 12$, 60%	4.75 ± 6.00	$n = 17$, 85%	5.00 ± 6.52
juvenile crow	78	$n = 18$, 23%	$n = 9$, 50%	11.00 ± 11.45	$n = 16$, 89%	6.25 ± 4.89
pigeon	77	$n = 26$, 34%	$n = 12$, 46%	5.92 ± 8.37	$n = 19$, 73%	4.53 ± 3.86
squirrel	76	$n = 29$, 38%	$n = 23$, 79%	3.78 ± 2.61	$n = 14$, 48%	5.29 ± 4.46
			aggressive behaviours			
	occurrence of pecking	average pecks ($\pm$s.d.)	occurrence of tissue pulling	average tissue pull ($\pm$s.d.)	occurrence of sitting	average stand time (s $\pm$ s.d.)
adult crow	$n = 9$, 45%	228.89 ± 292.46	$n = 7$, 35%	13.71 ± 20.94	$n = 7$, 35%	349.57 ± 326.20
juvenile crow	$n = 12$, 67%	67.08 ± 99.38	$n = 6$, 33%	11.33 ± 8.64	$n = 10$, 55%	102.30 ± 100.99
pigeon	$n = 19$, 73%	28.61 ± 37.49	$n = 10$, 38%	11.30 ± 22.94	$n = 14$, 54%	59.79 ± 72.69
squirrel	$n = 26$, 90%	49.12 ± 56.14	$n = 11$, 38%	2.82 ± 2.60	$n = 12$, 41%	47.58 ± 54.72
			sexual behaviours			
	total sexual events (n)	attempted copulation with stimulus (n)	copulation between stimulus and greater than 1 bird (n)	copulation with mate[a] (n)	solicitation posturing[b] (n)	
adult crow	4	4	1	0	0	
juvenile crow	2	2	1	0	0	
pigeon	4	1	0	2	1	
squirrel	0	0	0	0	0	

[a] Defined as copulation occurring following stimulus discovery and within 25 m of the stimulus. Identification of mated pair is based on nesting activity immediately before or after copulation event.

[b] Defined as drooped vibrating wings and erect tail.

Crows were less likely to peck the adult crow in dead posture than the other three stimuli (Pearson's $\chi^2_1 = 8.34$, $p = 0.004$); however, when they did, they administered more pecks to adults (table 1; mean ± s.d. = 228.89 ± 292.46; *Z*-score −2.03, $p = 0.042$). There was a significant interaction between date and stimulus on the likelihood of pecking (Date × Stimulus: Wald $\chi^2_3 = 8.13$, $p = 0.043$). This finding appears to be driven by an early season (March–May) bias towards pecking conspecifics (Date × Con/Heterospecific: Wald $\chi^2_1 = 4.63$, $p = 0.031$; figure 3). Among cases where birds stood on the stimulus, there was a difference in stand time on each stimulus ($F_{3,39} = 7.56$, $p < 0.001$). This was driven by responses to adult crows presented in dead posture, which were stood upon for the greatest length of time (Tukey's post hoc: Adult–Juvenile mean difference ± s.e. = 247.27 ± 71.97 s, Adult–Pigeon mean difference ± s.e. = 298.79 ± 67.60 s, Adult–Squirrel mean difference ± s.e. = 301.99 ± 69.46 s).

We observed sexual behaviour in $n = 10$ trials: $n = 4$ adult crows in dead posture, $n = 2$ juvenile crows in dead posture and $n = 4$ pigeons in dead posture (table 1). In two of these cases ($n = 1$ adult crow in dead posture and $n = 1$ juvenile crow in dead posture), a second live bird mounted and attempted to copulate during the initial bird's copulation event with the stimulus (see video footage in electronic supplementary material). It was not clear in these cases if the second bird was attempting to mate with the live bird or if it was also attempting to mate with the stimulus. Based on our knowledge of the territorial pair's whereabouts at the onset of the trial, in both these cases, we believed that the second bird was mated to the first bird (however, the study birds were not marked). In cases where copulation occurred, in $n = 3$ for adult crows in dead posture and $n = 2$ for juvenile crows in dead posture, the copulating bird(s) scolded immediately before or after the event and pecked the stimulus aggressively during or after the event. Among sexual events during the presentation of the dead pigeon, $n = 1$ was an attempted copulation with the stimulus and did not include scolding before, during or after the event, $n = 2$ were copulations between the presumed mated pair following stimulus discovery and $n = 1$ was a bird-making solicitation postures while on top of the pigeon (table 1). The observation of copulation behaviour was biased towards the first half of the breeding season (March–May). Only one event was observed after the end of May, and the observation of the bird soliciting from on top of the pigeon occurred 18 June 2015.

(b) Experiment 2: effect of stimulus posture on respondent behaviours

Crows did not appear to distinguish the adult crows in tucked dead posture ($N = 26$) from those in standard dead posture ($N = 52$). There were no differences in their response with respect to scolding (all trials resulted in scolding), mobbing (Pearson's $\chi^2_1 = 0.44$, $p = 0.51$), overall contact (Pearson's $\chi^2_1 = 0.029$, $p = 0.87$) or copulation attempts with the stimulus ($n = 1$ tucked dead crow; $n = 4$ with standard dead crow). As a result, we collapsed these stimuli into a single 'dead posture' category ($N = 78$) for all subsequent analyses.

Crows distinguished between the adult stimulus in dead posture ($N = 78$) and the life-like crow ($N = 45$). Crows scolded in response to the dead crow in all cases, but only scolded the life-like crow in 71% of cases (Pearson's $\chi^2_1 = 25.20$, $p < 0.001$). If scolding occurred, birds scolded more quickly after discovering the crow in dead posture (mean ± s.d. = 39.94 ± 118.03 s) than they did when they encountered the life-like stimulus (mean ± s.d. = 241.72 ± 477.77 s; $F_{1,108} = 12.24$, $p = 0.001$). Mobbing also occurred more frequently in response to a conspecific presented in dead posture (63% of trials) than to a life-like crow (31% of trials; Pearson's $\chi^2_1 = 11.49$, $p = 0.001$). By contrast, dive-bombing occurred most often in response to presentations of the life-like crow (Pearson's $\chi^2_1 = 15.08$, $p < 0.001$). Crows dive-bombed the dead crow in 9% of trials and the life-like crow in 38% of trials.

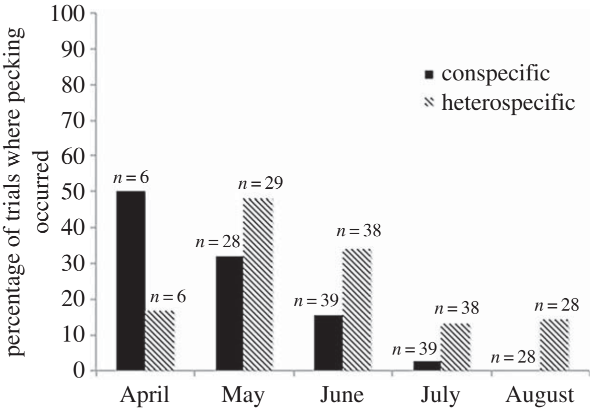

Figure 3. Pecking as a proportion of carcass directed contact in Experiment 1. Graph shows what percentages (Percentage is calculated as the number of trials that resulted in pecking out of the total number of trials where contact occurred for each stimulus type.) of trials resulted in pecking over each month of the 2015 field season. Black bars indicate trials using adult and juvenile crows presented in dead posture. Lined bars indicate trials using pigeons and squirrels in dead posture. The sample size per month for each stimulus is provided above the corresponding bar.

Although crows more often made contact with the life-like crow (49% of trials) than with crows presented in dead posture (33% of trials), this difference was non-significant (Pearson's $\chi^2_1 = 2.90$, $p = 0.088$). If contact occurred, there was no observed difference with respect to pecking (Wald $\chi^2_1 = 0.07$, $p = 0.79$) or touching (Wald $\chi^2_1 = 0.22$, $p = 0.65$). Crows did, however, engage in more feather pulling/dismemberment with the upright stimulus than the dead stimulus (Wald $\chi^2_1 = 4.59$, $p = 0.033$).

We observed $n = 8$ sexual events in response to crows presented in dead posture and $n = 4$ sexual events in response to life-like crows (table 2). Of the $n = 3$ attempted copulations with the upright mount, none of them were preceded or followed by scolding or pecking by the mating bird, whereas all $n = 5$ attempted copulations with the crow in dead posture were. All copulation events were observed before the end of May, with the latest event occurring on 25 May 2017.

4. Discussion

Among some mammals including dolphins, elephants and non-human primates, there are dozens of accounts detailing tactile interactions between living individuals and a dead conspecific, but to date no systematic studies have been done to determine how typical this response is. Our experimental study demonstrates that among one group of

Table 2. Occurrence of sexual behaviours in Experiment 2.

	total sexual events (*n*)	attempted copulation with the stimulus (*n*)	copulations with greater than 1 bird (*n*)	copulations with mate (*n*)[a]
dead adult crow	8	5	0	3
life-like adult crow	4	3	0	1

[a] Defined as copulation occurring following stimulus discovery and within 25 m of the stimulus. Identification of mated pair is based on nesting activity immediately before or after copulation event.

animals, wild American crows, contact with dead conspecifics is not characteristic of their response in that it only occurs in roughly one quarter of encounters, but when it occurs it is extremely varied. During these encounters, we found that crows are much more likely to scold and mob, something we observed significantly less often in response to dead heterospecifics or mounted, life-like crows. In addition, tactile interactions with crows were more often conflicting in nature (i.e. aggressive and sexual) in contrast to other stimuli. Although infrequent, we found that inappropriate contact like prolonged pecking or copulation generally occurred in the first half of the breeding season. Given these findings, we suggest that tactile interactions with dead conspecifics do not represent attempts to assess key information, typical scavenging or territorial behaviours. Our results suggest that costs associated with contact preclude most individuals from touching dead crows but that, in some birds, breeding season-induced changes may be responsible for overcoming more typical necrophobic responses.

Touching conspecific corpses may expose animals to disease or increase the risk of attack from dangerous scavengers, such as stinging insects or larger predators [5]. To avoid these risks, social insects such as ants, termites and bees have special undertaking procedures to efficiently dispose of conspecific corpses [26–28]. Rats (*Rattus norvegicus*) likewise bury cagemates that have been dead for more than 40 h [29]. For these colony living animals, any contact that occurs is therefore associated with body removal and the ultimate driver is maintaining colony health. Why some animals are motivated to engage with dead conspecifics in contexts outside of body disposal remains less clear, but some have suggested that they do it as a means to glean information from the body including attempts to identify the individual or assess its state [5,13]. Our observation that crows primarily responded to dead crows by scolding and mobbing in the absence of contact supports previous studies that crows and other corvids recognize dead conspecifics as indications of danger [14,16]. The finding that contact was uncommon may suggest that crows do not collect information via tactile interactions, tactile interactions are not necessary to collect such information or that the benefits of collecting such information are not outweighed by potential costs.

Although uncommon, we repeatedly observed that wild crows make contact with dead conspecific stimuli including juveniles and adults in varying positions. Contact could be exploratory, aggressive or sexual in nature. To our knowledge, this behaviour has not been previously reported in wild American crows. By contrast, California scrub-jays are not known to touch dead jays [14]. Further study is needed to determine if this behaviour is unique to crows among other corvids.

Our finding that interactions by wild crows with heterospecifics differed from interactions with conspecifics with respect to scolding, mobbing and the prevalence of aggressive and sexual behaviours suggests that interactions with dead crows are not food motivated. Specifically, that crows were significantly more likely to scold and mob in response to dead conspecifics both overall and during trials where contact occurred demonstrates a consistent danger response that was not observed in response to dead heterospecifics. This finding is supported by other observations that cannibalism (consumption of conspecifics) is rare among passerines [30]. To our knowledge, only one documented case of adult–adult cannibalism has ever been reported in crows [23]. Although most birds did not approach heterospecifics, this is not necessarily surprising given that in our area, predation and scavenging account for less than 25% of a crow's diet [22]. Furthermore, crows prefer open carcasses; therefore, carcass integrity may have kept some individuals away [31]. Those that did make contact appeared to be assessing and quickly determining that the specimens were of little food value.

Instead of foraging attempts, interactions with dead adults included behaviours more akin to territory defence such as intense physical aggression and scolding. In Experiment 2, however, we found that crows differed in their response to crows in a life-like versus dead posture in several key ways. In contrast to presentations of life-like crows, when crows encountered dead crows, they scolded more quickly and more often, were more likely to mob and were less likely to dive-bomb. These behaviours are consistent with the danger response hypothesis and suggest that the crows correctly identified the state of the dead bird. These findings are supported by a study on California scrub-jays that showed jays responded with alarm to a dead jay, but aggressively towards an upright jay [14]. Given that crows will attack intruders, and males appear to force extra pair copulations on non-receptive females, the finding that crows physically attacked or attempted to mate with the live mount is not unexpected [21]. With respect to interactions with the dead crows, it remains unclear what might account for the inappropriate and often conflicting nature of tactile responses including carcass destruction or attempts to mate, but we can begin to speculate as to their cause.

Observations of post-mortem contact that can be described as aggressive or sexual have been observed in a variety of animals. Following the death of a Rhesus macaque (*Macaca mulatta*), Buhl *et al.* [32] observed dominant group members interacting aggressively with the body including beating and biting for 50 min. Stewart *et al.* [33] described rough-handling and beating of a deceased female by young male chimpanzees after her death. Dolphins also sometimes direct aggressive and agitated behaviours towards dead conspecifics [4]. Such behaviours have been proposed as manifestations of frustration or confusion at being unable to elicit a response [33]. This would not account for the early breeding season bias when this behaviour occurred, however. Rather, social theatre or displacement behaviours that arise out of the heightened state of arousal experienced during the breeding season may better explain such observations [8].

Across both experiments, we observed $n = 11$ attempts to mate with a crow in dead posture (4.7% of $N = 234$ trials), 90% of which were coupled with scolding and all of which took place before the end of May. Sexual behaviours around dead conspecifics are rare, but not unique to crows. Hetero and homosexual necrophilia have been observed across a wide variety of taxa. Sexual arousal in response to dead conspecifics has been documented in bottle nosed dolphins [4] and humpback whales (*Magaptera novaeangliae*; [34]). Mating attempts with dead conspecifics have been observed in Richardson's ground squirrel (*Citellus richardsoni*), mallards (*Anas platyrhynchos*), sand martins (*Riparia riparia*) cururu toads (*Rhinella steuvax*) and great ameivas (*Ameiva ameiva*; [35–39]). The copulation posture typical of dead birds has been proposed as the releasing factor for such inappropriate attempts to mate, particularly among monomorphic birds [37]. In Experiment 2, however, we show that crows attempted to mate both with a life-like crow in neutral standing posture and a dead crow with the wings tucked close to the body. These observations call into question the validity of posture as the primary releasing factor for copulation events between crows and dead crows, and warrant further investigation.

Given the prevalence of scolding before, during or immediately following copulation events with dead, but not life-like, crows, alarm induced arousal, rather than reproductive attempts, might better explain copulation with dead crows. Increased sexual behaviour following alarm or excitement has been observed in the zebra finch (*Taeniopygia guttata*; [40]), vermillion flycatcher (*Pyrocephalus rubinus*, [41]) and pied avocet (*Recuruirostra avosetta*; [42]). Following the death of a group member, sexual behaviour occurring outside the breeding season was observed in rhesus macaques [32]. Likewise, we observed mating attempts between presumed pairs following discovery of a dead crow. It is possible in this context that distress induces arousal resulting in copulation attempts between mates if possible, but in the immediate absence of the mate results in displacement-mounting. In rooks (*Corvus frugilegus*), sexual displays by males sometimes stimulate reverse mounting by females [43]. In our study, females witnessing male precopulatory behaviour prior to mounting the stimulus may be responsible for the two possible instances of reverse mounting.

In addition to the multiple mating attempts with the dead and life-like crows, we also observed one attempted copulation with the dead pigeon. Attempts to mate with live heterospecifics have been observed in a variety of species including seals and non-human primates [44,45]. Although these events are rare enough that determining causal factors remains difficult, restricted access to conspecific females has been commonly observed in these cases. Such information about the crow involved in this case is not known.

Given that sexual and aggressive behaviours were often expressed simultaneously, it may be that breeding-related endocrine changes downregulate the ability of some birds to process conflicting information. Among primates, ambiguous or conflicting stimuli are processed in the anterior cingulate cortex (ACC). In humans, it has been shown that individuals with high anxiety show reduced ACC recruitment during tasks involving threat-related stimuli [46]. It is not yet known what area in birds may act as the functional homologue to the ACC, but the corticoidea dorsolateralis has been proposed as a possibility, given its similar pathways as the mammalian cingulate cortex [47]. Further study is needed to determine if the CDL is responsible for processing such information in birds, and if some individuals show reduced activation and lower suppression of inappropriate responses during periods of high excitement such as the breeding season or when exposed to threats. In addition, exploring endocrine differences with respect to adrenocorticosteroid hormone, testosterone and corticosterone between birds that do and do not engage in contact will further elucidate breeding season-induced changes on the release of inappropriate behaviours. Studies examining the change in rates and nature of contact within individuals across the breeding season will help verify that such behaviours wane in correlation to decreased reproductive activity.

This study is the first to demonstrate that American crows occasionally make contact with dead conspecifics. The nature of contact in crows can be exploratory, aggressive or sexual. We show that such behaviours are both atypical and, with respect to sexual and aggressive behaviours, seasonally biased. We suggest that rather than information acquisition, food or territoriality, contact with crows is attributable to an inability among some birds to process conflicting stimuli resulting in inappropriate or conflicting displacement activities. Similar aggressive and sexual behaviours have been anecdotally observed among cetaceans, non-human primates and elephants. It remains unknown, however, whether our findings apply to these animals. A crucial distinction between our study and the vast majority of observations among mammals is that most interactions involving mammals were between familiar individuals. The potential myriad ways this may affect the response of either mammals or birds are unknown. Given that crows maintain permanent pair bonds that can span over a decade, it is possible that responses to familiar individuals contrast with our findings, particularly with respect to affiliative behaviours. Understanding whether these differences exist and what form they take (which may be investigated in experiments employing sedation) will help us better elucidate the significance of death on group members and partners, and help guide best practices when we are confronted with animal death in captive settings.

Data accessibility. The raw data associated with this manuscript can be found within the University of Washington's ResearchWorks archive at https://digital.lib.washington.edu/researchworks/handle/1773/40753.

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Review

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Social relationships and death-related behaviour in aquatic mammals: a systematic review

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Some aquatic mammals appear to care for their dead, whereas others abandon their live offspring when conditions are unfavourable. This incredible variety in behaviours suggests the importance of comparing and contrasting mechanisms driving death-related behaviours among these species. We reviewed 106 cases of aquatic mammals (81 cetaceans and 25 non-cetaceans) reacting to a death event, and extrapolated 'participant' (*age class*, *sex*, *relationship* and *decomposition*) and 'social' characteristics (*escorting*, *calf dependence*, *alloparental care*, *herding* and *dispersal patterns*) from published and unpublished literature. A multiple correspondence analysis (MCA) was performed to explore the relationships between these characteristics and death-related behaviours, with species clustered based on MCA scores. Results showed that both cetaceans and non-cetaceans react to death but in different ways. Non-cetaceans, characterized by a short maternal investment, were observed to protect the dead (defending it from external attacks), while cetaceans spent much longer with their offspring and display carrying (hauling, spinning, mouthing with the carcass and diving with it) and breathing-related (lifting and sinking the carcass) activities with the dead generally in association with other conspecifics. Our work emphasizes the need of increased documentation of death-related cases around the world to improve our understanding of aquatic mammals and their responses to death.

This article is part of the theme issue 'Evolutionary thanatology: impacts of the dead on the living in humans and other animals'.

1. Background

'Death-related behaviour' [1], including grieving and other complex responses to dying or to distressed conspecifics, was long considered an exclusive prerogative of our species [2]. Darwin was one of the earliest to suggest that other animal species, like humans, are capable of pleasure, pain, happiness and misery [3]. Death-related behaviour is described as a subcategory of epimeletic or nurturant behaviours (i.e. a healthy individual gives attention to an injured or dead one, as summarized in [4]) and is usually seen as a consequence of the cooperative, succouring and protective nature of social mammals [4–8]. Considering that the individual receiving this attention is often an offspring, some authors suggested that this behaviour could be a consequence of the strong mother–offspring bond [9–12], or a revival attempt through violent manipulation of the bodies [13,14]. In certain cases where the dead or dying individuals were adults, a sexual component and/or a dominance display is involved as observers recorded erections, mounting attempts and other dominance display behaviours [15,16]. Generally, social structure features, anatomical constraints and ecological conditions could influence death-related behaviours, while an evolutionary or direct benefit is still far from being inferred [8].

According to the available literature, epimeletic death responses among land and marine mammals include stereotyped behaviours such as the carrying of dead offspring (primates using hands, cetaceans against their dorsal fin or similarly to *Canis* in their mouth) and having the mother–dead infant pair (or simply the dead infant) protected or escorted by other members of their groups, as observed in elephants, cetaceans and primates [4,7]. In cases where individuals were unable to carry the dead (e.g. lemurs, giraffes and elephants), these species are known to stay near a dead conspecific for extended periods and move back and forth between their groups and their distressed or dead offsprings [6–8]. Many aquatic mammal species react to the death of a conspecific, most often a calf, and adults can be observed staying close to, maintaining physical contact with, lifting, keeping at the surface or carrying the dead one, even in an advanced state of decomposition. While carrying the carcass adults may stop eating, focusing all their attention on it. They can also display defensive and aggressive behaviours if predators or conspecifics (e.g. pinnipeds) cross their paths, and have escorts accompany and defend them from intruders (e.g. cetaceans, [4,7]). There are also records of species (e.g. sea otters, [17–19], Antarctic fur seals [20]) that have been observed to routinely abandon their live pups, owing to environmental changes, illness or nutritional stress.

While death-related behaviours of dolphins are known to be highly variable [4,7], there has not been a comprehensive review of the available information on this topic including all cetaceans. The only exception is a recent encyclopaedia chapter focusing on epimeletic behaviour among cetaceans [4]. Regarding pinnipeds, sea otters and manatees, the current available information is lacking, and the few studies are often descriptive and include sporadic observations. However, in the majority of reported cases, a change in behaviour occurred after the death of a conspecific, suggesting that such event may have caused disruption/distress in the species displaying death-related behaviours. In this study, the association between aquatic mammal species' social characteristics and death-related behaviours was explored by using a multiple correspondence analysis (MCA) of the literature and available unpublished material. The aim was to answer the following questions: (i) Can behaviours displayed during death events be linked to certain species' social characteristics?, (ii) If so, which social characteristics can be used to categorize the type of behaviour displayed? and (iii) How do these behaviours differ among cetaceans and non-cetacean species? Sightings published in the literature and in the field were collected and were critically assessed, highlighting inconsistencies and identifying key areas for further work and future analysis.

2. Systematic and analytical literature review

We used the *List of marine mammal species and subspecies* [21] to create an updated list of aquatic mammals, distinguishing cetacean (odontocetes and mysticetes) from non-cetaceans (pinnipeds, sea otters and manatees) for this study. To find published cases, we used a combination of search words (see electronic supplementary material, table S1A for how these words were combined) including *calf*, *pup*, *adult*, *mortality*, *died*, *dead*, *death*, *mother* and *behaviour*, with the Latin name of each species, in the search engine Google Scholar. We also searched the reference section of online published papers to find additional articles not located in the online searches. Lastly, we contacted authors who had published several papers focusing on sociality, death and mother–calf bond among non-cetacean species. We added new field sightings from other researches to the literature review, and a complete list of all the cases including reference, species and participants characteristics is reported in electronic supplementary material, table S1B. Video and photographs available on the web and collected by a non-scientific audience were excluded owing to potential bias caused by cinematographic editing in videos (such as the loss of the correct temporal sequence of events owing to efforts to increase the dramatic nature of the images) and to the lack of detailed information about death events for photographs. A total of nine 'characteristics' (adapted from [22]) were gathered and were categorized as follows. Four of these were used to describe the 'participant characteristics': *age class* (adult, juvenile, subadult and calf), *sex* (male and female), *relationship* (between the alive 'giver' and the dead 'receiver': mother, inferred mother and unrelated) and *decomposition* (fresh, moderate and advanced; following [23]). Five provided information about the sociality, hereafter 'social characteristics' (see electronic supplementary material, table S2): *alloparental care* (presence and absence), *calf dependence* (defined as when a calf relies on its mother for food, protection, spending the majority of its time with her: 6–11 months, 1–1.5 years, 2–5 years, 4 years, 5.5 years, 6 years, 6–10 years), *herding* (mother–calf pair living in female groups, living in mixed-sex groups, living in mother–calf pair groups only and solitary), *dispersal patterns* (intended as the choice of offspring to stay, to leave their natal group once they reached sexual maturity or to return after a period of separation) and *escorting* (defined by the presence or absence of other conspecifics involved: helper, group and none). We chose these social characteristics because the death of a conspecific can affect group composition and survivability, with group composition potentially influenced by age class, sex, reproductive condition and kinship [24–26], and the social characteristics by group cohesion, parental care, social structure and reproductive success [27]. *Dependence*, *alloparental care*, *herding* and *dispersal patterns* categories were inferred and generalized from population studies found in the literature (see electronic supplementary material, table S2). The category *unknown* was used when the information was not certain, *not applicable* when the receiver was an object, another species or the receiver was severely wounded and close to death (*alive-then-dead*) and *not reported* when a parameter was not described in the literature.

An ethogram of death-related behaviours for cetacean and non-cetacean species was created consisting of a total of 23 behavioural types using terms that were found in the literature review we conducted. Potential sources of bias in our dataset are linked to (i) low frequencies of some behavioural components, and (ii) the species-specificity of some behaviours. In order to prevent the low frequency of some behaviours from biasing our results, we created behavioural categories and grouped multiple behaviours within them. To avoid creating categories that include behaviours displayed solely by one species, we included behavioural components displayed by both cetaceans and non-cetaceans. The only exception is the category 'protection', (see electronic supplementary material, table S3), which is only displayed by non-cetaceans. In some species of pinnipeds females display a protecting behaviour towards their young ones in response to aggressive juvenile male competitors wanting to separate them from their calves during the mating season. Given the uniqueness and importance of this category we decided to retain it. We therefore classified all behavioural types into the following six behavioural categories: (i) carriage: carrying, hauling, spinning, mouthing and diving; (ii) breathing: lifting and sinking; (iii) contacts: striking, licking, body contact, nosing, arousing, suckling and grooming; (iv) protection: protecting; (v) other: vocalizing, kidnapping, searching, unknown, sniffing and sexual; (vi) resting: laying beside the carcass and stationing. See electronic supplementary material, table S3 for the full list of types and categories.

An exploratory analysis of the potential relationships between aquatic mammal species and their death-related behaviours and social characteristics was performed using an MCA [28,29]. MCA allows the analysis of multivariate categorical data and visualization of the results in a graphical manner. For each species, each behavioural and social parameter was marked as a '1' if present and '0' if absent (see electronic supplementary material, table S4).

The matrix data, comprising 23 behavioural types for 28 aquatic species (see details below in 'Participant characteristics and death-related behaviour'), were then converted into dimensions that were structured from the most explicative to the least. To permit visualization, the scores from the two dimensions that account for the most variance are projected to create a factor plane. The scores on the factor plane can be used to explore the relationship between species where the distances between points reflect the similarities in type of social and behavioural characteristics, with the shorter the distance, the greater the similarity. We clustered species into groups by using the scores of the first *n* axes where *n* is defined by finding the cut-off where an increase in the axes does not provide significant discriminative properties (inertial gain). A hierarchical clustering is performed with the scores from these *n* axes using the Euclidian distance and Ward's clustering method. All analyses were performed using the R programming environment (R Core Team 2017) using *FactoMineR* [30] and associated packages for the MCA and clustering analysis.

3. Participant characteristics and death-related behaviour

A total of 106 cases were found (81 of cetacean and 25 of non-cetacean species), with 28 species involved (20 were cetaceans and eight non-cetaceans; see electronic supplementary material, table S1). For cetaceans, *Tursiops* sp., *Globicephala macrorhynchus* and *Sousa chinensis* were the most recorded species displaying death-related behaviours (see electronic supplementary material, histogram S5*a*), and *Otaria flavescens* and *Phoca vitulina* for non-cetacean species (see electronic supplementary material, histogram S5*b*). However, it must be acknowledged that the results presented in this study refer to the number of death cases found through search engines and do not indicate the total number of existing cases. The results in this study could also be biased downwards owing to a possible omission of pertinent papers, although care was taken by the authors to provide the most comprehensive systematic review of death-related cases across all aquatic mammals. For both cetaceans and non-cetaceans, 'givers' were adults, females and usually inferred mothers, while 'receivers' were most often dead calves in a fresh state of decomposition. 'Receivers' were calves in 84 cases, adults in 11, subadults in one and juveniles in seven, while an amniotic sac was targeted in one case (see electronic supplementary material, histograms S5*f,g*).

4. Social characteristics and death-related behaviour

Both cetaceans and non-cetaceans react to death but display different behaviours. MCA (figure 1) results highlight that parameters such as *calf dependence* and *the presence of alloparental care* are related to the behavioural type that is displayed and to the participation of other individuals during death events (i.e. *escorting*). Cetaceans with more dynamic moving patterns and with a longer time spent with their offspring are found to display carrying- (hauling, spinning, mouthing the carcass and diving with it) and breathing-related (lifting and sinking the carcass) activities, generally in association with other conspecifics. More than one individual commonly interacted with the mother–calf pair in cetaceans, either approaching the couple or contributing (see electronic supplementary material, histograms S5*h,i*). Conversely, non-cetacean species, with a shorter maternal investment, react to the death of a conspecific by displaying 'protecting' as a behavioural type. Both cetaceans and seals live in fission–fusion societies [31], so the different shades of gregariousness typical of these groups could explain the frequent involvement of other members of the same species during death events.

5. Cetacean versus non-cetacean species

For non-cetaceans, the dendrogram shows that Phocidae (*Phoca groenlandica*, *P. vitulina* and *P. vitulina concolor*), Trichechidae (*Trichechus manatus*) and the majority of Otariidae (*O. flavescens* and *Zalophus californianus*) are clustered separately from cetaceans (figure 2 and table 1). The grouping between cetacean and non-cetacean species mirrors the behavioural and social differences existing between these two animal groups (see §4 'Social characteristics and death-related behaviour'). Our data also show that females of *P. vitulina*, *P. vitulina concolor* and *O. flavescens* display protective behaviours towards their dead young. This could relate to the protective behaviour that mothers display towards their offspring after birth to defend them against danger. For example, females in *O. flavescens* protect their calves from juvenile male competitors who want to reproduce with them, separating mothers from their calves [32,33]. The remaining Otariidae, *Arctocephalus gazella*, clusters with *Enhydra lutris* (Mustelidae) as these species both display grooming during death events and, although abandonment was not considered in the analysis, both species are also reported to abandon their alive pups due to changes in environmental or body conditions [19,20]).

For cetaceans, the dendrogram (figure 2) shows *S. chinensis* and *S. sahulensis* clustering together, which is likely due to their display of carrying, lifting and stationing behaviours, and having a long period of calf dependence (5–10 years). In the death-event cases analysed for these two species, mothers initially stayed alone with the dead, but were later assisted by escorts in the carrying of the carcass. Another cluster was composed of *Delphinus capensis*, *Sotalia guianensis* and *Lagenorhynchus*

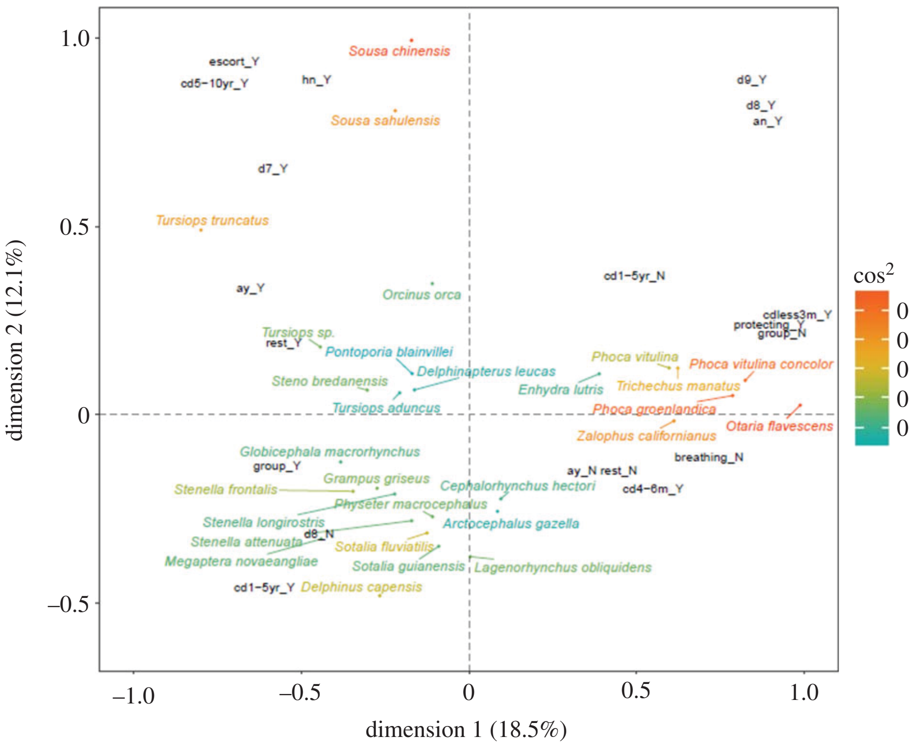

Figure 1. The first factor plane (dimension 1 and dimension 2) of the MCA which explains 30.6% of the total inertia within the dataset. Species are coloured by their cosine squared (cos^2) value with larger values, suggesting a stronger association with each axis. The categories that represent the greatest contribution to both the dimension 1 and dimension 2 axes are shown in black (see table 1 and electronic supplementary material, tables S4 and S3 for a description of each category).

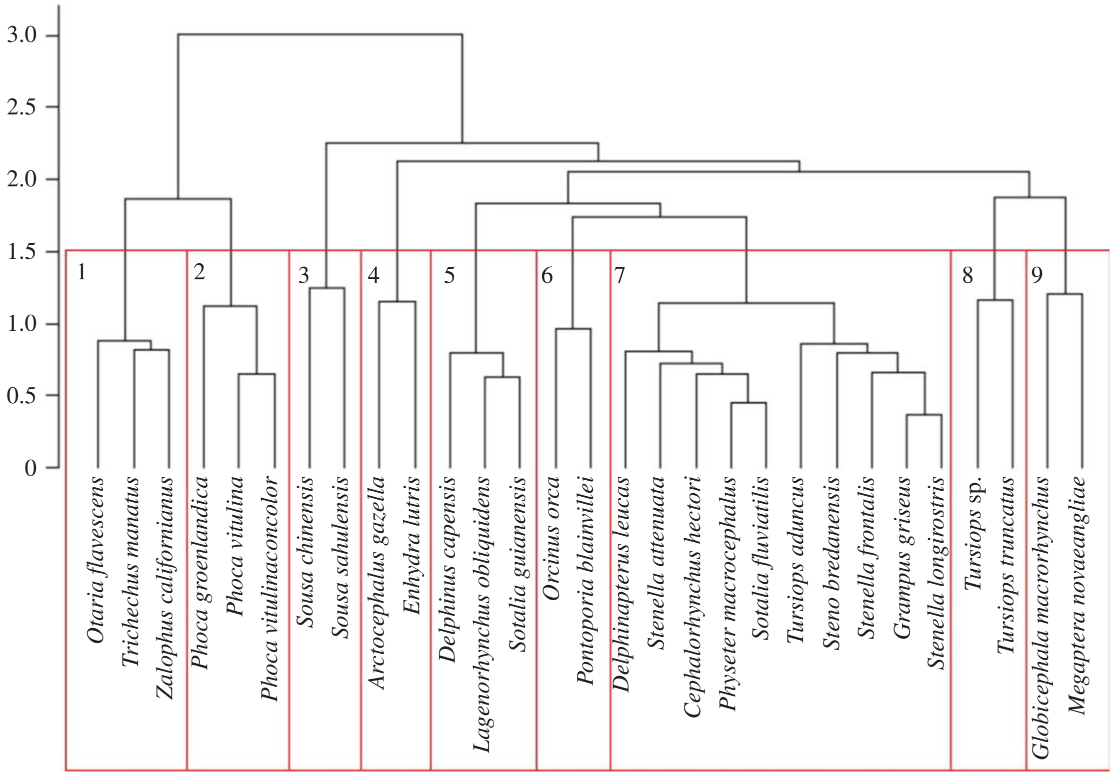

Figure 2. The results of the hierarchical clustering dendrogram using scores derived from the first eight axes of the MCA. Clusters were determined by finding the optimum level of inertia gain ($p < 0.05$).

obliquidens, which share a short calf dependence (less than 1 year), the tendency of mother–calf pairs to live in groups with other conspecifics [34–36] and the presence of escorts intervening and carrying the dead. Another group was made by *Orcinus orca* and *Pontoporia blainvillei*, which were clustered together owing to the fact that juveniles remain with the maternal groups for the duration of their lives [37,38], they both show *allo-parental care*, and during death events they always had at least one escort present with the mother. The largest cluster consisted of *Cephalorhynchus hectori*, *Delphinapterus leucas*, *Grampus griseus*, *Physeter macrocephalus*, *Sotalia fluviatilis*, *Stenella attenuata*, *S. frontalis*, *S. longirostris*, *Steno bredanensis* and *Tursiops truncatus*,

Table 1. The cosine squared ($\cos^2$) scores for the most important variables used to characterize the first two axes (dimension 1 and dimension 2) of the MCA with variables close to one are best represented by the two dimensions. Also shown is the percentage (%) contribution of the yes/no assignments for each category.

		dimension 1	dimension 2		% contribution	
category	ID	cos²	cos²	total	yes	no
dispersal	d8	0.52	0.26	0.78	16.9	6.16
calf dependence	cd5–10yr	0.18	0.44	0.62	16.44	5.23
herding (no)	hn	0.02	0.54	0.56	20.01	2.39
escorting	group	0.53	0.03	0.56	5.16	8.44
calf dependence	cd1–5yr	0.3	0.17	0.47	7.56	6.14
alloparental (no)	an	0.31	0.13	0.44	10.05	2.49
death-related behaviour	protecting	0.4	0.01	0.41	8.63	2.21
escorting	helper	0.13	0.23	0.36	9.49	2.42
calf dependence	cdless3 m	0.34	0.01	0.35	7.35	1.9
calf dependence	cd4–6 m	0.34	0	0.34	7.22	2.64
death-related behaviour	breathing	0.31	0.01	0.32	2.9	4.74
death-related behaviour	rest	0.25	0.04	0.29	3.97	3.22
alloparental (yes)	ay	0.22	0.06	0.28	4.94	1.92
dispersal	d9	0.15	0.07	0.22	6.07	2.87

which all displayed carrying, diving, mouthing and lifting as death-related behaviours. Lastly, *Globicephala macrorhynchus* and *Megaptera novaeangliae* were clustered together, sharing lifting and sexual behaviours directed towards dead adults (erections and intromission of a male towards dead female for *G. macrorhynchus*; erection and genital slit opened for *M. novaeangliae*). They also displayed their death-related behaviours in the presence of other individuals, a calf dependence period lasting 1–5 years and a tendency of mothers and calves to group together [39,40].

6. Conclusion and future recommendations

An important step when summarizing the findings of this work is to address the three aims we outlined at the beginning of this study that relate to the investigation of the association between aquatic mammals' species' social characteristics and death-related behaviours. (i) *Can behaviours displayed during death events be linked to certain species' social characteristics?* A high number of species show death-related behaviours that can occur due to a mix of ecological, taxonomical, cultural and abiotic factors. Here, we have shown that the behaviours displayed during death events in marine mammals can be linked to certain social characteristics. (ii) *Which social characteristics can categorize the type of behaviour displayed?* Death events represent for highly social species the definitive breaking of a strong social bond. Outcomes of this work highlight that for marine mammals, some social characteristics, such as calf dependence and the presence of alloparental care, can categorize death-related behavioural patterns. Lastly, (iii) *How do these behaviours differ among cetaceans and non-cetacean species?* Social characteristics, like alloparental care and calf dependence, differ among cetacean and non-cetacean species and consequently their behavioural patterns are influenced by this variation. Our results highlight that the differences in social characteristics shown by these two groups exert a strong influence on the variation of the observed death-related behaviours.

In the context of the new interdisciplinary area of comparative thanatology [41], which incorporates animal cognition, social behaviour, inter-individual relatedness and emotion, this study provides scientific advances in understanding how aquatic mammals face death through a systematic and analytical approach to link behaviour and social characteristics. However, fully understanding how aquatic mammals perceive and react to death will require more time. As a future consideration, a larger number of death-related events is needed to improve our understanding of grieving, abandonment and neglect towards the dead. We therefore hope to encourage an increasing number of researchers to report sightings of similar events, collecting acoustic recordings alongside photographs and videos with scientific rigour, and strictly accompanied by an accurate description of all behaviours displayed in chronological order. Future analysis could also include the use of mortality rate and predation risk as parameters investigated, as they are known to affect group cohesion and composition, which might ultimately influence how mammals relate to death.

Data accessibility. Data are available in the electronic supplementary material.

Authors' contributions. M.A.L.V.R. and C.G.B. conceived the work, performed the systematic literature review, participated in data analysis and drafted the manuscript. L.E. contributed to most of the cetacean literature review. E.P. contributed to a field case, participated in data analysis and drafted the manuscript. G.A.deL. contributed with E.P. to a case described in the paper. N.McG. analysed the data, prepared all figures present in the paper, drafted the manuscript and helped revise the use of English. All authors gave final approval for publication.

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Behaviour of nonhuman primate mothers toward their dead infants: uncovering mechanisms

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Opinion piece

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In comparative thanatology, most reports for nonhuman mammals concern mothers' behavioural responses to their dead offspring: most prominently, dead-infant carrying (sometimes of extended duration); but also inspection, proximity, maternal care such as grooming, protective behaviours and filial cannibalism. Documented across many primate species, these behaviours remain poorly understood in all. The literature is dominated by relatively brief qualitative descriptions of isolated anecdotal cases in apes and monkeys. We argue for quantitative coding in case reports, alongside analyses of longitudinal records of such events to allow objective evaluation of competing theories, and systematic comparisons within and across species and populations. Obtaining necessary datasets depends on raised awareness in researchers of the importance of recording occurrences and knowledge of pertinent data to collect. We review proposed explanatory hypotheses and outline data needed to test each empirically. To determine factors influencing infant-corpse carriage, we suggest analyses of deaths resulting in 'carry' versus 'no carry'. For individual cases, we highlight behavioural variables to code and the need for hormonal samples. We discuss mothers' stress and welfare in relation to infant death, continued transportation and premature removal of the corpse. Elucidating underlying proximate and ultimate causes is important for understanding phylogeny of maternal responses to infant death.

This article is part of the theme issue 'Evolutionary thanatology: impacts of the dead on the living in humans and other animals'.

1. Introduction: How do mothers behave towards their dead infants?

In the emerging discipline of comparative thanatology, most reports for nonhuman mammals concern mothers' behavioural responses to their dead offspring, continued transportation being most evident. Mothers may carry the corpse of their infant for hours, days or months—sometimes after all resemblance to a living infant ceases, beyond bloating and mummification, clutching only skeletal remains or a disintegrated fragment. Extended duration carrying is not exceptional (table 1). Most commonly, however, transportation lasts between one and several days, and mothers typically direct caretaking behaviour to the dead infant as if it were still alive, such as grooming and apparently protective behaviours. Despite reports across a diverse array of species, both captive and wild, from apes, monkeys and manatees to dolphins and dingoes [2,17,18,21], this striking phenomenon remains poorly understood. Proximity after death and 'inspecting' the infant-corpse are seen even more broadly across taxa (e.g. in giraffes, table 1). Elucidating underlying proximate and ultimate causes is an important requirement for understanding the phylogeny of maternal responses to death in infants.

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Table 1. Range of dead infant-directed behaviours observed across taxa: selected individual examples. Behaviours are as reported by authors of the respective papers. Note that the absence of a tick does not necessarily mean that the behaviour did not occur, only that it was not reported. Duration of carry (days) relates to one particular individual case.

		infant-corpse directed behaviour by mother														
				investigate				caretaking			other	protect/defend				
category	species	duration in proximity to corpse (if no carry)	approach/ retreat repeatedly	peer	sniff	lick	touch-inspect with hand/fin	groom	hold/ carry	duration of carry (days)	cannibalism	wasp/fly swat	block crows	block others'[r] interaction	references	captive (c); wild (w); provisioned free-ranging (f), rehabilitant (r)
apes	chimpanzee[a]	—						✓	✓	≥ 27		✓			[1]	w
		—			✓		✓	✓	✓	68		✓			[2]	w
		—	✓	✓			✓		✓	2		✓			[3]	c, r
	bonobo[b]	—						✓	✓	≥ 1	✓			✓	[4]	w
		—							✓	~ 1	✓	✓		✓	[5]	w
	orangutan[c]	—					✓	✓	✓	10	✓				[6]	f, r
	gorilla[d]	—						✓	✓	>20				✓	[7]	w
monkeys (Old World)	Japanese macaque[e]	—	✓	✓	✓	✓	✓	✓	✓	28	✓	✓		✓	[8,9]	c
	Taihangshan macaque[f]	—				✓			✓	≤ 1	✓				[10]	f
	Tonkean macaque[g]	—		✓		✓	✓	✓	✓	25	✓				[11]	c
	gelada baboon[h]	—						✓	✓	≥ 48					[12]	w
	Hanuman langur[i]	—		✓		✓		✓	✓	27			✓		[13]	f
	Yunnan snub-nosed monkey[j]	—						✓	✓	≥ 3					[14]	f
(New World)	capuchin monkey[k]	—	✓			✓		✓	✓	1		✓			[15]	w
prosimian	ring-tailed lemur[l]	$\sim$6 hr	✓		✓	✓	✓			—					[16]	w
cetacean	Risso's dolphin[m]	—	✓				✓		✓	±				✓	[17]	w
canid	Dingo[n]	—	✓						✓	2[q]					[18]	w
ungulate	Rothchild's giraffe[o]	3 days	✓		✓					—					[19]	w
	Thornicroft's giraffe[p]	2 hr			✓					—					[20]	w

[a] *Pan troglodytes*; [b] *P. paniscus*; [c] *Pongo abelii*; [d] *Gorilla beringei beringei*; [e] *Macaca fuscata fuscata*; [f] *M. mulatta tcheliensis*; [g] *M. tonkeana*; [h] *Theropithecus gelada*; [i] *Semnopithecus entellus*; [j] *Rhinopithecus bieti*; [k] *Cebus capuchinus*; [l] *Lemur catta*; [m] *Grampus griseus*; [n] *Rhinopithecus bieti*; [o] *Giraffa camelopardalis rothschildii*; [p] *G. c. thornicrofti*; [q] four confirmed instances of transporting corpse; [r] 'others' refers to conspecifics, humans, boats; ± unknown.

The currently available literature is dominated by relatively brief, qualitative descriptions of isolated, anecdotal cases. Remarkably, despite hundreds of reported instances of dead-infant care and portage, virtually none include quantitative coding of behavioural responses. Further, only one study has analysed longitudinal records of multiple cases [22], leaving a major source of potential insight unexplored.

Why is it necessary to take a quantitative approach? With qualitatively similar behaviours seen across taxa in response to infant death, quantitative data will enable direct systematic comparisons between as well as within species and across populations. Mothers' response to their dead infant is a highly emotive topic; therefore, conclusions based on objective, quantitative evidence are of particular importance. In seeking to understand behavioural responses to infant death, we must avoid both over-interpretation and speculation as much as under-interpretation, and define often-loaded terms like 'grieve' and 'mourn' operationally. Most fundamentally, quantitative evidence will be necessary to reveal causal mechanisms, to allow us to test proposed theories empirically.

We cannot yet explain why some mothers abandon their infant soon after it dies, but others continue carriage for weeks. Why do mothers carry at all? What causes carrying of extended duration, followed by eventual discard? It is sometimes assumed that strength of the maternal–infant bond alone underlies transport and care of the infant-corpse, especially for animals with complex cognitive capacity, but influencing factors are likely to be numerous and complicated. Several researchers have highlighted the need to consider alternative explanations, such as climate [12]. Furthermore, extended carrying is seen in a wide variety of Old World primates (table 1) [12]. Intriguingly, both monkey and ape mothers have been observed to perform behaviours of opposite extremes toward their infant-corpse: both protective, nurturant care and carrying, and cannibalism (table 1). Strikingly, carrying can overlap cannibalism. One monkey mother carried her dead infant for a further three days after cannibalizing [8,9] with no further cannibalism events subsequently observed. Any explanatory theory must account for such apparently contradictory behaviours.

Many hypotheses for post-mortem attentive behaviours towards infants have been put forward and discussed [21]; however, the literature generally lacks explicit suggestions for testing such hypotheses directly. Focusing on nonhuman primates, we review the proposed hypotheses and delineate the data that will be required for systematic analyses of contributing factors. For case reports, we outline variables to be coded quantitatively, and discuss stress in relation to infant death, carrying and early removal of the corpse. Although our review concerns mainly nonhuman primates, much of the discussion and many suggested quantitative measures are equally applicable to a wider range of taxa. We focus on mothers' responses to infant death (not sick or dying infants or adult death) and observational not experimental approaches (e.g. [23]).

2. Possible explanations

Care towards and carriage of dead infants have generated considerable interest and speculation across several disciplines. To uncover underlying mechanisms, we must consider all existing hypotheses, generate additional interpretations, examine evidence for and against and accumulate quantitative data for empirical evaluation. Hypotheses are listed in table 2, with the quantitative data needed to test each. Consideration of influencing factors should ideally be driven by predictive theory. While some hypotheses stand in direct opposition, other sets of hypotheses may not be mutually exclusive.

Continued maternal care and carrying following the death of an infant have been interpreted as a direct index of maternal-bond strength [2,14]. However, distinguishing this measure from related variables, including disentangling mothers' emotional from biological investment, presents challenges. Potential hormonal influence has been highlighted, with authors suggesting that pregnancy hormones underlie post-partum attentive behaviours [7,24] and that resumption of cycling leads to discarding the corpse [2]. It is unlikely that maternal affection represents the sole underlying cause across all taxa for at least three reasons, outlined below.

First, nurturant care and/or dead-infant carrying are in some instances combined with [4,5,10] and, importantly, may even overlap, the mother ingesting flesh or dried flesh from the corpse, with careful carrying resumed afterward for hours to days [6,8,9,11]. The juxtaposition of care and cannibalism is puzzling. For example, a wild bonobo mother groomed her infant-corpse immediately before cannibalizing it [4]. If cannibalism always occurred at the end of carrying, immediately before discard of the corpse, this would be consistent with a gradual weakening of the mother–infant bond, from treating it as if alive (grooming, protecting and carrying it) to treating the body eventually as an object/food. The incidence of overlap, continued carrying after cannibalizing, suggests simultaneous, conflicting impulses. If carrying behaviour is driven purely by maternal affection, it is difficult to explain recommencement of carrying after eating part of the corpse. Although cannibalistic mothers may simply be carrying around an easy source of food, this interpretation seems unlikely because of the apparent care with which they carry it, the length of time that is probably energetically costly and the lack of subsequent cannibalism or further missing fragments observed before discard. Elucidating what drives the maternal cannibalism element, considered a natural behaviour, could help to unlock the motivations underlying the phenomenon of dead-infant carrying.

Second, corpse-carrying and care are not limited to mothers, or even to females, and it extends across species boundaries. Other females within a group may carry the infant-corpse (gorilla: [7]; gelada baboon: [12]); even females of a different group [12]. Dead-infant transportation and care by males can be explained by neither maternal bond nor hormones. A male bonobo carried, protected and groomed the body of his dead sister [25]; a rhesus monkey behaved similarly toward an adopted infant for a day after it died [26]; a baboon carried the corpse of an infant killed during a fight for a week [27]. Such behaviour is perhaps less surprising for species in which males are heavily involved with infant care and thus social bonds between males and infants may be formed pre-death. Male barbary macaques (*Macaca sylvanus*) of all age categories carry, protect and groom dead infants, using them in species-typical social interactions including agonistic buffering [28]. Cases of interspecific corpse care include a female captive guenon monkey inspecting, grooming and carrying a dead rat for two days [27]. Most

Table 2. Potential explanations for mothers' behavioural responses to dead infants and the data required to test each empirically.

category	hypotheses	ref.	data required
mother	maternal-bond strength	[1,2,11,14,16,24]	proximity to corpse over time [3,8,9]; effect of age of infant at death (time to bond)
	post parturition hormones	[2,7,24]	hormone metabolite levels in urine/faeces (prolactin, oxytocin): pre-mortem and post-mortem (compare for 'carry'/'no carry' mothers), during carrying and after discard (for 'carry' mothers), association with frequency/duration of nurturant behaviours; compare: carrying rate, 'carry' versus 'no carry', for infants dying within period of hormonal influence versus dying older, stillborn versus dying $\geq$1 day old; observe when cycling resumes relative to discard
	'unawareness' of death	[13,22,24]	submersion of corpse in water [21]; experimental approaches
	lack of experience with dead individuals	[22]	number of dead individuals interacted with in lifetime prior to dead infant: 'carry'/'no carry', behavioural responses observed
	learning about death	[3]	quantitative coding of inspection behaviours/sensory cues, especially directed to face/head [3]; does likelihood of inspection decrease with higher frequency of previous inspection events?
	'learning to mother'	[7,24]	primiparity; number of previous successfully reared infants; age of mother at infant death; record of nulliparous females interacting with dead infants: subsequent rearing success versus that of comparable nulliparous females without such interaction; do females handle others' dead infants while pregnant? (hormonal influence); quantitative coding of nurturant behavioural responses observed
	maternal experience	[2]	primiparity; number of previous successfully reared infants
	mothers' age at infant death	[13,22]	age of mother at infant death
	'wait and see' strategy	[13,18,24]	primiparity; number of previous successfully reared infants; age of mother at death
	individual differences	this paper	longitudinal records: repeat carries by same individual; carrying durations between and within individuals; measures of individual differences: 'personality', reaction norms in relation to 'carry'/'no carry' and type of behavioural responses observed
	social facilitation	[a]	number of mothers in same group carrying live infants at time of infant death: 'carry'/'no carry'
	cultural transmission	[2]	number of other mothers in same group carrying dead infants in lifetime of mothers that 'carry'/'no carry'; evidence for social learning (gaze orientation/observation)
	costly signalling of maternal diligence[c]	[b]	relative reproductive success/quality of males copulated with: for females of comparable age, parity and rank (etc.) for females that have carried versus have not; coding of gaze orientation of males toward females carrying dead infant (evidence of selective attending)
	social rank	this paper	social rank of mother; social network analysis
	dead-infant carrying mitigates stress in mother[c]	this paper	glucocorticoid levels and negative behavioural indicators observed (stress-related, 'depressive'): pre-mortem and post-mortem (compare for 'carry'/'no carry' mothers), during carry and after discard (for carry mothers)
	parallels to species-specific infant developmental stage	([22], this paper)	age of infant at death in relation to species-specific developmental stages
	species differences in handling dead infants of different sexes	this paper	sex of infant—'carry'/'no carry', carrying duration, behavioural responses observed for various species in relation to species-specific differences in relating to live infants of different sexes

(*Continued.*)

Table 2. (*Continued.*)

category	hypotheses	ref.	data required
infant	age at death	[14,22]	age of infant at death; developmental stage at death
	sex	[22]	sex of infant
	morphological resemblance to live infant[c]	[11][d]	over time: % body remaining; objective rating state of corpse over time, carrying duration
	cause/context of death: (traumatic versus 'peaceful')	[21]	cause of infant death (peaceful: perinatal death, disease; traumatic: death from injury, infanticide)
ecological/ environmental factors	extreme climatic conditions slow decomposition[c]	[12,21[d]][5[d]]	seasonal influence—climatic conditions: rainfall, humidity, temperature, season; comparisons across various climates [21] – 'carry'/'no carry', carrying duration
	arboreality[c]	[21]	population carrying rates, carrying durations: in arboreal/non-arboreal species; frequency corpse dropped from trees/height; comparisons across various terrain difficulty
	demands of foraging[c]	[22][d]	compare provisioned populations versus non-provisioned: carrying durations

[a] JR Anderson 2015, personal communication.

[b] CP Van Schaik 2015, personal communication

[c] Relates to dead-infant carrying and carrying duration only.

[d] Relates to carrying duration only.

strikingly, a post-menopausal wild female bonobo groomed, protected and carried a dead red-tailed monkey for 43 days, latterly only a skeleton [29]. These latter cases suggest that carrying and nurturant behaviour towards a corpse is not dependent on pre-mortem bond formation. This also applies to tending, carrying and extended carrying by mothers of stillborn infants [30], though hormonal factors may influence such responses.

Third, if maternal-bond strength alone determined carrying, presumably infants surviving longer prior to death, allowing more time for mothers to form a strong bond, would more likely be carried than those dead soon after birth [14,31]. However, longitudinal evidence indicates the converse [22]. In a pioneering study systematically assessing three influencing factors (mothers' age, infant age and sex) in a population of Japanese macaques over 9 years, 80% of carried infant-corpses died within 30 days of birth. Further, mothers carried less than 5% of infants that died between 31 and 253 days old. When considering influence of infant age at death, predictions should correspond to biologically meaningful infant developmental stages. In Japanese macaques, 30 days coincides with a transition from high to lower dependency; from travelling while clinging to their mother and getting pulled back/retrieved if they wander, to following behind more independently [22]. If maternal behaviour to infant-corpses is interpreted as a continuation from pre-morbid tendencies [22], we might expect infants dying at a stage of relatively higher dependency as more likely to be carried, and similarly kept close, by their mothers in death as in life.

For perinatal infant deaths, any hormonal influences (oxytocin, prolactin) on behavioural responses to the infant-corpse are likely to be particularly potent, with primates predisposed to mothering behaviour in the last few weeks of pregnancy [7,24]. Intriguingly, Sugiyama *et al*. [22] found that 90% of Japanese macaque infants that died one day (and no longer) after birth were carried versus less than a quarter of infants that died within a day of birth (or were stillborn). This suggests that handling the infant alive may be an important precursor for hormonal effects to initiate carrying and nurturant behaviour. Perhaps when cycling later resumes the mother continues to transport the corpse, but 'views' the infant-corpse differently. This further underlines the need for hormonal sampling. However, increased time for bonding may still be a predictor among mothers whose infants die above a certain age, e.g. without influence of perinatal/lactation hormones.

An intuitive assumption is that mothers must recognize their infant as dead due to the lack of response when they direct behaviour toward it. However, this is difficult to establish with any certainty. In fact, one explanation for continued care and carriage rests on the opposite assumption, that mothers do not 'realize' the infant is dead [22], instead considering it unconscious/unanimated [24]. Perhaps females inexperienced as mothers or at encountering dead individuals are more likely 'confused' and so more likely to carry than more experienced mothers [22]. Indeed, apparent 'grief' may be difficult to distinguish operationally from possible 'confusion'. Inspection by a chimpanzee mother of her dead infant has been interpreted as potentially gaining sensory cues, leading to learning about death [3]. Some authors have suggested that nulliparous females may be predisposed to handle dead infants to learn mothering skills [7,24]. This may extend to some inexperienced mothers, for example, if their first infant is stillborn or has died at an early age, whether handling their own dead infant or another's. Females that handle infant corpses potentially increase the likelihood of future offspring surviving through infancy. Although handlers may include females other than the dead infant's mother, if they are kin, 'allowing' others to hold the corpse may increase her inclusive fitness. Common to all these explanations is the expectation that younger, inexperienced mothers and females are more likely to carry the infant-corpse than experienced mothers;

however, these various interpretations should be distinguishable according to the identity of the females handling the dead infant and the types of behaviours observed. For example, if nulliparous females are most motivated to handle the corpse, showing mainly maternal behaviours, then the learning-to-mother hypothesis would be supported, whereas a high frequency of behavioural responses to gain sensory cues would suggest individuals are handling the corpse to learn about death.

Other authors have made the opposite suggestion that more experienced mothers are more likely to carry, and for longer, than inexperienced [2], or that older mothers will carry their dead infant for longer than younger mothers [13]. Inconsistent with the former hypothesis are extended carries by primiparous mothers [8,9,11] and the fact that almost a third of carriers were primiparous in the longitudinal study of Japanese macaques [22]. Further, the same study found no influence of mothers' age on likelihood or duration of carrying [22]. Rather than treating parity as dichotomous, a continuous measure such as number of infants previously reared successfully by a given individual would allow a more fine-grained evaluation, for sufficiently large datasets.

Evolutionary thanatology must include consideration of ultimate function. It may be adaptive to continue carrying and caring for an immobile infant, 'just in case' it is still alive, given the heavy biological investment already made [18,24]. However, carrying is energetically costly, more so the older and heavier the infant [22], and extended carrying is potentially maladaptive [18,22]. Presumably, there is a trade-off between discarding too soon and holding on too long. Further, if carrying delays resumption of cycling, or impedes copulation, it might adversely affect reproductive success. However, carrying an infant-corpse does not preclude copulation; indeed, a chimpanzee mother that copulated while carrying her dead infant showed visual signs of cycling [1] and subsequently gave birth, indicating that she had been fertile during corpse-carriage. A mother gelada baboon copulated frequently two weeks before discarding the corpse [12], indicating that hormonal changes leading to cycling are not sufficient to end carrying [12,31]. Another possible way in which dead-infant carrying may increase fitness indirectly, relevant only in species where there is some sort of partner choice, is that females might 'use' carrying to show males they are skilled, 'good' mothers (CP van Schaik 2015, personal communication). Such females would potentially gain access to a better quality male and improve their reproductive success, although depending on males' perception of the situation, the opposite may be true: a mother investing time and energy into a dead infant may indicate inexperience.

Ecological factors may also exert an influence on dead-infant carrying. That extremes of climate (arid, cold) might delay decomposition making carrying more likely, and extend carrying, was proposed initially as an alternative to the maternal-bond hypothesis [12]. Counter to this proposal are multiple reports of extended carrying by mothers in hot, humid, tropical climates (e.g. [6,8,9]), including over 140 infant-corpses carried in the most humid months despite swift putrification [22]. Similarly, inconsistent with continued carrying requiring that corpses resemble live infants morphologically, are the many examples of mothers continuing to transport bloated, misshapen corpses, bodies with missing parts or holding only a single body part; for example, an orangutan mother persisted in carrying only the spinal cord [6]. Arboreality has also been proposed to curtail carrying [21], with the infant-corpse expected to be less likely retrieved upon falling to the ground. Faster decomposition and tree-living may well place an upper bound on carrying duration. However, arboreality does not necessarily prevent dead-infant carrying of extended duration in wild populations. For example, a free-ranging Japanese macaque mother carried her infant-corpse for 30 days, across densely forested terrain, retrieving the corpse repeatedly whenever it fell from the tree (S Matsuoka 2016, personal communication).

Context of death is another proposed influencing factor, with continued caretaking and portage considered more likely and prolonged following a 'peaceful' death, through illness, than a traumatic death through injury or infanticide [21]. Counter-examples demonstrate this is not categorical: two gorilla infants were carried after presumed violent deaths [7]; a wild barbary macaque mother inspected and carried the corpse of her infant killed by a road vehicle [32]; and an adult male Hamadryas baboon carried and tended an infant after killing it [27]. Context of death may be a better predictor for carrying duration compared to predicting whether or not a mother will carry at all.

Repeat carries by the same mother, i.e. for more than one infant death event [2,8,9,11,22], suggest individual differences in the proclivity for the behaviour. In the only longitudinal study [22], 12 Japanese macaque mothers were repeat carriers. One chimpanzee mother carried her dead infants for 27 and 68 days, respectively [2]; a Japanese macaque mother carried and cared for her dead infant for 29 and 28 days on successive births, each time also cannibalizing [8,9]. This raises an intriguing question: do individuals that carry more than once, carry consistently, i.e. at every opportunity? If not, what causes carrying after some deaths yet not others, by the same individual? Do repeat carrying mothers show a consistent pattern, e.g. always carry for extended duration (nominally defined as longer than 10 days [12]); always combine with cannibalism [8,9]? Might these outcomes reflect genetic influence, individual or social learning? Might 'personality' and individuals' reaction norms influence tendency towards particular behavioural responses to dead infants? Do repeat carriers differ from one-time carriers? The longitudinal study of Japanese macaques found no appreciable difference in the ages of repeat carrier mothers or the duration of carrying observed compared with one-time carriers [22]. Importantly, data on repeat carriers might help to clarify the role of (or eliminate) some other factors, such as parity, age and context of death.

It has been suggested that multiple carriers within a social group may be indicative of cultural transmission [2]. Cultural influence might also be evident in the manner, or 'group-style', in which other members respond to dead infants: interest and investigation [2,13] versus no apparent interest [22]. More immediately, social contagion or social facilitation [33] might be a proximate cause of dead-infant carrying. Seeing other mothers in the group holding young (live) infants might motivate a mother to similarly keep holding onto her lifeless infant (JR Anderson 2015, personal communication). This would perhaps be especially likely in species with a fixed birth season and large groups (many mothers carrying at once). Mediating factors might be the total number of other mothers in the group carrying live infants and the degree of association between these individuals and the bereaved mother, with a higher number and stronger association increasing the likelihood of social facilitation.

Social rank of the mother is a potential influencing factor, but as yet unlinked to predictive theory and without indication of a hypothesized direction of difference. Given that carrying is energetically costly, high-ranking mothers may be physically more able to carry for longer, with more access to more and higher quality food, even while still carrying or keeping the corpse in proximity. Conversely, perhaps lower-ranking, more peripheral females will carry the corpse for longer, with fewer baseline social associations. There is scope for application of social network analyses [34].

For other putative contributory factors not yet associated with specific hypotheses, conceivably, species differences in the way mothers relate to their live infants, such as disparity in behaviour according to sex of the infant, may similarly influence responses to dead infants. However, in the longitudinal study of Japanese macaques, no significant difference in the proportion of male and female infant-corpses carried was found [22].

What influence might wild or free-ranging, provisioned versus captive context have on post-partum attentive care, likelihood of continued carrying and carrying duration? Carrying, including extended duration carrying, is seen in all three population types (table 1). Wild populations likely show the highest rate of infant mortality, leading to more opportunities for dead-infant care and carrying but higher energetic costs. Free-ranging, provisioned groups, such as the Takasakiyama group [22], have access to supplementary food, but not veterinary care. Mothers in populations with a poor abundance of food, high foraging demands [22] and a large home range with difficult terrain presumably face the highest energetic costs of continued carrying; extended carrying under such circumstances indicates high underlying motivation. Captive groups inhabit a restricted area, presumably making carrying less energetically taxing, though captive areas may still be relatively large and complex [3,8,9]. None of the observed behaviours by mothers toward their dead infant are considered abnormal (but see [6]).

3. Longitudinal data

Which parameters have explanatory and predictive power for dead-infant carrying behaviour? Long-term datasets of multiple records of mothers' care for and carriage of infant-corpses, from captive and field populations, represent vast potential for elucidating underlying mechanisms. Typically, case reports discuss implications for only a few hypotheses, and risk skew from small sample sizes (e.g. [14]). Longitudinal data will enable systematic evaluation of possible contributing factors (table 2), and multivariate testing. Despite obvious prospective benefits, so far there exists only one set of population-level quantitative analyses for dead-infant carrying [22], indeed for any nonhuman mammalian behavioural response to death. The data come from one population of one species (Japanese macaques). Accumulating longitudinal datasets necessary for future analyses will require wider appreciation of the importance of recording occurrences, alongside awareness of which data to collect to test different hypotheses empirically (table 2). To allow a comprehensive, systematic analysis of potential influencing factors, many relevant variables should be included, along with relevant data on other group members (table 2). At long-term field-sites and for captive populations, demographic data are already recorded. Collecting additional data on events can be relatively straightforward, provided it is added to the site protocol. As such events are relatively infrequent, collaboration and combining data will be important. Scientists with sufficient foresight may already possess the necessary datasets.

One alternative is meta-analyses of published cases but this may result in missing data points and certainly incomplete data across all factors listed in table 2, as required to test proposed hypotheses empirically. Another important consideration for pooled datasets is careful evaluation of how directly comparable cases are in captive compared to free-ranging, provisioned and wild contexts. Examining potential influences such as parity, individual differences (repeat carriers), social facilitation and social transmission will depend on continuous records of infant-corpse-carrying events within populations over time. So too will calculating carrying rates (number of carrying cases per infant deaths in a population) (after [22]). Importantly, the dataset should include only cases where there was sufficient opportunity for the mother to carry directly following infant death, applicable to both captive conditions and the field. For example, cases of infants stillborn during veterinary intervention or where the infant corpse is removed forcibly from the mother should be excluded. Similarly, carrying duration is invalidated if portage is interrupted artificially or by conspecific intervention.

We suggest a novel approach to analyses—direct comparison of influencing factors between infant deaths after which mothers carry, and deaths after which mothers have the opportunity to carry the corpse yet do not. Note that, due to the infrequent observation of death events and thus limited feasibility of establishing complete absence of carrying, especially in the field, 'no carry' may in fact apply to carrying for no more than a few hours. Effects of multiple potential contributory factors, both nominal and interval level, on the nominal dependent variable (carry/no carry), could be analysed together using logistic regression.

4. Quantitative coding in case reports

(a) Behavioural responses

Case reports could contribute more substantially to this field. Several researchers [3,21] have highlighted the need for more detailed, objective, quantitative data on behavioural responses to death. Behaviours directed by nonhuman primate mothers toward their dead infant include: inspection, proximity, sustained/frequent gaze orientation, continued maternal care, protective behaviours, carrying (sometimes for extended duration), and filial cannibalism (figure 1). Because infant death and mothers' responses cannot be predicted, continued interaction with corpses is observed opportunistically. Most thanatological papers on nonhuman species are contributed by researchers for whom this topic is a side-line. Researchers with a comparative thanatology focus could set out to selectively target populations with high infant mortality, especially those with a high carrying rate, periods of highly expected infant mortality, e.g. birth seasons, and, within such populations and periods, individuals that have previously carried once or repeatedly [8,9]; nonetheless timing remains unpredictable. Scientists, especially in the field [21], should be well prepared in advance to record responses to infant death at short notice, and have adequate equipment (video camera, spare batteries) and knowledge of which data to collect. Table 3 summarizes pertinent behavioural variables to code quantitatively, those used in previous studies and suggestions for future inclusion.

Conducting observations continuously from infant death to mothers' eventual discard is ideal, yet rarely feasible [22]. Infant death, like birth, is infrequently observed in free-ranging nonhuman primates [22,35]. Researchers quantifying responses in densely vegetated landscapes are limited to windows of time when the mother and infant-corpse are visible; for example, a chimpanzee coming into view as she begins to separate from her dead infant, videoed over a period of 45 min [3]; a carrying mother macaque emerging from thick undergrowth for feeding, videoed for 30–90 min daily over a month [8,9]. Nonetheless, careful coding of even short durations can yield much useful information. Video records enable more detailed coding than can be achieved accurately live; multiple, mutually exclusive measures can be coded for objective comparison. Use of more than one video camera allows different viewpoints, both wide-frame and focused, allowing, for example, coding of both mother's responses to the corpse and proximity/interaction of and with other group members [3]. Videos can be synchronized for simultaneous viewing [3]. Responses of other group members to a dead adolescent [36] and a sub-adult [37] chimpanzee have been coded quantitatively with the help of video records.

Researchers have noted mothers' transition between constant contact with the infant-corpse and discard [3,11,24], but very few have quantified this process. A retreat/approach pattern has been described across several taxa (table 1), with the mother moving away and returning to the corpse repeatedly. Specifically in nonhuman primates, mothers often lay the corpse down to feed, moving further away and for bouts of increasing duration over time. Quantitative coding has been used successfully to track this tendency over minutes (chimpanzee: [3]), hours (lemurs: [16]) and weeks (Japanese macaque: [8,9]).

Infancy is a period associated with high mortality risk, which is partly why reports on responses to dead infants are so numerous. Ideally, coding should take into account species-typical behaviour and proximity of a mother to a live infant of equivalent age. Nonhuman primate infants are dependent on adult care for survival, and are either in constant physical contact with their mother or allomaternal carer(s), in close proximity or visually monitored. Cronin *et al.* [3] suggested that quantifying mothers' proximity to and gaze orientation toward or away from the infant-corpse offers an objective index of mother–infant bond strength. These represent two important measures to code. They should be interpreted in concert with ad libitum quantitative coding of infant-directed behaviours (table 3) because, for example, like maternal care, episodes of maternal cannibalism also involve close contact/proximity [8,9].

It might be informative to code the mode of carrying over time (table 3). Carrying typically starts off in arms and hands, even when the mother is moving. Later, however, the corpse may be carried in her mouth while she moves [8,9]. Baboon and chimpanzee mothers may carry their dead infant slung across their back [2]. Although live infant monkeys and apes cling, and hence are not usually carried in hands/arms or mouth or across the mother's back as corpses are, deformed, sick or experimentally anaesthetized infants may be carried in their mothers' arms [22,24].

Inspection of her dead infant by the mother was first coded quantitatively in a chimpanzee mother [3], and later a Japanese macaque [8,9]. Some researchers have noted that mothers selectively direct more attention to the face and/or eyes [3,12,13,27,38] of dead infants. The anal area is also often inspected [15,30]. Because inspection is seen widely across taxa, a comparative approach may be informative especially when combined with reports of inspection of sub-adult (e.g. [37]) and adult corpses.

Importantly, quantitative coding of particular infant-directed behaviours will allow evaluation of proposed hypotheses. For example, whether a mother allows her dead infant to be submerged in water or not may relate to awareness of death [21]. Similarly, protective/defensive behaviour of the infant-corpse, including preventing contact by others, may represent maternal behaviour or 'bereavement-related' behaviour, but this must be distinguished operationally from possessive behaviour towards a 'found' object [39], tool, or corpse of another species. Collecting and analysing hormonal samples, as part of case studies, is necessary to assess theories related to hormonal influence, discussed above (§2), and to assess stress related to infant-death, considered below. Detailed quantitative coding of case studies will be most valuable and informative in the context of longitudinal population-level data.

(b) Stress

Do nonhuman primate mothers experience stress when their infant dies? Researchers have studied stress in surviving group-mates following adult [40,41] but not infant death. Female baboons showed increases in glucocorticoid stress hormones after adult kin died. Anecdotal cases provide evidence that mothers do experience stress, but we lack quantitative data. For example, a barbary macaque in a tree above her infant-corpse displayed extended bouts of self-grooming and distress calls [32]. How does the death of an infant and carrying affect the mother's social behaviour and social integration? Japanese macaque mothers with dead infants reportedly showed decreased social grooming [22] though this was not quantified. Might this be linked to behaviour indicative of 'depression', with potential for comparison with humans?

For human mothers whose neonate is stillborn, contact, looking at and holding the dead baby, and treating it as a live baby, spending time with, dressing and bathing it, creating memories over the time-limited period available, can benefit psychological well-being [42]. Dead-infant carrying appears phylogenetically ancient. Might carriage and caretaking of the infant-corpse mitigate stress in nonhuman mothers? If so, benefit to fitness may outweigh energetic cost of carrying, at least for short-durations.

Furthermore, it may be asked whether stress increases for bereaved mothers if the infant corpse is removed while she remains motivated to carry it. In captivity, standard procedure is to remove corpses at the first opportunity [21]. Reasons for this include: performing a necropsy while feasible [7], concerns about public perception, lack of knowledge about dead infant-carrying behaviour, or misinterpretation as an abnormal response. Indeed, authors have suggested that early removal might stress mothers [7]. Even with a

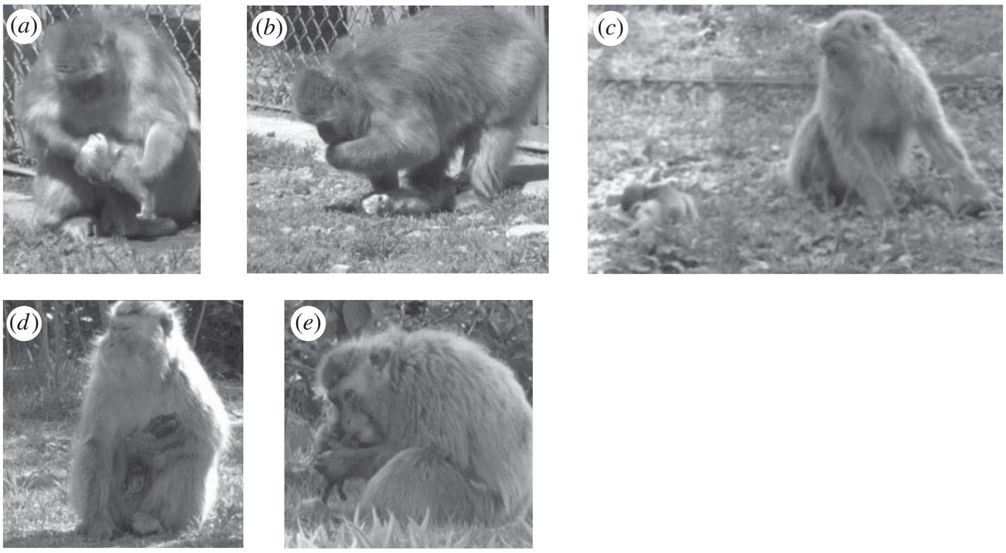

Figure 1. Behavioural responses to infant death: an adult female Japanese macaque holds and inspects her dead infant (*a*) and lays the infant-corpse on the ground while she forages (*b*); another female with gaze oriented toward her dead infant (*c*); a third adult female [8,9] holds/carries the mummified body of her infant 15 days after death (*d*) and cannibalizes it on day 23 (*e*). Photo credits: Claire FI Watson. All individuals were captive, socially housed, in large vegetated enclosures (approx. 1400 m^2). (Online version in colour.)

Table 3. Behavioural variables to code quantitatively in case reports of mothers with dead infants.

category	focal	behavioural variable
proximity	mother	distance to infant-corpse [3,8,9,16] (interval sampling e.g. every second)
		approach/retreat to corpse [8,9] (freq.)
		move between corpse and social group/troop [16] (freq.)
mode of carry	mother	arms/hand, mouth [8,9] (dichotomous)
gaze orientation	mother	head oriented towards/away from corpse [3] (dichotomous)
ad libitum behaviours: — infant-directed behaviours	mother; conspecifics	'inspection': peer, touch with hand, inspect [3,8,9] (body; face; anal region); sniff, lick (not anogenital)[8,9]
		% inspect corpse events followed by hand-sniff [3]
		'nurturant': groom [8,9,14]; play [8,9]; lick anogenital region, hold to teats
		'protective/defensive': swat fly [3,8]; prevent/block others' interaction with corpse (chase/attack)[8,9]; allow/prevent submersion in water [8,9]
		cannibalize: eat flesh/dried flesh [8,9]; other: suck/draw past lips [8,9]
— other-directed behaviours	mother	social groom [8,9], number of grooming partners; copulation (while carrying infant-corpse), compare social behaviour and degree of social integration before and after: infant death and carrying period
— self-directed behaviours	mother	species-appropriate behavioural stress indicators: self-groom; self-scratch
— vocalizations	mother	calls [16]; call types

progressive policy of deferring corpse-removal until mothers lose motivation to carry, judgement can be problematic with appearances potentially misleading without extended observation. Large distances between mother and corpse at any one time may simply represent a repeated approach/retreat pattern. For example, after 22 days of carrying, a macaque mother moved up to 20 m, from her infant-corpse, yet always returned [8,9]. Staff perceived disinterest and removed the corpse. However, when it was returned to the enclosure 10 minutes later, the mother ran towards it immediately and retrieved it, while threatening nearby humans. This case also underscores the benefit quantitative coding can provide.

Going beyond captivity, we suggest that issues surrounding early removal extend to the field and other taxa, with implications for best practice in husbandry and field policy as well as scientific accuracy and validity. For example, nature-reserve staff retrieved a snub-nosed monkey infant body for burial when, on the fourth day of carrying, the mother climbed a tree, leaving it below. The mother began vocalizing within half a minute, and continued to search for the corpse all afternoon [14]. A decomposed infant-corpse being pushed along by an adult dolphin was removed by biologists and towed, by boat, to shore for burial. The presumed mother followed, circling and touching the corpse, and remained in shallower waters long after the body was removed [17]. These anecdotal reports together suggest early removal does stress mothers, evidencing strong motivation to continue carrying (but see [15]). Motivation-based approaches to welfare indicate that being prevented from performing behaviours animals are intensely motivated to perform is stressful [43].

If mothers are stressed when their infant dies, does carrying mitigate this stress? Does early removal of the corpse cause stress, and if so, what implications does this have for captive management and field policy? How does the death of her infant in itself, and carrying, affect a mother's social behaviour? To answer all these questions objectively, we need quantitative data on both physiological and behavioural measures before and after infant death and before, during [31] and after infant-corpse carrying. This includes species-appropriate behavioural indicators of negative welfare and stress, for example, increased self-directed behaviours and distress-related vocalization rates. Measures of mothers' social behaviour, for example, social grooming rates and social integration are likely to prove valuable and such data may also allow for better comparisons to behavioural reactions by humans, for example, depressive symptoms of grief including changes in activity patterns and social withdrawal. Because infant death and infant-corpse carrying are unpredictable events, scientists focused on observing this behaviour are unlikely to have taken the relevant pre-mortem measurements in advance. Such important baseline measurements may then necessarily depend on data and hormonal samples gathered for unrelated research and recorded by researchers investigating non-thanatology topics.

5. Conclusion

Understanding nonhuman primate responses to dead infants can contribute to elucidating the evolutionary origins of human responses to death. However, to fully understand phylogeny, a truly comparative approach will be needed; gathering data from wide-ranging taxa will be key [19], along with interdisciplinary discussion and collaboration. We expect that evidence of inspection and other behavioural responses to dead infants will be found for a wide range of species. Within nonhuman primates alone, current estimates [17] of the number of species displaying infant-corpse carrying and care are probably conservative because many instances go unreported (e.g. wild *Mandrillus sphinx*: M Charpentier 2017, personal communication).

Although documented across many species, mothers' behavioural responses to their dead offspring: dead-infant carrying, inspection, proximity, maternal care such as grooming, protective behaviours and filial cannibalism, remain poorly understood in all. Despite the plethora of proposed explanations, we still lack objective, quantitative data to test each one empirically. Quantitative coding of behavioural responses in individual cases combined with analyses based on appropriate longitudinal records will allow objective evaluation. Potential foci for future observations of death responses are summarized in tables 2 and 3. We seek to encourage and facilitate comparative, quantitative approaches to researching behavioural responses of mothers to their dead infants and have provided a framework to inform future work. Asking the right questions and accumulating relevant observational data will be critical for a more comprehensive understanding of nonhuman responses to death in infants.

Data accessibility. This article has no additional data.

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Chimpanzees and death

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Information about responses to death in nonhuman primates is important for evolutionary thanatology. This paper reviews the major causes of death in chimpanzees, and how these apes respond to cues related to dying and death. Topics covered include disease, human activities, predation, accidents and intra-species aggression and cannibalism. Chimpanzees also kill and sometimes eat other species. It is argued that, given their cognitive abilities, their experiences of death in conspecifics and other species are likely to equip chimpanzees with an understanding of death as cessation of function and irreversible. Whether they might understand that death is inevitable—including their own death, and biological causes of death is also discussed. As well as gathering more fundamental information about responses to dying and death, researchers should pay attention to possible cultural variations in how great apes deal with death.

This article is part of the theme issue 'Evolutionary thanatology: impacts of the dead on the living in humans and other animals'.

1. Introduction

Given favourable social and environmental conditions—such as abundant food, few predators, absence of epidemics and little disturbance from humans—chimpanzees might live until at least 50 years of age. However, as a result of various challenges to their survival at different stages of life most chimpanzees do not live as long, and males generally die earlier than females [1–4]. At Mahale (Tanzania), around half of all infant chimpanzees die before they are weaned [5].

Deaths have been witnessed or inferred by researchers at all long-term chimpanzee study sites. Because female chimpanzees tend to emigrate from their natal communities, unexplained disappearances are conservatively assumed to reflect possible transfer. By contrast, if infants, juveniles or adult males disappear researchers often consider them to have died, although this often goes unverified. Even when dead chimpanzees are found it is not always possible to establish the precise cause of death [6–9]. Known and inferred mortality factors in wild chimpanzees include disease, hunting by humans, nonhuman predators, general senescence, accidents and intra- and inter-group aggression [3,4]; some factors reported in captivity [10] are also likely to apply to wild populations. The aims of this paper are to (1) review causes of death in chimpanzees, (2) consider how chimpanzees respond to death and death-related cues and (3) address the question how chimpanzees' 'psychology of death' compares with that of their nearest evolutionary neighbours, namely humans. The broader, overall aim is to stimulate primatologists to gather and present further information to help progress in the field of comparative evolutionary thanatology.

2. Causes of death

(a) Disease

Chimpanzees in the wild are susceptible to a range of potentially fatal diseases such as pneumonia, human respiratory viruses, simian immunodeficiency viruses, Ebola and anthrax [11–16]. Diseases accounted for most deaths of

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known cause in the early years of research at Gombe (Tanzania) [11,17,18]. Cross-infection may occur from humans (researchers, park employees, local people, tourists) to chimpanzees [14,19]. Following the establishment of improved prevention protocols for humans at Gombe, respiratory disease-related deaths in chimpanzees declined sharply [9]. Some diseases might cause death indirectly; for example, severely weakened individuals may be more prone to accidents or more vulnerable to predatory attacks. Chimpanzees naturally infected with *Toxoplasma* have been found to show abnormal levels of interest in leopard urine, which would likely be maladaptive under normal circumstances [20].

(b) Humans

In many areas where they live chimpanzees are deliberately killed by humans for meat, for body parts in traditional medicine (or as charms), or to obtain infants as pets or to sell. It is estimated that 5–10 chimpanzees are killed for every infant captured alive [21]. Poaching poses a serious threat to many populations, especially in areas where armed conflicts result in food shortages and a breakdown of law and order, and when mining or timber-felling operations open up new roads that facilitate access to forests [22,23]. Chimpanzees are also killed in retaliation for crop raiding or aggression toward humans [8,24–26].

The replacement of traditional weapons (e.g. spears, bows and arrows) by guns has made it easier to kill chimpanzees and other wildlife. Snares and mantraps are sometimes set specifically for chimpanzees, although they are generally more often used to capture other animals [27,28]. Many chimpanzees lose fingers, toes, hands or feet after getting caught in snares, and some survivors have wire embedded in their flesh for a long time [29–31]; death from infection must befall some injured victims [28,32,33]. Snare-injured chimpanzees in Budongo (Uganda) carry higher helminth parasite loads than non-injured controls, indicating secondary and/or long-term effects on health [34].

Another anthropogenic cause of deaths in chimpanzees is motor vehicles [35]. A recent report described the case of an adult female in Uganda killed by a fast-moving taxi as she tried to cross a road [36]. The mortality risk to chimpanzees from vehicular traffic seems bound to increase with the massive expansion of road building and vehicles travelling at greater speeds [37].

(c) Nonhuman predators and other species

Lions and leopards are known predators of chimpanzees [38–41], although in the absence of direct evidence scavenging cannot always be ruled out [42]. One or more leopards was the primary cause of chimpanzee mortality during a 5-year period in the Taï Forest (Ivory Coast) [43], and at least eight individuals at Mahale were presumed killed by lions over a 2-year period [40]. Among other potential predators, hyenas and African hunting dogs [44,45] are probably of little threat to healthy adult chimpanzees owing to the latters' strength and agility, but capable of finishing off sick or injured individuals.

Despite no records of chimpanzees being eaten by pythons, these snakes are also considered as potential predators [46]. Similarly, given that they consumed early hominids and kill modern humans [47], crocodiles in and around rivers and water holes should be considered as potential predators [48]. Finally, although venomous snakes such as cobras and vipers do not prey on chimpanzees, their bites could be fatal; researchers frequently encountered these species in the savannah-woodland habitat of chimpanzees at Mount Assirik (Senegal) [49].

(d) Accidents

Falling out of trees presents a real danger to large-bodied primates, as indicated by direct observations of the fall-related injuries and post-mortem signs of bone damage [8,9,50,51]. It has been even been argued that fractures on the skeleton of the australopithecine 'Lucy' indicate death from a fall [52]. Fatal falls represented 10% of the sample in a study of Kibale chimpanzee corpses [8]. Gombe adults were most likely to fall during fights [11], and all falls witnessed during a 17-year period at Taï were fight-related [30]. An aggression-related fatal fall was recently reported in a zoo-housed chimpanzee group [53].

One fatal fall at Gombe was by an adult male who died instantly from a broken neck when he hit the ground after the branch supporting him broke [54]; another was by an infant who got blown out of a tree by a gust of wind and who died from suspected internal injuries a few days later [11]. Usually when youngsters fell it was during play and resulted in fewer injuries than in adults, who fell from greater heights [11]. The death of one Taï infant was attributed to a fall [30]. Post-mortem examination of an adult female at Mahale revealed six fractured ribs, suggesting haemorrhagic shock and death shortly after a fall [55]. Researchers at Mahale also reported an unusual but fatal arboreal accident. An abandoned dead infant was found jammed between two overlapping tree boughs. Death was attributed to one bough springing back after being displaced by a heavier, stronger individual—most likely the mother—and crushing the infant [56].

Chimpanzees are not good swimmers, and several deaths by drowning have been reported. Although no reports concern fully wild chimpanzees, some captives released onto an island drowned [57], probably after wading too far into the water. Several zoo-housed chimpanzees have drowned after jumping or falling into moats [58–60].

(e) Conspecifics

Numerous killings of chimpanzees by other chimpanzees have been observed, and further cases have been inferred from wounds on fresh corpses or results of post-mortems [61]. Conspecific killing was the most important cause of death at Gombe between August 2004 and January 2010 [9]. Over a 50-year period at Mahale at least 29 chimpanzees were possible victims of lethal aggression by conspecifics, although when stricter criteria are applied the number drops to 12 [62]. In all 12 cases both attackers and victims were male, a sex bias that emerged also in a multi-site study of 152 intraspecific killings (males accounting for 92% of attackers and 73% of victims) [61].

Intraspecific killing includes infanticide—typically by adults—as well as fatal attacks on adults by other adults [11,61,63]. Whereas a single adult can quite easily kill an infant, it takes a sustained onslaught by several individuals to kill an adult [64]. At Gombe inter-group killings eventually resulted in the elimination of an entire neighbouring community [11], and by wiping out most of their neighbours over a

10-year period a chimpanzee community at Ngogo (Kibale) significantly expanded its home range [65]. In keeping with a direct competition/territorial expansion hypothesis, most victims in 152 observed, inferred or suspected intraspecific killings at five study sites across Africa were members of other communities [61]. Within-group killings of adults have also been reported, both in captivity and in the wild [66–71].

3. Responses to dead animals

(a) Conspecifics: non-cannibalistic responses

Reports about how captive and free-living chimpanzees respond to dead conspecifics vary in details about circumstances of the death and the behaviours shown. The well-known phenomenon of mothers continuing to transport and care for dead infants (and others' reactions) have been well documented elsewhere [72–74]. Here, other categories are considered. Two early accounts are notable for the contrasting responses of young captive chimpanzees to the death of their cagemate. One youngster was found sitting silently and subdued beside his dead companion, who was covered by a blanket. When the body was removed the youngster became agitated, but after being released from his cage he reportedly calmed down and watched as the corpse was dissected [75]. Another youngster vocalized loudly and threw a temper tantrum when his companion died, vigorously pulling, pushing and lifting up the head and hands; he remained agitated for the rest of the day after the body was removed [76]. In both of these cases the survivor may have been frightened by the dramatic change in the companion, from active and interactive to inert and unresponsive.

Fright and heightened arousal characterized Gombe chimpanzees' reactions to the sudden death of an adult male who fell out of a tree [54]. The ensuing general frenzy included loud vocalizations and displays, and mutual embracing, as well as frequent visual and olfactory inspection of the corpse. Gradually, the chimpanzees calmed down and engaged in quiet social activities; several individuals approached and peered at the corpse, but none physically contacted it in the several hours before it was finally abandoned.

Outbursts of vocalizations and aggressive displays interspersed with periods of silence were also recorded at Taï when a leopard killed an adolescent female. By contrast to the post-accident scene at Gombe, however, the Taï chimpanzees frequently touched the dead female, including grooming, and holding and gently pulling her hand; adult males even dragged the corpse along the ground for several metres [30]. Adult males also prevented some individuals from approaching the corpse, notably infants and a low-ranking female. On discovering another (adult) female's body with no obvious signs of injury, Taï chimpanzees sporadically alarm called, screamed and pant-hooted during the 5 h that they remained nearby. They mostly looked down at the corpse from overhead branches, but a few descended to the ground and touched it, one male doing do aggressively [33].

At Gombe, the corpse of an adult female who died after being visibly sick for several days received aggressive treatment from some of the 16–18 individuals present [77]. This account is especially notable for the bouts of rough handling and dragging of the body by young males; other members of the party did little more than look at, sniff or groom the body. Among several females present, only the dead female's daughter physically contacted the body.

The possible influence of the pre-death social relationship with the dead individual on post-death responses is illustrated by a recent case involving a dead 9-year-old male. After discovering the corpse, members of a sanctuary-housed group of chimpanzees sat quietly nearby for most of a 20 min period during which the scene was video recorded [78]. Many individuals looked closely at and sometimes clustered around the body, with at least nine physically contacting it. Two individuals—an adult male and an adult female—were briefly aggressive; the adult female slapped the body. One male who showed special interest had been the closest companion of the dead individual after the latter's mother died 3 years earlier. Towards the end of the observation period an adult female closely inspected the corpse and cleaned the teeth with a grass stem, which she occasionally also put in her own mouth.

(b) Conspecifics: cannibalism

Not only are some chimpanzees killed by conspecifics, they also get cannibalized: the killers and sometimes bystanders eat parts of the dead body [11]. Most reports concern infants of 'stranger' females getting killed and eaten, but intra-group cases also occur [79]. The rate of post-infanticide cannibalism is higher in chimpanzees than other species of nonhuman primates [80]; a review of 40 cases revealed that 23% of chimpanzee infanticide victims were consumed wholly, and another 37.5% partially [81].

More rarely, adults may also be cannibalized, as happened following the killing of a former dominant male at Fongoli (Senegal). Several of the victim's attackers and others abused the corpse, and several individuals ate parts of it; one adult female in particular tore pieces off the body with her teeth and ate them [71]. Following a lethal gang attack on a lone male from another group in the Taï forest, a participating adult female reportedly ate the victim's severed genitals [39].

(c) Non-conspecifics

Chimpanzees occasionally eat parts of dead animals that they have not themselves killed, but scavenging is generally uncommon. The predominant response towards discovered non-conspecific corpses is short-lived curiosity [74,82–85]. However, Gombe chimpanzees reacted with fear-related 'wraaah' calls when they encountered a recently killed adult bushpig; several individuals sniffed the surrounding ground and vegetation, in what van Lawick-Goodall [74] suggested might be an attempt to get olfactory information about the cause of death (the bushpig was killed by humans).

4. Responses to danger and death-related contexts

The above overview sets the scene for examining how chimpanzees behave when confronted with cues that are related to death and dying. Such cues include dead individuals (discussed above), sick individuals and potentially dangerous situations such as being high up in a tree, near a territorial boundary or in proximity to humans or predators. Consideration of these aspects paves the way for discussion of what chimpanzees might understand and feel about death.

(a) Diseased conspecifics

An individual stricken with a potentially fatal contagious disease presents a risk to its companions. Do chimpanzees show evidence of awareness of this? Little is known about responses to visibly ailing or dying conspecifics in the wild [86]; overall reactions have been described as 'ambivalent' [16]. Reported responses include adults attacking newly partially paralysed victims of polio [74], slowing down to allow an old, sick female to keep up [87], tending and sharing food with a sick, injured old relative [11] and mothers giving extra support to sick infants that cannot cling normally, or resettling them if they shows signs of discomfort [11,74,88]. Non-relatives showed no negative reactions to a disabled infant [88]. Empathic responses towards sick and dying companions have also been described in captivity [89–91].

Injured chimpanzees, for example those bearing wounds resulting from intra-group fighting, may receive 'comforting' attention and grooming from companions [40]. At Gombe kin or close friends in particular tended others' wounds [11], whereas at Taï wounded chimpanzees—including those injured by leopards—also received care from non-relatives [33]. With the exception of the reported attacks on polio victims at Gombe, chimpanzees in the wild do not appear to discriminate against or shun sick or injured companions.

(b) Humans

Unhabituated wild chimpanzees usually flee when they first encounter researchers [92,93]. Habituation may take months or years, but groups with less negative exposure to humans may show less avoidance, and some may appear relaxed or even intimidate human intruders [94–96]. Chimpanzees high up in trees, males, and those in large parties are less skittish than those on the ground, females, or those in small parties [95,97]. Occasionally, chimpanzees living near humans have attacked them, usually in response to provocation or harassment [98]. Previous experience and current context likely combine to determine responses to humans, eliciting a range of anti-predator-like behaviours in at least some populations [99].

Responses on discovering snares indicate recognition of potential danger. At Bossou (Guinea), when chimpanzees discover snares they try to destroy or deactivate them, sometimes successfully. The rarity of snare injuries at Bossou may reflect not only recognition of the danger, but also possible inter-generational transmission of how to deal with snares [100,101]. Snared individuals sometimes receive help from others to get free [33,102]. Clearly, experienced chimpanzees know that snares are dangerous, and they empathize with snare-injured victims.

Humans drive vehicles, and these can kill chimpanzees. At Bossou, chimpanzee parties crossing a wide road that bisected their home range were usually large and contained the alpha male [103]. The chimpanzees visually scanned the road before starting to cross cautiously; parties with no adult male ran quickly to the other side. If an adult male was present he was usually first to scan and then lead the party onto the road, where he often stood 'guard' while the others crossed [104,105]. Chimpanzees crossing a road at Sebitoli in Kibale National Park also scanned in both directions; healthy adult males usually led the progressions and frequently guarded or checked on other individuals, especially trailing, 'vulnerable' members of the party [106]. Compared with Bossou, Sebitoli chimpanzees crossed in smaller subgroups, possibly an adaptive response to heavier traffic at this site. Despite their caution and vigilance, however, chimpanzees did not avoid crossing the road at points where visibility was restricted (e.g. at sharp bends). It seems reasonable to suggest that in the case of death following serious injuries as a result of getting caught in a trap or hit by a vehicle, survivors might make the association between physical injury and death.

(c) Nonhuman predators and other species

Mount Assirik chimpanzees responded with interest and vocalizations to visual or auditory signs of lions and leopards; they responded less intensely to hyenas and wild dogs [44]. More generally, responses to large cats vary from fear and alarm to overt aggression—at least towards leopards [43,107,108]. Taï chimpanzees chased leopards away on several occasions [33], and a radio-tracked leopard avoided noisy groups of chimpanzees [109]. At Mahale a party of chimpanzees pulled a leopard cub from a hole and killed it [110]. Wild-caught chimpanzees in Gabon were averse to leopard urine, but this response was lost in chimpanzees with high *Toxoplasma* loads [20]. Free-ranging West African chimpanzees vocalized loudly, and showed fear, 'reassurance frenzies' and aggression to stuffed leopard models, and used tools to attack them [111,112]. Survivors of non-fatal leopard attacks at Taï receive care from other members of the community, who lick and groom their wounds [33]. Together, these observations indicate chimpanzees' awareness of the threat posed by big cats, and of suffering in victims of predatory attacks.

Rare encounters with pythons elicited a combination of curiosity and fear in Gombe and Mahale chimpanzees [74,113]; snakes at Bossou elicited similar responses, and none was voluntarily touched [114]. Taï chimpanzees give distinct vocalizations when they see a python or a viper, and in field experiments individuals aware of the presence of a (model) viper called to inform ignorant companions approaching the snake [115,116]. Again, these behaviours suggest awareness that snakes can be dangerous, and also concern for others' safety. Yerkes [117] noted that young captive-born chimpanzees showed little fear of snakes compared with adults; normal, mature attitudes towards snakes are probably more heavily influenced by social learning than direct aversive experiences. Finally, there are no accounts of wild chimpanzees' reactions to live crocodiles, but a young wild-born captive showed no fear of water unless it contained crocodiles, for which he had no 'particular friendship' [118, p. 37].

(d) Other dangers

All or most chimpanzees likely experience painful falls, and see other others falling from trees. They clearly try to avoid falling, but it is not clear when they start to do so. Unlike monkeys [119] infant chimpanzees have never been tested on the 'visual cliff' apparatus used by psychologists to test various species' depth perception and fear of falling [120]. However, infants making exploratory excursions from their mother sometimes fret about not being able to regain contact with her [121]. Mothers clearly guard against their infant falling: when moving in the canopy they carefully support the offspring with one hand or foot, or in the groin pocket by flexing one thigh [11]. They wait to help if older offspring struggle to cross a gap between branches, and quickly grab the youngster if it looks like falling; allomothers do likewise [40]. To avoid falling, chimpanzees must be constantly vigilant while moving around in trees; careful planning of arboreal routes might have been a selection factor in the evolution of self-awareness in large-bodied ancestral apes [122].

Chimpanzees are not good swimmers, and most avoid entering deep water [123], possibly for fear of drowning. The fact that many rivers and waterholes attract crocodile may add to wild chimpanzees' wariness of water, but at least one group regularly cools down in hot weather by soaking in a waterhole once [124]. The sign-language-trained chimpanzee Washoe once rushed to the rescue of another chimpanzee who was drowning in a moat. Washoe held on to a support, grabbed the other's arm and pulled her out of the water [60]. Again, this act suggests an understanding of the danger the other was in.

(e) Conspecifics

Like many other animals, chimpanzees show clear awareness that they can be hurt or injured, if not killed, by conspecifics. They employ a range of appeasement and reconciliatory behavioural mechanisms to control the amount of within-group aggression, including simple avoidance of potentially dangerous others, various gestural and tactile signals [74,125], and impartial interventions by third parties (policing) [126]. Participants in territorial boundary patrols are clearly tense, and they try to remain silent and inconspicuous [11,39,127]. This may indicate increased readiness for aggressive action against enemies while also reflecting fear of being detected and attacked.

5. Understanding death

Based on the above review of illness, injury and death in chimpanzees and how they respond to events and cues relating to these events, this section deals with the issue of the psychological significance of death for chimpanzees: how do they perceive it, and what is their understanding of it? The discussion is framed in terms of four elements or 'components' that typify adult humans' concept of death [128,129]: irreversibility (death is final; it cannot be undone), universality (all living things will die), non-functionality (dead individuals do not think, perceive or act) and causality (death results from non-survivable organ failure or damage). In addition to the literature already reviewed, it is important to keep in mind chimpanzees' known abilities in a range of relevant physical and social cognitive domains, including inferential reasoning, object permanence, self-awareness, metacognition, social learning, empathy, perspective-taking, mental attribution, cooperation and turn-taking [130–135].

(a) Irreversibility and non-functionality

By the age of 5 or 6 years most children view death as irreversible. Do chimpanzees share this view? Given the material already discussed it seems reasonable to suggest that sufficiently mature and experienced chimpanzees know that a dead individual will not come back to life. 'Sufficiently mature and experienced' here refers to adolescent or adult chimpanzees with direct experience of corpses and knowledge of how others respond to corpses. Unlike individuals who are asleep, regardless of what gets done to them dead individuals neither act nor react. This inert state often—although not always—occurs after one of the events leading to death reviewed above.

Here it is also worth considering that wild chimpanzees kill a variety of small-to-medium size animals including insects, reptiles, birds and mammals including other primates [74,82,83,136,137]; some are eaten opportunistically, others are deliberately hunted. Captive chimpanzees also capture and kill various animals (e.g., rabbits, squirrels, rats, birds, reptiles), which they often dismember and/or consume [138–140], although death sometimes appears to be an inadvertent consequence of rough, playful handling. In fact, all contact interactions between Bossou chimpanzees and other nonhuman mammals resulted in the death of the latter, which were often at least partially eaten ([114], but see [141]). All of these experiences seem likely to help chimpanzees construct the knowledge that death, once inflicted, is permanent, and that the dead individual is non-functional.

As mentioned in the Introduction, some chimpanzees simply disappear from their community without trace. Do chimpanzees, like researchers, infer that long-term absentees are dead? How to answer this question is not obvious, but it has been shown that chimpanzees remember long departed others for many years [142]. Future experiments might shed further light on chimpanzees' understanding of the permanence of death. In the meantime, however, a case can be made for reconsidering the widespread management practice of quickly and permanently removing seriously ill or dead individuals from their group, including freshly dead infants from their mothers. Might such interventions interfere with chimpanzees' evolved cognitive and emotional mechanisms for coping with death, including grief reactions [91,143]?

(b) Universality

Young children do not view death as universal; for them death happens to other individuals, not members of their own family or themselves. The universality component of the death concept is achieved by middle-to-late childhood. Unlike children, chimpanzees cannot be questioned directly, so whether they also understand that all creatures will die is not easy to determine. A useful distinction might be made between 'will' and '*can*.' As already discussed, adult chimpanzees in the wild may be well acquainted with death: family members and others die (or disappear); animals are killed for meat or other reasons, they get injured, and injured individuals sometimes die. It is conceivable that all of these experiences contribute to the formation of a category of 'animals that can die.' If such a cognitive category exists, how broad it is would be an interesting topic for research.

The notion of universality includes oneself, and integral to a mature human concept of death is the knowledge that *oneself* will die. Although chimpanzees have been credited with the capacity to know that they will die [144], there is no strong evidence for such knowledge, and in the absence of adequately language-competent chimpanzees it is hard to see how we could be sure. Again, it might be useful to distinguish between 'will' and 'can.' Conceivably, given their experiences of others' deaths, and their own self-awareness [130], chimpanzees may understand that they could be killed by a predator, by falling out of a tree, or if attacked by other chimpanzees. However, alternative explanations for self-preservation behaviours can be proposed that do not require explicit knowledge of the reason for fear of dangerous situations. Three such explanations invoke fear of pain or injury rather than death itself, socially learning to fear specific stimuli without explicitly knowing why they should be feared, and the activation of 'evolutionary fears' that have evolved for their survival value, again without knowing why [145–147].

One striking consequence of humans' understanding of their own mortality is the ability to intentionally kill oneself [148,149]. Unlike many humans, however, chimpanzees do not deliberately kill themselves; nobody has ever seen a chimpanzee intentionally jumping to its death, drowning itself or ingesting a lethally poisonous substance. In some humans, ruminative and self-evaluative processes can lead to suicide as the chosen way to escape from unbearable psychological distress [149,150]. Despite their self-recognition abilities, however, there is no strong evidence that chimpanzees share the cognitive-emotional self-evaluations or real versus ideal self mismatches [151] that typify human self-awareness.

(c) Causality

Biological explanations of death come late in childhood. What knowledge do chimpanzees have about what causes death? It seems beyond argument that they know that they can inflict death on other creatures. Before eating smaller animals—including infant chimpanzees—they typically kill them by biting them in or around the head. Captured young colobus monkeys at Taï were invariably killed this way, whereas adult prey usually died only after chimpanzees began eating them, starting with the viscera [136]; live prey may be torn apart by several individuals competing for meat [33,137]. At Gombe, bites to the head were almost the most common way of killing small prey; bigger animals such as adult monkeys and juvenile bushpigs were flailed against a hard substrate [11]. In some cases death occurred only after chimpanzees started eating captured prey. With smaller prey the head region might be bitten first for fast access to the highly nutritious brain [152]. The predominance of this killing method led Videan *et al*. [138] to comment on the deliberateness of the act. The ontogenetic emergence of the 'craniocervical killing bite' in various predatory species including primates [153] merits further study, as does the development of killing (or stunning) larger prey by flailing them against a hard substrate [11,137].

With regards to the causality component of the death concept it is noteworthy that descriptions of lethal attacks on adults often mention wounds around the throat and genitals of the victim (in males the testicles are sometimes severed), along with various other crush, slash and puncture wounds [39,66–68,71,154]. Death is usually attributed to shock and loss of blood. It is tempting to speculate that adult chimpanzees target the throat because damage there can cause profuse bleeding. In any case, the range and flexibility of ways that chimpanzees kill suggest some rudimentary knowledge about biological causes of death.

The causality issue also arises in the frequently cited case of Flint, an 8-year-old Gombe male whose demise has been described as an example of a chimpanzee losing the will to live [11], or fatally 'shutting down emotionally' [143]. Although physically healthy, Flint was unusually emotionally dependent on his mother. After her death he became increasingly lethargic and withdrawn; he refused to eat, and died three weeks later [155]. Was it suicide? Although Flint was clearly depressed, deliberately bringing about his own death in this manner would have required (a) the abstract causal knowledge that starvation causes death and (b) some reason for preferring this method to an alternative, such as jumping from a tree. As described earlier, non-avoidance of disease victims may reflect a lack of awareness about slowly acting causes of death such as contagious diseases. Before they attain a mature biological concept of death children tend to focus on observable external causes, such as guns or cars. Whereas chimpanzees appear likely to associate some specific external events with death (e.g. violent attacks, guns, predators, falls), there is no evidence for awareness of the link with less obvious causes, such as disease or starvation.

6. Questions for future research and conclusion

There is still much to discover about behavioural and psychological reactions to death in chimpanzees, including their understanding and feelings about death. One obvious question is whether they show any evidence of human-like taboos about killing. They clearly relish killing and eating other animals, and sometimes show no qualms about starting to eat their prey alive (many humans also have no moral issues about eating or cooking live animals), but do chimpanzees have a moral code against killing other chimpanzees? It can be assumed that most chimpanzees are not murderers, but killing sometimes appears to be acceptable, as in some territorial encounters and cases of infanticide. Similarly, although some individuals actively refrain from participating and may even try to protect the victim of lethal gang attacks [68,69], others do not hesitate to join in. Precisely how outbreaks of collective lethal violence come about in chimpanzees is unknown, or when conspecific killing is 'acceptable' and when it is not. The only pertinent experimental study to date asked whether intra-species infanticide might be perceived as a violation of a social norm: 'infants should not be harmed.' Captive chimpanzees watched video clips of unfamiliar chimpanzees (1) aggressively attacking and killing an infant, (2) hunting a small colobus monkey, (3) showing nonlethal aggression among adults and (4) nut-cracking [156]. Although chimpanzees looked longest at the infanticide scenes, there was no evidence of heightened emotional arousal during these presentations. The authors suggested that unfamiliarity of the chimpanzees in the clips might have dampened any emotional responses. Combined behavioural and physiological studies of responses to death-related stimuli could be useful for learning more about affective responses to death.

What about the morality of cannibalism? Are dead chimpanzees simply perceived as potential food, like captured bushpigs or monkeys? The answer appears to be no. First, most dead chimpanzees do not get cannibalized. Second, less of the corpse of cannibalized infants is consumed compared

Table 1. What chimpanzees might learn from experiences of death and death-related contexts, and possible contributions to their understanding of four cognitive components of a death concept.

		contribution to cognitive component of death concept?			
danger/death context	**potential learning**	**irreversibility**	**non-functionality**	**universality**	**biological causes**
disease	Sick individuals may weaken, die. No avoidance of diseased or dying others. Some empathic responses.	no	no	no	no
injuries	Injured or wounded may die. Injuries and wounds are painful. Injured and wounded may receive care.	no	no	yes	possible
humans	Humans sometimes injure, kill. Snares, traps, vehicles also injure, kill. Caution and evasive action often required.	yes	no	no	possible
predators	Predators and some other species (e.g. snakes) can injure or kill. Caution and evasive action often required. Aggression sometimes appropriate.	yes	no	possible	possible
accidents	Falls from trees can injure, kill. Deep water is dangerous. Caution, avoidance required. Help given to others (e.g. youngsters) in difficulty.	yes	no	possible	possible
conspecifics	Chimpanzees sometimes injure, kill, eat others. Avoid getting attacked. It is possible to kill.	yes	yes	yes	possible
non-predatory animals	Other animals die, get killed, eaten. It is possible to kill animals, using different methods.	yes	yes	yes	possible
corpses	Corpses do not act or react. Corpses never come back to life.	yes	yes	possible	no

with similar-sized monkey prey [81], suggesting a psychological difference between eating a conspecific and another species. Third, intra-community infants are eaten less completely than extra-community infants [81]. The psychology of cannibalism in chimpanzees requires further study.

In many humans, from late childhood a fifth element of the death concept takes on increasing importance, namely, the notion of some kind of afterlife, sometimes referred to as a metaphysical concept of death [157,158]. Chimpanzees have been prematurely described as engaging in 'ritual practices' in in the presence of dead conspecifics, contributing to evidence of an analogue to human religion [159]. However, although death in chimpanzees appears psychologically more impactful that death in other species, compelling evidence for any notion of a spiritual life after bodily death in chimpanzees is not forthcoming.

As reviewed above, chimpanzee responses to conspecific deaths are highly variable and include frenzied excitement, loud vocalizations, displaying, attacking and rough treatment of the body, consuming it, tending it carefully, sitting quietly and looking at it, making soft vocalizations before abandoning it and, especially in the case of deaths of unknown cause, partly covering it with vegetation [33]. Some individuals have been seen to return to where they last saw the body of a familiar conspecific [68,71]. Systematic comparisons of reactions across communities remain to be conducted. Like many other behaviours [123,160], responses to death might show cultural variations (see [72] for one suggested example).

In conclusion, chimpanzees, in common with many other animals, strive to stay alive by avoiding potential causes of death or minimizing risks. Their experiences with death in other chimpanzees and other species—including individuals they have killed themselves—may well contribute to construction of a human-like understanding that dead individuals no longer behave or feel anything (non-functionality), and that they will stay dead (irreversibility) (table 1). As in humans [157], direct experience of death in childhood possibly facilitates maturation of the death concept in chimpanzees. Chimpanzees—and probably other great apes—understand that death 'is different from life and permanent' [161, p. 196]. Taï chimpanzees groom and lick wounds of injured, but not dead kin and companions [33]. Whether chimpanzees understand that all creatures will die (universality) is less clear, but a reasonable suggestion is that they know that other creatures can die. This knowledge probably includes a notion of their own vulnerability, if not the inevitability of their own death. Although there is little evidence for a mature human-like understanding of the 'biology' of death (causality), they do have some knowledge about effective ways of killing, which they apply to conspecifics and other targets flexibly (see [162] for another example of flexibility in killing techniques). Comparative evolutionary thanatology needs more information on nonhuman species, not least to improve our understanding of the evolution of our own species' psychology of death [163–165]. Primatologists clearly have a role in this endeavour. In view of the precarious survival prospects of many great ape populations, we must hope that valuable information on how death is dealt with and represented in great ape communities can be discovered before their cultures die out.

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The Late Upper Palaeolithic and earliest Mesolithic evidence of burials in Europe

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Burials of the Late Palaeolithic (14 000–11 600 cal years before present, henceforth BP) are a rare phenomenon in Europe. Several sites possess burials of single and double individuals. As with the preceding Magdalenian, the burial of more than two individuals in the same grave cutting seems to be unusual, but does occur occasionally. The deposition of isolated and disarticulated human remains with or without cut marks seems additionally to belong to the Magdalenian context. In the final Palaeolithic phase (13 000–11 600 cal years BP) there is evidence for cemetery-like clusters of burials, which contrast to the Magdalenian evidence, instead showing some similarities with the succeeding Mesolithic. The earliest Mesolithic burials 11 600–10 500 cal BP) are a very rare phenomenon, covering a short time span between the beginning of the Preboreal and the beginning of the Boreal phase of the early Holocene. Here the evidence includes single inhumations, cemetery-like structures and a number of isolated human remains. Caves and rock shelters were the most common places for inhumations in both the final Palaeolithic and the early Mesolithic. Although the number of sites with a chronological continuity from the LUP to the Early Mesolithic burial is low, several aspects indicate a general continuity in burial patterns over this period. Apart from this continuity, the Mesolithic burials in general seem to represent a new level of diversity in burial practices.

This article is part of the theme issue 'Evolutionary thanatology: impacts of the dead on the living in humans and other animals'.

1. Introduction

The Late Upper Palaeolithic (LUP) begins with the late Magdalenian around 14 000 calibrated years before present (cal BP) and ends with Dryas III and the last glacial at the Pleistocene–Holocene boundary around 11 600 cal BP. Regardless of a transitional phase, the earliest Mesolithic starts with the beginning of the Preboreal and continues to the Boreal around 11 000 BP. There are a number of uncertain burials that probably belong to this period but which have not been directly dated by AMS radiocarbon, and hence which have been omitted from this review, which focuses on primary and secondary burials which are relatively well understood. Isolated human remains might additionally represent the very end of a complex ritual treatment of the deceased, and this 'loose human bone phenomenon' has recently been brought to the fore in a study of the Mesolithic of North Western Europe [1].

2. Late Palaeolithic burials

At the end of the Magdalenian around 14 000 cal BP, the number of burials in the sense of single inhumations varies dramatically region to region [2,3]. In Central Europe the number is extremely low, with Bonn-Oberkassel being the only secure example. In Western Europe, mainly in France, several single inhumations and a possible further multiple burial are attested for the post-Magdalenian Azilian technocomplex. In Spain only one—and possibly a second now lost—burial is attributable to the Azilian. On the Italian peninsula, however, the data on late

Palaeolithic burials belonging to the broadly contemporary Epigravettian or late Epigravettian is significantly richer than anywhere else.

Two sites in Central Europe are dated to the very end of the Magdalenian or already at the beginning of the Late Upper Palaeolithic and Federmesser Group. Two adults—a female and a male—seem to have been buried together in the same grave cutting or close to each other in Bonn-Oberkassel, Germany [4,5]. Direct dating of the skeletons indicates an age of 11 600–12 200 BP (13 500–14 200 cal BP) (table 1) for the burial of a male and female, suggesting a Late Magdalenian and/or Late Upper Palaeolithic cultural association ([36], pp. 83–84). Although details are lacking for early excavation, the remains of the two bodies were found together, each intensely stained with haematite (red ochre). The bones of the cranium and upper body of the female were particularly stained on their outer surfaces, indicating that the colorant was applied to clothing rather than to disarticulated bones. The partial skeleton of a dog, a bone pin, and a flat carving of a cervid seem to have been associated with the burial. According to the information available, it has to remain unclear whether Bonn-Oberkassel was a double burial or two single burials in close proximity to each other.

Fragmentary human remains from the open-air site of Neuwied-Irlich in the Rhineland represent an adult, two children and a neonate ([5,38], p. 568). Other details of this burial are unknown due to the circumstances of the find (in a secondary position during construction works). AMS radiocarbon dates range between 14 500 and 13 800 cal BP (table 1). The bones are ochre-stained, and the remains are accompanied by a burin spall, a backed blade, one perforated and decorated cervid tooth pendant, and an antler point [38]. According to preliminary investigation results, the adult individual might have suffered from vitamin C or D deficiency. Street *et al.* ([5], p. 568) noted how both the Neuwied-Irlich and the Bonn-Oberkassel burials seem to have been isolated—deposited away from occupation sites—which may suggest a regional tradition of separation of the dead from the world of the living, or at least a distinction between burial and domestic space. The evidence of red ochre on the bones and the discovery of objects, although in a secondary position, probably indicate a burial. It is, however, impossible to decide between a multiple or several single burials.

The Italian Peninsula has rich sets of Upper Palaeolithic burials belonging to Mid Upper Palaeolithic (Gravettian, approx. 31 000–22 000 cal BP) and Late Upper Palaeolithic (Epigravettian, less than 19 000 cal BP) context [7]. The Epigravettian examples, where they are dated by AMS measurements, seem to date to no older than 15 000 cal BP, i.e. form a relatively late Pleistocene phenomenon [9]. The sample can, however, be divided chronologically into two groups; an early (and smaller) one between 15 000 and to 14 000 cal BP and hence contemporary with the Magdalenian north of the Alps, and a later (and larger) group between 13 000 and 12 000 cal BP of post-Magdalenian age [12]. Lack of precise AMS dates measured directly on the human remains leads to several cases of uncertainty, however. Six examples constitute the earlier period; Riparo Tagliente, Riparo di Villabruna, Grotta Maritza, San Teodoro, Grotta Addaura Caprara and probably Grotta Vado All'Arancio. The burials from both chronological groups are found all over Italy with a certain trend towards a regionalization in grave goods ([9], p. 349).

In the Riparo Tagliente (Venetie), an adult male was buried in an extended position in a vast rock shelter. The burial had been partially destroyed by digging during historic times and only the lower part of the skeleton was preserved. The grave was covered by stone blocks, one bearing linear incisions and the other the outline of a lion's head and an aurochs' horn. The bones were stained with ochre, and a fragment of bison horn and a pierced shell were recovered from the grave. There are no direct dates from the burials available, but the Epigravettian occupation level that the grave is associated with dates to between 15 070 ± 70 cal BP (OxA-3531) and 15 270 ± 170 cal BP (OxA-3532) ([9,10,12,39,40], 28).

A single burial of an adult male around 25 years old was placed in an extended position on his back in a grave in the Riparo di Villabruna. Subsequent road works had destroyed the lower extremities. The grave pit was filled with stones, of which five were decorated with geometric motifs drawn with red ochre. Several objects—a bone point, a backed knife, a flint blade, a flint core, a retoucher and a ball of resin and wax—were found close to the left forearm. The burial is associated with a Final Epigravettian occupation of the site. A direct AMS ^{14}C measurement from the burial indicates an age of 14 171 ± 243 cal BP (KIA-27004) ([9,11,40], 28–29). This dating places the burial at the very end of the first Italian chronological group.

Another burial of an adult male (A) and a nearby child (B) was found in the Grotta Vado All'Arancio (Tuscany). Burial A was placed extended on his back on a surface of red ochre within an oval grave pit, the fill of which was covered by large stone blocks. Several objects were found in the grave: a fragment of roebuck jawbone, a horse molar, an aurochs premolar, three smooth pebbles, about 10 pierced shells, two flint scrapers and a flint flake. Burial B has no evidence for a grave pit, and is represents the fragmentary remains of a child of approximately 18 months age apparently placed in a supine position. Objects found close to the skeleton, such as perforated shells and stone artefacts, may represent grave goods but it is impossible to establish this with confidence ([40], 29). No direct dates are available, but the burial presumably belongs to the late Epigravettian phase around 15 400 cal BP [12].

In the Grotta Maritza (Abruzzo), the skeletal remains of an infant of about 7–8 years (Maritza 1) were found close to the cave's wall, next to which was found the partially disturbed and partially articulated remains of an adult (Maritza 2). Maritza 2 was subsequently disturbed by carnivores, as several bones were found dispersed about the area, with the skull missing ([12,40], 29). However, the excavations did not produce clear evidence for a burial pit, nor for grave goods or the use of red ochre ([40], 29). However, it is noted that some flint artefacts and perforated shells were associated with Maritza 2 [9]. The preservation and the partially articulated remains of both individuals may indicate that it was a purposeful burial. The Maritza 1 remains derived from levels later than 14 000 cal BP ([40], 29), but direct AMS radiocarbon dates are not available. The direct dating of both individuals would be desirable to verify their association with the late or final Epigravettian.

The remains of four male adults and an individual of undetermined age and sex, in addition to two isolated crania, were apparently buried in the San Teodoro cave on northeastern Sicily, probably between 14 000 and 13 000 cal BP ([40], 35;

Table 1. The Late Upper Palaeolithic burials.

site	^{14}C-dating	individuals	grave features	objects	references
Arene Candide, cave, Italy	VIb: 10 585 ± 55 BP (OxA-11000) VIII: 10 655 ± 55 BP(OxA-11001) XII: 10 720 ± 55 BP (OxA-11002) XIV: 10 735 ± 55 BP (OxA-11003) X: 11 605 ± 445 BP (GX-16960-A) XII: 11 510 ± 385 BP (GX-16964-K) direct dates, Epigravettian	20 (infants, adults both sexes)	grave pits, single and double burials, secondary burials, disturbed burials	red ochre, perforated red deer canines and shells. 2 pairs of elk antlers	[6–8]
Grotta Romanelli	level A: 10 320 ± 130 BP (GrN-2305) 9880 ± 100 BP (GrN-2056) 11,800 ± 600 BP (R-58) 9050 ± 100 BP (R-54) level B: 11 930 ± 520 BP (R-56) level C: 9790 ± 80 BP (GrN-2154) 10 390 ± 80 BP (GrN-2153) level D: 10 640 ± l00 BP (GrN-2055) final Epigravettian	1 adult male 2 children			[7,9]
Grotta Polesini	10 900 ± 80 BP (R-1265) Epipalaeolithic	14 (MNI)—10 adults, 4 children		red ochre on bones, perforated red deer canines, shells	[9]
Riparo di Villabruna	10 040 ± 120 BP (R-2022) layer; 12 140 ± 70 BP (KIA-27004)—direct date, final Epigravettian	Adult, male∼25 years	stone block covering, decorated w. red painted geometric motifs grave pit		[9–11]
Grotta Maritza	13 000–10 000 BP final Epigravettian	1: adult male, partially preserved and articulated 2: 7–8-year-old child—partial skeleton	close to the cave wall	flint tools, perforated shells	[7,9,12]
Riparo di Tagliente	13 070 ± 70 BP (OxA-3531) 13 270 ± 70 BP (OxA-3532) direct dates, final Epigravettain	1: adult male 2: child	covered by stone blocks with red ochre, one with engravings (lion)		[9,10,12,13]

(*Continued.*)

Table 1. (*Continued.*)

site	^{14}C-dating	individuals	grave features	objects	references
Riparo di Romito	10 250 ± 450 BP (R-298) 11 150 ± 150 BP (R-300) 4: 11 340 ± 90 (LTL3032A) 5: 10 862 ± 70 (LTL3033A) 9: 13 915 ± 70 (LTL3034A) Epigravettian	9 (MNI) in 7 graves (5 single, 2 double burials)	grave pits, stone block with engraving		[9,13–16]
Grotta Vado all'Arancio	~ 13 400 BP Epigravettian	adult male with 1–2-year-old child in extended position	grave pit	flint tools and perforated shells	[7,12,17]
Grotta dei Fanciulli	level C: 11 130 ± 100 BP (GifA-94197) direct date, Epigravettian level B: younger than 11 000 BP Epigravettian	two infants, 2 and 3 ± 1-year-olds, extended position adult female, poorly preserved	grave pit grave pit	several hundred perforated shells on the waist and pelvis area perforated shells in level, association unclear	[9,12]
Grotta di San Teodoro	12 200 ± 400 BP (charcoal from overlying heath) Epigravettian 12 580 ± 130 BP (ETH-34451) direct date, San Teodoro 1	5 (MNI), 4 male and one female (?)		use of red ochre, antler small cobbles	[7,13,18–20]
Grotta Addaura Caprara	12 890 ± 60 BP (KIA-36055) direct date, Addaura 1	1 adult female			[20]
La Madeleine	10 190 ± 100 BP (GifA-95457) direct date, Azilian	2–4-year-old infant	grave pit, stones around the head	use of red ochre, perforated shell pendants, 2 perforated deer canines, 2 fox canines	[21,22]
Roc de Cave	11 210 ± 140 BP (GifA-95048) direct date, late Magdalenian or Azilian	juvenile incomplete skeleton		perforated deer teeth necklace	[21,23]
Rochereil	Azilian (1 + 2?) and probably late Magdalenian (3)	1: male, 40–50 years 2 unknown, fragmented/ cremated? 3 child skull		red ochre	[24–26]
Le Peyrat (Saint Rabier)	11 430 ± 140 BP (GifA-99117) Azilian level	5: adult male		red ochre on the bones	[27,28]

(*Continued.*)

Table 1. (*Continued.*)

site	^{14}C-dating	individuals	grave features	objects	references
Los Azules	9540 ± 120 BP (CSIC-260) layer above 9430 ± 120 BP (CSIC-216) – layer below Azilian	male, 40–50 years	grave pit	red ochre, painted cobbles, atypical animal remains, shells, harpoons, endscrapers, burins and debitage (tool kit)	[29–31]
La Paloma (lost)	Azilian	young child	grave pit		[31]
Aven des Iboussières	10 210 ± 80 BP (OxA-5628) Fauna from layer 4C) Azilian	4 adults 5 children (MNI) fragmentary remains (426 fragments)		red ochre on bones (layer 4C), red ochre, flint artefacts, faunal remains within layer, engraved animal bones, fish vertebrae, shells, perforated animal teeth (197 red deer canines), perforated stones and bones within find horizon	[32–35]
Bonn-Oberkassel	11 570 ± 100 BP (male) (OxA-4790) 12 180 ± 100 BP (female) (OxA-4792) direct dates, Late Palaeolithic	adult male and female		red ochre, domestic dog bone or antler animal figurine, bone pin	[4,5,36,37]
Neuwied-Irlich	12 310 ± 120 (OxA-9736) 11 910 ± 70 (OxA-9847) 11 965 ± 65 (OxA-9848) 12 110 ± 90 (UtC-9221) direct dates, Late Palaeolithic	4 (MNI) adult female (?), 2 infants, 1 neonate		red ochre, perforated red deer incisor with carvings on the root, 2 flint tools, 1 antler point	[5,38]

[13]). Although the burials are rather insecurely dated, an overlying hearth was dated by AMS to 12 200 ± 400 BP ([2], Tab. 7.1), which would indicate a late Epigravettian age. The exact chronological position of the burials remains unclear, however; only San Teodoro 1 is dated directly. The age of 12.580 ± 130 BP (approx. 14 500 cal BP) places it in the older group of Late Upper Palaeolithic Italian burials ([19], 538, [20]). If the dates of the other burials at the site are consistent with this dating of San Teodoro 1, this would indicate that burial groups were already present on the peninsula before 14 000 cal BP. Little information is available for these burials, however, since they were disturbed by unauthorized individuals before excavation was carried out under difficult circumstances. Burials 1 and 4 were the most complete, and while San Teodoro 2 and 4 were placed in an extended position, burial 1 seems to have been placed on its left side. Burial 5, which may have been inhumed a little later than the rest, may have been a secondary burial, i.e. having been collected from another location before being buried here. Burials 1–4 were grouped below an approximately 5-cm thick layer of red ochre, although it remains an open question as to whether it was used as a deliberate covering ([40], 35; [41], 550). San Teodoro 4, the probable adult female, was buried with a cervid antler and with several stone cobbles. A flint flake, probably the distal part of a geometric microlith, was embedded in its pelvis [18]. San Teodoro 1, an adult male, seems to have been equipped with a set of 12 red deer canines, although the context is not indisputable ([40], 35; [41], 550).

An amateur discovered the remains of Addaura 1 in 1916, and any documentation relating to this is missing. The remains consist of several postcranial elements (scapula, ulna, ilium and fibula) and seem to belong to an adult female ([20], 3096). This attribution is supported by the similar state of preservation of the bones and by the same colour of deposit encrusting them, which suggests that they might derive from a burial. A radiocarbon date of 12 890 ± 60 BP, 15 472 ± 300 cal BP (KIA-36055) places this individual in the older LUP group ([20], 3096).

The second group of Italian Epigravettian burials dates between the final Epigravettian and the beginning of the Sauveterrian or early Mesolithic (Preboreal and Boreal) industries. The sites representing this group are: Grotta Romanelli, Grotta Polesini, Riparo di Romito, Grotta dei Fanciulli and Arene Candide. No direct dating is available for the sites of Grotta Romanelli and Grotta Polesini, so their stratigraphic position remains unclear although they were found within a final Epipalaeolithic sequence. In the case of Grotta Romanelli several radiocarbon measurements were produced by different laboratories, with somewhat contrasting results, even if a quick rate of sedimentation of Levels A–D is accepted ([9], 296). Any details on the burials themselves, excavated at the beginning of the twentieth century, are lacking. The Grotta Polesini remains are also undated, but a single radiocarbon date of 10 090 ± 80 BP (R-1265) from the middle of the sequence (level 7) provides a direct indication of the final Pleistocene age of the bones. The remains of a minimum of 14 individuals (4 children, 10 adults) seem to have been found dislocated, and isolated from the main anatomical context. However, the bones show red ochre staining, which might indicate a funerary ritual. Additionally, some of 260 fish vertebrae also showed traces of red ochre and were possibly associated with the human remains, as were 80 perforated deer canines and more than 200 perforated shells ([9], 292–293).

Nine skeletons were discovered at the Grotta or Riparo del Romito (Rom 1–9). The skeletons are generally well preserved and belonged to young adults between 20 and 30 years (Romito 1, 3, 5, 7, 9) and adolescent or nearly adult individuals (Romito 2, 4, 6, 8). Determination of sex revealed three females (Romito 1, 4 and 5), one probable female (Romito 2) and five males (Romito 3, 6, 7,8) [16,42]. Romito 2 was affected by a serious genetic disease which caused a form of acromesomelic dwarfism [15]. Unfortunately direct dates are only available for two burials so far; one of 11 340 ± 90 (LTL-3032A) for the single inhumation Romito 4 from inside the cave and another of 10 862 ± 70 (LTL-3033A) for the double burial. Indirectly, measurements of 10 250 ± 450 BP (R-298) and 11 150 ± 150 BP (R-300) from charcoal associated with Romito 5 (and 6) from the rock shelter confirm the direct dates [16,42]. At least one new burial (Romito 9) seems to be older than 14 000 cal BP [42], but further information on the burials is sparse.

One of the best known Late Palaeolithic burials is probably that of the double burial of two infants from the Grotte des Enfants (Grotta dei Fanciulli) discovered in 1874/1875. In fact two burials are known from the site, with a less well-known adult female found in level B, stratigraphically slightly higher than the double burial of the children at a depth of 1.90 m from the surface ([26], 63–64). The burial is not dated but may belong to the final Epigravettian or Azilian. A few objects might be associated with the burial, notably two perforated shells, several unperforated shells, faunal remains and a flint scatter. The two children, aged between 2 and 3 years, were found lying side by side in level C at a depth of 2.79 m from the surface ([26], 63). Several hundred perforated shells were found in the area of their waist and pelvic girdle, probably arranged in parallel rows. It seems convincing that the shells were sewn on the clothing; the children were wearing as they were buried. Apart from these ornaments some faunal remains were found in association with the burials, but no use of red ochre was recorded. Surprisingly, a triangular flint projectile was found embedded in a thoracic vertebra of the older infant; presumably the cause of the individual's death. Apart from the deadly injury probably caused by an arrow shot, both children had suffered from periostitis, and the younger individual showed bone deformation most probably caused by vitamin D deficiency [17].

These examples of single and double primary burials of adults and children clearly indicate a Late Pleistocene/Late Epigravettian burial tradition across Italy. Simple inhumation with the body lying extended on its back and with little or no grave goods, except basic equipment such as flint tools and personal ornamentation such as perforated shells, is dominant. In most cases, adults and children were buried in the same way, sometimes even together in the same grave. However, due to the lack of documentation of the early excavations this is not confirmed in every case. By contrast, isolated human remains do not seem to be frequent phenomena in the Italian Epigravettian. More direct AMS radiocarbon dates of the Italian Epigravettian burials would be highly desirable.

By contrast, the evidence for late Palaeolithic burials on the Iberian Peninsula is extremely rare. The single inhumation of Los Azules in Asturias and the lost grave of a child from La Paloma are the only apparent examples [43]. The burial of Los Azules was discovered in 1975 within the entrance area of the cave and with some degree of damage in the area of the skull. There are no direct dates available, but the stratigraphic evidence places the burial in the first half of the ninth millennium cal BC. There is evidence for a grave pit, and the body was associated with several objects that have been interpreted as grave goods. There were some Azilian painted cobbles, red ochre, the skull of a badger (*Meles meles*), a fragment of a deer antler, an accumulation of unperforated shells with remains of ochre inside, and several harpoons, endscrapers and burins, as well as some production waste. This inventory of different objects has led to the idea that the deceased was equipped with a tool kit, raw material and symbolic items [30,43].

Late Upper Palaeolithic burials in France are represented only by a couple of single burials. One of them is the famous burial of a 2–4-year-old child found in a grave pit during excavations in the large rock shelter of La Madeleine in 1926. The burial was found within a Magdalenian level (Magdalenian IV) and attributed to this period. A direct date on the human remains, however, revealed an age of 10 190 ± 100 BP (GifA-95457), according to which the burial belongs to the subsequent Azilian and was presumably intrusive (dug down) into the underlying Magdalenian occupation level. The very rich body ornamentation of at least 1275 perforated shells, as well as 2 perforated deer canines and 2 fox canines, is reminiscent of some of the richly equipped burials of the broadly contemporary Italian Epigravettian [22]. The small size of the objects indicates that they were collected and selected for the child on purpose, i.e. to distinguish it from adults, again in accord with the Italian Epigravettian burials. The La Madeleine child could be interpreted as a high status individual who received a complex burial ritual, additionally indicated by the use of red ochre and its large grave pit.

A Late Magdalenian (Magdalenian VI) cranium and mandible of a 2–4 year old with supposed evidence of post-mortem trepanation on a hydrocephalus was found in the Rochereil cave, Dordogne [44]. However, the supposed trepanation of the child (Rochereil III) was later identified as a pathological lesion (lacuna) of unknown aetiology and the hydrocephalic nature of the skull was not confirmed [45]. The placement of a child's head within the Magdalenian levels, however, presumably reflects a deliberate treatment/deposition of the human remains, as the postcranial bones were absent. An AMS date of 13 159 ± 93 cal BP (OxA-16932) places the skull chronologically in the Late Palaeolithic/Azilian. Two further burials have been found in an Azilian context. Rochereil I, an older male, was found in a 'hyper flexed' position lying on its right side and lacking any obvious grave goods. Only red ochre was visible in the area of the head. The second burial has been described as a cremation but further details are unfortunately not available ([26], 121). The dating of Rochereil II is insecure, as no cremation for the European Late Palaeolithic is otherwise known; it is probably of Mesolithic age. Rochereil I, although similarly undated could belong to the Azilian.

In 1928, the partially incomplete skeleton of a juvenile, a 13–15-year-old probable female, was excavationed in Roc de Cave (Saint-Cirq-Madelon, Lot). Given the lack of information on the excavation, little is known about the position of the body or the existence of a grave pit. Several perforated deer teeth may belong to a necklace worn by the deceased. A direct AMS date of 13 107 ± 166 cal BP (GifA-95048) once again indicates a final Magdalenian or earliest Azilian age, or perhaps a transitional period between the two [23]. The burial from Le Peyrat (Saint Rabier) is dated to the same period. The remains of an adult male (Peyrat 5), which were found close to a partially preserved adult female (Peyrat 6) and within Azilian levels, has been dated to 13 330 ± 180 cal BP (GifA-99117). The female individual was, however, dated to the Middle Ages and is, therefore, intrusive ([27], 35–36). No grave goods were reported, but the human remains seem to have been covered with red ochre ([26], 122).

At the site of Aven des Iboussières (Drôme), a karstic sinkhole in the Rhône valley, approximately 426 human remains were recovered during rescue excavations in 1994 in the cave's 'salle supérieure'. Further excavations were cancelled due to the partial collapse of the roof. The remains of four adults and four juveniles and a new-born (MNI = 9) were found in layers 4B and 4C. These were mostly fragmented and mixed with archaeological material. Anatomical connections were not recorded. Some of the human remains from layer 4C and the sediment itself were stained with red ochre. The human remains were found mixed with faunal remains deriving from the occupation of the cave. A large number of personal ornaments were also recorded, as well as a few flint tools [32]. The assemblage of personal ornaments contains engraved and perforated pebbles of small size, naturally perforated fish vertebrae, perforated and ornamented animal long bones and some other mostly fragmentary animal bones bearing decorations, decorated animal mandibles, more greater than 1000 perforated shells, alongside approximately 200 incised and perforated red deer canines. The human remains may be attributable to the Azilian, although confirmation of this in the form of direct dates on the human remains is still lacking. An isolated date from faunal remains from layer 4C revealed a terminal Palaeolithic date of 10 210 ± 80 BP, 11 911 ± 200 cal BP (OxA-5628) ([32]; [33]). The material could date to a transitional period between the end of Dryas III and the beginning of the Preboreal. Other than a palaeopathological thesis and a general description of the human remains [34,35], a taphonomic analysis is still lacking. The find situation could indicate that the human remains of Aven des Iboussières represent a multiple and/or secondary deposition. However, the existence of primary burials which were subsequently disturbed by taphonomic factors cannot be excluded. The funerary character of the material seems to be indicated by the use of red ochre and the various personal ornaments within the find layer.

With regard to the objects associated with the burials—mostly personal ornaments—the grave from La Madeleine and the remains from Aven des Iboussières are comparable to those of Arene Candide and Grotta dei Fanciulli from Italy. The mode of deposition of Aven des Iboussières could also be comparable to the remains of Grotta Polesini. Although both sites lack a precise date for the human remains, there are similarities concerning the fact that the human remains were found without anatomical connection were stained with red ochre. Additionally, the occurrence of a number of personal ornaments, such as perforated red deer canines, fish vertebrae and shells, in both sites might indicate a similar funerary behaviour at the very end of the Pleistocene or the transition to the Holocene.

3. Early Mesolithic (Preboreal and early Boreal) burials

The Preboreal/early Mesolithic evidence for burials is exceptionally sparse across Europe. However, several sites between

10 300 and 9300 BP (12 000–10 200 cal BP) contain a number of individual burials ranging from single inhumations to 'collective burials' of isolated and mostly fragmented human remains. Probably due to the narrow time span of the Preboreal—between the end of the Final Pleistocene and the beginning of the Boreal phase—the number of sites containing human remains is exceptionally limited. This need not indicate a low population density, however. The oldest dates for the Preboreal are from the Arene Candide cave in Ligura, Italy. The calibrated values of two individuals (III and Vb) are just on the border between the Final Pleistocene and the earliest Holocene, falling between 11 700/11 600 and11 500/11 400 cal BP. Burial III seems to be slightly older than burial V, which is a double burial of an adult and a child. Burial III is an accumulation of bones, which is interpreted as a secondary burial rather than a disturbed single inhumation [13]. The intact double burial V, which contains an adult male and a child of 4–5 years of age on its left side, is one of the earliest examples of human burial in the Holocene/Preboreal (table 2). This double inhumation disturbed the double inhumation of another adult and child, burial VI, leaving only their lower limbs in place. Burial VI was organized in the same way, however, with the bodies extended on their backs with the child on the left side of the adult. The fact that this double inhumation dates to the very end of the Pleistocene, 10 585 ± 55 BP, 12 549 ± 131 cal BP (OxA-11000) (based on a date on the remains of child VB) shows a continuity of funerary patterns between the final Pleistocene and early Holocene. This scenario is supported by the older date of double burial VI [8]. No grave goods or personal ornaments were recorded on the possible secondary burial III, but a considerable number of objects have been found in close context with double burial V ([62], 277–279). However, there is uncertainty, not only in the case of this double burial, about whether the personal ornaments were worn by the deceased person or were deposited as grave goods, i.e. as 'offerings' for the dead ([62], 278–279). In fact, double burial IV is among the richest in the 'necropolis' of Arene Candide, indicating the continuity of this burial tradition from the Late Palaeolithic to the early Mesolithic. In addition to fragments and powder of red ochre, several pebbles, some bearing traces of red ochre, and a flint scraper have been found close to the right hand. A similar set of objects was found in the pelvic area alongside two beaver mandibles and a bone point in other areas of the body. Personal ornaments were found both in close contact with and further away from the body. Several perforated red deer canines were lying below the skull and the right shoulder, one shell together with the pebbles in the pelvic area. Several perforated red deer canines along with a perforated shell close to the right hand, where other objects noted above had been discovered. The objects associated with the child were similar. Various small pebbles, some with traces of red ochre, in addition two small pieces of red ochre were found close to the body of the child. Several shells lay close to the skull and the ribs. On the child's thorax, some 80 squirrel vertebrae were deposited together with another shell. In close contact with the right hand, 26 shells, and in the area of the feet, two perforated shells, were discovered. Finally, together with the pieces of red ochre, 22 shells were found on the left side of the body. This set of body ornaments is not only among the richest in Arene Candide but links this double burial to the Epigravettian and Gravettian burials in Italy, and also to the La Madeleine burial in France.

According to the radiocarbon dates from the cemetery of VasilEvska III in the Ukraine a series of three burials seems to be older than originally supposed [59]. Although the necropolis had been divided into an older and a younger phases (both however attributed to the Late Mesolithic), the three burials from the older burial area have calibrated ages similar to those of Arene Candide burials V and III, i.e. between 11 700 and 11 500 cal BP) (table 2). These burials were all placed in a crouched position within oval grave pits. No grave goods or personal ornaments were reported, although sporadic traces of red ochre were found within grave 6 ([59], 281, 350–357). This clearly indicates that either the whole cemetery is earlier than previously thought or at least that the burials were accumulated over a considerable period of time. Further dates from VasilEvska III and other cemeteries from the area are, therefore, highly desirable.

A similar situation is found at Padina in Serbia. The dating of several burials revealed that the dates of the various inhumations on the site, sometimes close to housing structures and concentrated in three sections, were chronologically distinct. While several dates reveal a middle and Late Mesolithic attribution, at least six dates represent an earlier inhumation in the late Preboreal and early Boreal time range [60]. For these burials two phases are, therefore, evident. The first and oldest group (burials 11, 15 and 21), is dated between 12 100 and 11 500 cal BP (or between 11 700 and 10 900 cal BP when corrected for freshwater carbon reservoir effects on the dating). The second group (burials 12, 14 and 39_ falls between 11 300 and 11 200 cal BP (corrected around 10 500 cal BP). All burials are single inhumations and none was accompanied by grave goods. The mode of deposition is quite diverse, however; within the older group are two rare seated burials, while the remainder were buried in extended positions, with only burial 12 flexed.

Another example of Mesolithic cemeteries originally dated to the Boreal or even Atlantic phases, but which have now been shown to have older origins, is Olenij Ostrov in Karelia, Russia. Burial 100—a seated an adult male—dates to 9910 ± 80 BP (GIN-4836) (11 413 ± 145 cal BP), and was accompanied by a rich set of animal teeth, 126 lamellae of beaver teeth, 303 elk incisors and 2 perforated bear canines. This grave is the only one of the cemetery dated to the Preboreal; all other dates are much later, i.e. between 7700 and 5700 BP (8600–6600 cal BP) ([59], 250). If this date is correct we have to suggest that the largest Mesolithic cemetery so far with more than 160 graves has its origins in the Preboreal around 11 400 cal BP.

This shows that Arene Candide III, V, VasilEvska III graves 6, 7 and 16, Padina graves 11, 15 and 21, in addition grave 72 at Vlassac, Serbia, are in fact the oldest known burials to date to the Preboreal. At Worm's Head (South Wales, UK), some isolated bones relating to a minimum number of four individuals were found. It is, however, unclear whether these belong to burials, as they were found isolated within the cave's sedimentary fill. A scapula was dated to 9920 ± 160 BP, 11 489 ± 252 cal BP (OxA-13 131) indicating an imprecise date between the early Preboreal and early Boreal. The other bones were dated to the late Preboreal or early Boreal (table 2) ([47], 32–33; [63]).

A radiocarbon date of 10 879 ± 164 cal BP (ETH-6668) was measured on a calvarium found close to the Höhlesbuckel rock shelter near Blaubeuren-Altental in Baden-Württemberg [57]. The remains were discovered between 1949 and 1951 during the construction of a car park, unfortunately without

Table 2. Early Mesolithic (Preboreal and early Boreal) burials. *Commingled sample (46 fragments).

site	chronology direct dates	individuals	grave features	objects	references
Aveline's Hole	8890 ± 45 GrA-22421 8925 ± 45 GrA-22431 8960 ± 50 GrA-22938 8980 ± 50 GrA-22605 9020 ± 50 GrA-22555 9060 ± 50 GrA-22546 9075 ± 45 GrA-22428 9090 ± 45 GrA-22433 9095 ± 45 GrA-22422 9100 ± 45 GrA-22429 9120 ± 50 GrA-22557 9130 ± 60 GrA-22621 9155 ± 45 GrA-22432 9170 ± 50 GrA-22547 9170 ± 50 GrA-22548 9180 ± 50 GrA-22607 9200 ± 50 GrA-22552 9210 ± 70 GrA-22558	~ 50 Individuals	single inhumations double burials? Secondary burials?		[46,47]
Gough's Cave	9100 ± 100 (OxA-814) 9080 ± 150 (BM-525)	1 (Cheddar Man)	single inhumation		[47–49]
Badger Hole	9360 ± 110 (OxA-1459) 9060 ± 130 (OxA-679)				[47–50]
Worm's Head	9920 ± 160 (OxA-13131) 9450 ± 50 (OxA-11128) 9420 ± 55 (OxA-11083) 9360 ± 50 (OxA-11129) 9294 ± 49 (OxA-16607) 9255 ± 45 (OxA-19844)	isolated bones, 2 femur, ulna, scapula, 2 crania			[47]

(*Continued.*)

Table 2. (*Continued.*)

site	chronology direct dates	individuals	grave features	objects	references
Greylake	9118 ± 37 (Wk-30930) 9134 ± 37 (Wk- 30931) 9170 ± 40 (OxA -25666)	2 skulls, mandible, postcranial remains	burials?		[51]
Grotte Margaux	9190 ± 100 (Lv-1709)* *9590 ± 110 (GifA-92345) 9530 ± 120 (GifA-92355) 9260 ± 120 (GifA-92362) 9530 ± 120 (OxA-3533) 9350 ± 120 (OxA-3534)	MNI: 9 adult females	collective burial in a pit	red ochre on bones	[52]
Abri des Autours	9500 ± 75 (OxA-4917)	1 mature female	grave pit		[53]
	9090 ± 140 (OxA-5838)	collective burial, MNI: 6 (1 cremated)	pit		
Grotte des Sarrasins (Loverval)	9640 ± 100 BP (GifA-94536) 9090 ± 100 (Lv-1506)	2 adult female burials	disturbed		[52–55]
Fissure de Claminforge	9525 ± 60 (OxA-10552) 9320 ± 75 (OxA-5451)	MNI: 5 3 adults, 2 children 8–9 years	disturbed by modern activity (collective burial)		[54,55]
Faille du Burin	9520 ± 55 (OxA-10585) 9345 ± 75 (OxA-8938) 9335 ± 65 (OxA-10595) 9315 ± 50 (OxA-10564)	MNI: 6 4 adults, 2 children	collective burial		[54,55]
Bois Laiterie	9515 ± 65 OxA-8910) 9445 ± 60 (OxA-8878) 9420 ± 65 (OxA-8911) 9235 ± 85 (GX-21380)	MNI: 6 4 adults, 2 children (one~2 years)	collective burial	red ochre on some bones	[54,55]
Grotte Lombeau	9410 ± 70 (OxA-6441) 9360 ± 75 (OxA-6440) 9015 ± 80 (OxA-6445)	several individuals	collective burial	red ochre on some bones	[54,55]
Grotte de Petit-Ri	9270 ± 90 (OxA-5042)	MNI: 4 (adult)	collective burial		[54,55]

(*Continued.*)

Table 2. (*Continued.*)

site	chronology direct dates	individuals	grave features	objects	references
Bourg Charente	9330 ± 50 BP (Beta-283143)	1: adult	single inhumation grave pit flexed position	2 flint flakes 1 limestone pebble (usewear)	[56]
Houleau	9250 ± 50 BP (OxA-5683)	2: bone remains			[27]
Blaubeuren-Altental	9520 ± 80 BP (ETH-6668)	adult male			[57]
Blätterhöhle	9700 ± 30 (KIA-45012) 9475 ± 50 (OxA-14466) 9435 ± 40 (KIA-26265) 9470 ± 45 (OxA-14463) 9460 ± 45 (KIA-37515) 9390 ± 35 (KIA-24689) 9370 ± 45 (KIA-37509) 9355 ± 40 (KIA-37516) 9275 ± 45 (KIA-37511)	MNI: 7 (2 children, 5 adults) individuals isolated remains			[58]
Arene Candide, cave, Italy	III: 10,065 ± 55 BP (OxA-10998) Vb: 9925 ± 50 BP (OxA-10999)	III: 1 Ind. V: 2 Ind.	double burial, secondary burial	red ochre, grave goods?	[6–9]
VasilEvska III	V6: 10,060 ± 105 BP (OxA-3807) V7: 9980 ± 100 BP (OxA-3808) V16: 10,080 ± 100 BP (OxA-3809)	6: adult 7: infant 16: adult/mature female	all flexed positions all single inhumations	6: red ochre	[59]
Olenij Ostrov	100: 9910 ± 80 BP (GIN-4836)	100: adult male	sitting position single inhumation	126 lamellae of beaver teeth, 303 elk incisors, 2 perforated bear canines	[59]

(*Continued.*)

Table 2. (*Continued.*)

site	chronology direct dates	individuals	grave features	objects	references
Padina	12: 9331 ± 58 BP (BM-1146)	12: mature male	12 flexed		[59,60]
	14: 9198 ± 103 (BM-1147)	14: adult male	14, 39, 11 extended		
	39: 9292 ± 148 (BM-1404)	39: infant	15 and 21 seated		
	11: 10,000 ± 60 (OxA-11104)	11: infant	single inhumations		
	15: 9480 ± 55 (OxA-11105)	15: –			
	21: 10,095 ± 55 (OxA-11106)	21: –			
Vlassac	72: 9850 ± 130 BP (OxA-5824)	72: late adult–mature female	extended single inhumation	dark red sediment with charcoal	[61]

any proper excavation. It, therefore, remains unclear whether the remains from the Höhlesbuckel site represent a disturbed inhumation of one to three Mesolithic individuals or an accumulation of isolated remains.

Several Belgian sites with human remains fall within this time range from 9500 to 11 300–11 000 cal BP are known from the area between the rivers Meuse and Sambre, close to Namur and Dinant [55,67]. Grotte des Sarrasins (Loverval), Grotte de Claminforge, Grotte de Petit Ri, Grotte du Bois Laiterie, Abri des Autours and the Grotte Margaux, for example, contained human remains in early Mesolithic (Preboreal and early Boreal) contexts. These sites have been excavated during the last 30 years of the twentieth century, but some have suffered from damage by construction and quarrying or have been excavated by speleologists. In these cases, there has been a considerable loss of information, and additionally bioturbation has limited the archaeological information available in some cases. Modern archaeological excavations have been carried out at the Grotte Margaux and Abri des Autours that makes them key sites for an understanding of early Mesolithic funerary behaviour in the region [52,65].

Most of the identification of the remains as Mesolithic is due to direct AMS radiocarbon dating carried out on a number of the sites [54,55]. Remarkably most of these sites dated to the Preboreal or early Boreal, and there is a considerable lack of sites dating to the subsequent middle or even late Mesolithic. The early Mesolithic sites show various characteristics; remains were typically found within small cavities, the only exception is the site of Grotte Margaux were the human remains were found in the narrow rear part of the cave [52], and usually little or no archaeological (i.e. occupation) material was associated with them. This is probably because these sites simply were too small to be occupied. Any kind of personal ornament in association with the human remains is completely absent, and the use of red ochre on the human remains was recorded in only a few cases. One of the main similarities of the Mesolithic remains in the Meuse area is the lack of anatomical connection between skeletal elements. Bones are mostly found in fragmented state, although some complete bones and skulls have been recorded. Occasionally, the remains of several individuals (MNIs = 4–9) were deposited in pits, but mostly the bones must have been deposited on the surface (i.e. floor) inside the caves. Although fragmented, manipulations on the remains are rare; exception is a skull from Grotte Margaux with perimortal cut marks on the cranium. This activity seems to be linked with the funerary practice at the site [66].

The Blätterhöhle at Hagen, Germany contains a number of Mesolithic human remains similar to the Belgian sites, radiocarbon dates for which range between 11 500 and 11 300 cal BP (table 2). An MNI of seven individuals (five adults and two children aged between 5–6 and 8–10 years) was recovered from the narrow cave, scattered within the sediment of the cave's interior in a very good state of preservation, if generally fragmentary. The deliberate placement of three boar skulls in context with the human remains is so far unique for the Mesolithic [58].

The newly discovered isolated burial of Bourg Charente, southwestern France falls within the same period. The body was found in a tightly flexed position within a grave pit. The AMS date of 10 544 ± 78 cal BP (Beta-283143) (table 2) places it in the late Preboreal between 10 700 and 10 400 cal BP. Three objects—two flint flakes and a used limestone pebble—were found close to the body and can reliably be regarded as grave goods [56]. Owing to missing information, the Houleau 2 burial in the Gironde remains largely uninformative. The remains were dated to 9250 ± 80 BP (10 600–10 400 cal BP), i.e. the transitional phase between the Preboreal and the Boreal ([27], 16) (table 2).

Despite the 'Cheddar Man' skeleton found in Gough's Cave in 1903, another site that is of great importance for the early Mesolithic burials is Aveline's Hole, both in Somerset, UK. The human remains from Gough's Cave seem to belong to a single inhumation or deposition in a side chamber of the cave [47,48,50]. The situation at Aveline's Hole is, however, more complex [46]. The site has suffered from a rather early discovery beginning in the eighteenth century, with successive activities inside the cave including the removal of sedimentary material. Of greater importance are the excavations of 1914 and between 1919 and 1930. Reports on these suggest a relatively simple stratigraphy and human and faunal remains in large numbers, whereas lithics only represented in lower numbers, suggesting less of an occupation of the cave. The human remains were mostly preserved in form of a bone scatter, but at least two burials of complete bodies were recorded. A double burial (A) was found below a hearth, whose relation to the burial is unclear. The bones of the two adult individuals were unburned, although 18 red deer incisors, which were found in a possible relation to the burial, showed signs of burning. The dating of this double burial is unclear, and it could even be late Upper Palaeolithic in age ([46], 171–181). A second inhumation of a single adult individual (B) was found near the double burial (A). Although heavily affected and destroyed by a massive rock fall, a number of objects were recorded in close contact with the skeleton, including six flint blades, numerous red deer teeth and the tooth of a young brown bear. Nearby, close to the cave wall, three red deer antlers with cranial fragments attached to them were found. As the collection of the human remains was heavily damaged during the Second World War, the number of individuals is rather vague. Based on the surviving collection of 860 bones the MNI is 21, but the real number could originally have been much higher, possibly up to 50. If correct this would make the Aveline's Hole collection the largest sample of human remains from the early Mesolithic of Europe. The dating of the assemblage is based on 18 AMS radiocarbon measurements on 17 left ulnae and 1 cranium, therefore representing an MNI of 17 individuals. The dates between 11 200 and 10 900 cal BP indicate a use of the cave as a burial place in the transitional period between Preboreal and early Boreal. This relatively short time span and the fact that subadult individuals, especially small children, are underrepresented, could indicate that the cave was selectively used as a burial place by a larger group or by several smaller groups over 100 or 200 years.

Similar radiocarbon dates have been found at two skulls and a mandible from a sandpit at Greylake, Somerset, UK (table 2). The human remains including postcranial fragments representing a minimum of five individuals were excavated in 1928, but dated only recently to the early Boreal. The facts that skulls and long bones, together with some smaller skeletal elements were preserved might indicate the presence of complete burials at the site.

4. Conclusion

This review of the Late Upper Palaeolithic and early Mesolithic (Preboreal and early Boreal) European funerary record may be incomplete, as several burials are still undated or insecure and were, therefore, omitted from the study. In various cases, new AMS radiocarbon dates have changed previous attributions to the Late Upper Palaeolithic (LUP) or the Mesolithic and further direct dating will inevitably bring more changes to the sample.

The occurrence of burials from the European LUP is relatively diverse. It is quite obvious that the sample from the Italian peninsula is the richest one. In this case, the single and double inhumations of adults and children clearly reflect an Epigravettian and (earlier) Gravettian tradition. In most cases, adults and children were buried in the same way, occasionally even together in the same grave. The dominant rite was of inhumations with the body lying extended on its back and with little or no grave goods excepting basic equipment such as flint tools and personal ornamentation such as perforated shells.

Burials in other parts of Europe (Spain, France and Germany) are quite rare. Where present they seem to follow the general pattern, although there is a considerable lack of information on several of these. However, the use of red ochre, the occurrence of a limited number of personal ornaments and rare provision with stone artefacts seems again to have been a common practice. An exception to this pattern is the La Madeleine burial, which was richly equipped with personal ornaments, and that of Los Azules, with its possible tool kit. Concerning the objects associated with the burials, the personal ornaments from the La Madeleine burial, the objects from Aven des Iboussières are comparable to those from Arene Candide and Grotta dei Fanciulli in Italy, and furthermore the mode of deposition of Aven des Iboussières could be comparable to the remains of Grotta Polesini. Although both sites lack a precise date for their human remains, there possess similarities in that the human remains were found in disarticulated state and were stained with red ochre. Additionally, the occurrence of a number of personal ornaments, such as perforated red deer canines, fish vertebrae and shells, at both sites could indicate a similar funerary behaviour at the very end of Pleistocene or the transition to the Holocene. These two sites can also be interpreted as a form of cemetery where the incomplete remains of several humans were deposited in what could be interpreted as secondary burials. Additionally, such 'cemetery-like' structures are also visible in other cases, with a considerable number of single and double inhumations involved at San Teodoro, Riparo di Romito and most convincingly Arene Candide.

For the early Mesolithic burials of the Preboreal and early Boreal, it seems obvious that single inhumations in either flexed or extended positions within caves and rock shelters still played an important role. As this is comparable to the traditions of the Late Upper Palaeolithic, we could suggest that this is an important aspect to argue for continuity in traditions between these environmentally distinct periods. There are, however, several nuanced differences between the LUP and early Mesolithic burials. It seems quite striking that there is an almost complete lack of personal ornaments and a much reduced inventory of objects which can be identified as grave goods in the latter. Grave 100 at Olenij Ostrov—so far the only one from this large Mesolithic graveyard dated to the Preboreal—and the double burial V from Arene Canide are the only exceptions to this. The use of red ochre is recorded in several cases, but descriptions emphasize the fact that the red ochre was found mostly on the bones themselves and not within the fills of the graves on the level of the burials. Possible secondary burials of individuals were identifiable at Arene Candide III for the Preboreal and possibly also at Aveline's Hole in the early Boreal phase. A new aspect in these burial traditions is the occurrence of assemblages of human remains, often of adults and infants alike. These assemblages were found mostly within caves and rock shelters in the Meuse region in Belgium and in the Blätterhöhle in Germany almost 300 km distant. These so-called 'collective burials' contain the disarticulated and sometimes fragmented remains of a minimum of 4–10 individuals. Grave goods are not identifiable, but the use of red ochre was recorded several times in the Belgian sites. Whether these collective burials can be seen as an equivalent of cemeteries is an open question. Cemetery-like structures with single and double inhumations have not been identified in the Preboreal. In the early Boreal, by contrast, sites such as Aveline's Hole, and maybe the open-air site of Greylake as well can be seen as one of the first Mesolithic cemeteries [67]. The Mesolithic double burial V and the secondary burial III at Arene Candide clearly show that the LUP tradition of a cemetery was transferred to the postglacial period, at least at this site. According to the AMS radiocarbon dating of later cemeteries, it becomes evident that sites such as Olenij Ostrov, VasilEvska III, Padina and Vlasac all had earlier origins in the Preboreal. Further dating of other burials from these sites and AMS radiocarbon dates from as yet largely undated Mesolithic cemeteries may yet reveal that the tradition of burials within cemeteries is also liked with the Preboreal. The fact that the first cemeteries can be dated to the LUP links this burial tradition with the Final Pleistocene. Most certainly we are dealing with local burial traditions in the LUP and the early Mesolithic, but given the sparse findings these are sometimes hard to identify. The LUP burials in Italy and the Mesolithic collective burials in the Meuse area seem to be part of such a tradition. Further on it is important to note that the Mesolithic burial practice is not only to be seen in the tradition on LUP burials, but shows a high amount of variation. The Mesolithic burial practice is highly diverse including single, double, multiple burials, cremations, manipulation of bodies, secondary single and collective burials, burials in cemeteries, in caves, rock shelters and open air sites, as well as water burials and head burials. This diversity is in many aspects already visible in the Upper Palaeolithic, but reaches a new level in the Mesolithic.

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Hominin evolutionary thanatology from the mortuary to funerary realm: the palaeoanthropological bridge between chemistry and culture

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Research

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Palaeoanthropology, or more precisely Palaeolithic archaeology, offers the possibility of bridging the gap between mortuary activities that can be observed in the wider animal community and which relate to chemistry and emotion; to the often-elaborate systems of rationalization and symbolic contextualisation that are characteristic of recently observable societies. I draw on ethological studies to provide a core set of mortuary behaviours one might expect hominoids to inherit, and on anthropological observations to explore funerary activity represented in the Middle and Upper Palaeolithic, in order to examine how a distinctly human set of funerary behaviours arose from a more widespread set of mortuary behaviours. I suggest that the most profound innovation of the hominins was the incorporation of places into the commemoration of the dead, and propose a falsifiable mechanism for why this came about; and I suggest that the pattern of the earliest burials fits with modern hunter–gatherer belief systems about death, and how these vary by social complexity. Finally, I propose several research questions pertaining to the social context of funerary practices, suggesting how a hominin evolutionary thanatology may contribute not only to our understanding of human behavioural evolution, but to a wider thanatology of the animal kingdom.

This article is part of the theme issue 'Evolutionary thanatology: impacts of the dead on the living in humans and other animals'.

1. Introduction: bridging chemistry and culture in evolutionary thanatology

How would the scientific community react to reports of the deliberate burial of a dead chimpanzee by its conspecifics? Let's say in the context of apparently rule-bound social theatre, investigation and grooming of the corpse by specific individuals, use of tools to clean it [1] and its eventual disposal in a shallow grave, communally excavated in an intense activity area in close proximity to night nests? The burial is hypothetical of course, although everything else that I list as its context has been observed. I do not think it is unfair to suggest that many palaeoanthropologists, for whom 'burial' is often interpreted as one of several marks of behavioural 'modernity' that emerged among large-brained members of the genus *Homo* [2], would not hesitate to welcome chimpanzees into the 'behaviourally modern' symbolic club. They would have to, given their repeated emphasis on the behavioural sophistication of the act of burial in shallow graves. But what would this achieve in terms of understanding the evolution of mortuary behaviour? What would its implications be for those Miocene hominoids and Plio-Pleistocene hominins that we often use chimpanzees as a heuristic for, or the large-brained Late Middle and Upper Pleistocene examples of *Homo sapiens* and *H. neanderthalensis* that we see as the epitome of hominoid cognitive evolution? If we conceive of the answer to this in terms of a dichotomy—as archaeologists often do—we might conclude either that all hominoids

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were as 'sophisticated' as our own species in this light, or that the act of burial is not so special after all. Burial is a time consuming and difficult thing to do, particularly when corpses can alternatively just be abandoned, floated off down rivers, or tucked away in nature's nooks and crannies, so why is it seen to be so important? Palaeoanthropologists have been drawn to the heuristic potential of burials for a century; we tend to interpret hominin mortuary behaviour in terms of a 'before' and 'after' the invention of burial, a simple dichotomy that has little helped us develop the field of thanatology as applied to long-term hominin behavioural evolution.

My purpose here is to examine how palaeoanthropology—the study of hominin biological and behavioural evolution—might contribute towards an understanding of how mortuary activities we regard as distinctly human arose from those we may regard as distinctly animal. By doing so, I aim to nuance the information from all these areas—evidenced by the papers in this issue—in order to develop our understanding of the archaeological record in terms of how treatment of the dead evolved in early human societies over the long term. To begin this, I have previously drawn on primatological data in order to establish a set of 'core' mortuary activities that I suggest may reasonably have been practised to varying degrees by early hominoids and hominins [3], and I develop this here by reference to wider animal activities on the one hand and anthropological observations among the small-scale/non-industrial societies of the past century or so on the other. I am aware of the dangers of universal generalizations, which are problematic in anthropology where one can talk to informants [4], let alone prehistoric archaeology where one cannot, although I believe that advancing some broad generalizations will at least enable us to begin a more sophisticated dialogue about exactly how and why certain treatments of the dead arose, and how they became selectively elaborated over the course of human evolution. I do so using four categories of behaviour that may be seen as increasingly conscious and complex while at the same time cumulative and complementary: chemical, emotional, rational and cultural. I read the existing archaeological record in the light of these categories. Overall, I suggest that only palaeoanthropology—more specifically the Palaeolithic record—can address the question as to how a distinctly 'human' mortuary behaviour observed by anthropologists, psychologists and sociologists arose from the more 'animal' one documented by ethologists and biologists.

2. Palaeoanthropological heuristics: from *mortuary* to *funerary* behaviour

Across the world, human reactions to corpses are ubiquitously strong [4]. The same can be said for many animal taxa, whether or not they are at base chemical or emotional. In a review of the emerging field of comparative thanatology, James Anderson [5] posited a spectrum of responses to death in animals, from hardwired, mechanistic responses probably lacking emotional components, to socially malleable behaviours that likely incorporate emotional states such as sadness and grief. For human evolution, the difficult task is to tease out how such behaviours may have developed over the course of the Pliocene and Pleistocene, and at what point they become archaeologically visible. Archaeologists have long since been particularly attracted to mortuary activity: our subjects are all long-dead, and burials and excavation of the occasionally labour-intensive and conspicuous constructions associated with them are often rewarding. In palaeoanthropology, however, we suffer from a paucity of heuristics that could be applied to the study of the long-term evolution of mortuary behaviour. In the field of Palaeolithic archaeology, the terms 'mortuary' and 'funerary' are often used synonymously. If, however, we are to develop a hominoid evolutionary thanatology, we will need to develop specific concepts and associated terminology that will enable us to begin to move away from simple concepts to nuanced specifics.

We can start by tightening these definitions. *Mortuary* activity is a broad term, describing anything relating to death and to the treatment of the dead; by contrast, *Funerary* activity is more specific, describing activities relating to the disposal of the dead and to their subsequent commemoration.[1] Examples of the former might include the examination of corpses for signs of life or explanations of the cause of death, behaviour I have defined as *morbidity* [3]; disposal of corpses for hygienic or other reasons; curation of the corpse prior to emotional detachment from it and deliberate disposal of the dead in specific places of the landscape, which I have *termed funerary caching* [3]. Hence, *mortuary behaviour* describes a spectrum of emotional and intellectual beliefs relating to and arising from the occurrence of death and presence of the dead (e.g. confusion, emotion, inquisitiveness), followed by a variety of physical behaviours that either facilitate these (morbidity) or express them (e.g. display, curation, caching) [3–10]. *Funerary behaviour* may come to be part of mortuary activity, I suggest, when artificial forms of disposal (graves, cremations) are introduced, or when forms of active remembrance (commemoration) of the deceased supplement others (e.g. spatial segregation of the dead from the living in the form of tombs and cemeteries, grave markers and grave goods). Hence all funerary behaviour is mortuary behaviour, but not all mortuary behaviour need have a funerary element; an evolutionary trajectory from mortuary to funerary is implicit.

For heuristic purposes, I want to define this difference between the two further. Mortuary behaviour occurs face-to-face between individuals and in the moment. Most importantly, the deceased continues to function as part of the social group only as long as the corpse-focused activities continue; when they stop, the dead are abandoned. By contrast, funerary behaviour deploys a variety of symbols by which the dead *continue* to remain part of the social group. This is achieved by a process of transferring the temporary mortuary behaviours into the wider landscape, by means of intelligible symbols such as relics or marked burial places, by which a longer temporality can be accorded to the dead by their incorporation into places, or landscapes, of the dead [11]. While the mortuary realm occurs face-to-face, funerary behaviour adds place, and consequently, time, to it. Hence the major transition from one to the other is from a peripersonal activity to an extrapersonal one.

It follows that the basic research questions for palaeoanthropology in the long term are: What might we expect the earliest (presumably simplest) mortuary behaviours to have been? When did a wide range of such mortuary activities begin to include behaviours that are specifically funerary, or to put it another way, when did the treatment of the dead begin to include aspects of commemoration? To translate this into a specifically archaeological concept, when did the dead become symbols to their contemporaries? The dead can become symbols in many ways that are archaeologically invisible (song, storytelling, curation of perishable material culture such as hair, wearing black clothing and so on), although archaeologically, a funerary aspect may be inferred, I suggest, by the artificial provision of space for the dead (graves); the segregation of the dead from the living and the accumulation of the dead in such places, often in some number (cemeteries), the creation of places of deposition that are meant to be seen; age, gender or other biases in the treatment of the dead that plausibly reflect social 'rules' about how specific deaths or specific individuals should be treated; elaborate behaviours such as secondary burial, retention and/or deliberate deposition or alteration of body parts.

3. Chemistry

We can assume that the physical and conceptual separation of the dead from the living has very ancient roots. Diverse animal species recognize the dead and modify their behaviour in order to reduce the impact of deleterious effects on their health [12]. As the avoidance of contagion is one of the most powerful agents of natural selection, numerous insect taxa are repelled by their own body fluids, avoiding the fatty acid necromones associated with decomposition, a form of behaviour-changing biochemical death signalling that likely predates the divergence of crustaceans and terrestrial insects more than 420 Ma [13]. The power of necromones should not be underestimated; traces of these seem to allow woodlice to recognize and avoid places where insects have been killed [13]. We may safely assume that early hominins would inherit from substantially earlier evolutionary ancestry a concern with blood as well as a revulsion towards the corpses of conspecifics, and possibly an ability to identify places where conspecifics have been killed, and from these one might expect them to have practised corpse management strategies.

It is not surprising that eusocial insects manage corpses, given that they aggregate in relatively dense numbers and are highly organized socially [14]. The practice minimizes the threat of epidemic disease caused by exposure to corpses. Corpses may simply be consumed by a conspecific (cannibalism or necrophagy) [15], particularly during periods of food shortage or when inter-colony violence has resulted in dead enemies [12]. Otherwise the simplest, most common (and evolutionarily earliest) means of avoiding contact with corpses is simply to remove them from the nest [12], which has been termed *necrophoresis* [16] and which might informally be termed *undertaking* [12,14]. Archaeologists should not, therefore, interpret examples of undertaking in hominin groups as necessarily sophisticated. Among ants, corpses of conspecifics are investigated by repeated antennal palpation, licked and moved about by co-workers before being carried to refuse piles or 'kitchen middens' [14], and among established colonies, sloughed cocoons and pupae are removed in such a manner that they can accumulate in craters around colony entrances [17], forming a spatial patterning that it may be tempting to interpret as deliberate 'cemeteries'. With termites, durations of 2 h of licking and grooming of the corpse are common, in addition to repeated displacements of it [15]. Furthermore, injured and dying workers leave the nest themselves, 'their last act as living workers' [15] to die in isolation, as an altruistic means of reducing risk to their group [18]. Typical responses of the living to such alarms include relatively intensified, 'highly excited' movement such as faster locomotion and circling patterns, which spreads among the group as a 'wave of excitement' [19] involving up to 25 individuals within a few seconds [20] .Where physical factors preclude the removal of corpses from termite nests they may be buried by accumulating sediment atop them to form a 'claustral [enveloping] chamber' [15], and a similar process has been observed as a group activity among ants while other individuals continue to palpate the corpse [20]. Among the latter, burial is a four-stage process, involving carrying and depositing building (i.e. burial) material, plugging gaps in this with smaller sedimentary material, packing down and reordering of materials. A social element is reflected by the ants' ability to distinguish between group and alien conspecifics and to react accordingly, by necrophoresis and agonism (attacks, bites), respectively [20]. The accompaniment of necrophoresis and burial by additional behaviours including antennal palpation, licking, aggression and biting and corpse displacement in fits and starts [20] is remarkably similar to the range of behaviours exhibited by chimpanzees around corpses [3–10], and a degree of task specialization in how individuals respond towards the corpse is observable in both [12].

Understanding that death has occurred, that the corpse may be a source of contamination and hence threat, and consequently distancing it from the living are clearly important for survival [9]. In particular, understanding the cause of injury and the nature of danger are of great importance to group fitness; chimpanzees, for example, stay near the bodies of the dead or injured who have obvious wounds, but conversely avoid those that are diseased, a difference that is also manifest in distinct vocal reactions [9]. Given the concern with purity (or more specifically, avoidance of contamination), we should not be surprised by the presence of elaborate morbidity among various animal taxa, including compassion and empathy towards the wounded and dying. In terms of a hominin evolutionary inheritance in the mortuary realm we may, therefore, expect a very deep-rooted appearance of self-removal of the dying from living company; morbidity, grooming and movement of the corpse, cannibalism and agonistic behaviour towards it; and it burial by accumulation of materials or by digging; shared, excited responses and intensified movement among the living; and a degree of elaboration of all these, varying with social organization. As the complexity of the social brain grew, emotional responses to death began to complement these initial chemical stimuli.

4. Emotion

Only in recent times have humans become relatively isolated from an otherwise ubiquitous frequent and visceral experience of the death, decomposition, and butchery of conspecifics and animal prey [21]. Like non-human animals, hunter–gatherers routinely deal in death, which is for them 'a way of life' [22]. The overwhelming emotions that are evoked by death are so obvious that they have often been used as a direct explanation of the funerary rituals and 'rites' that are observed across the world [4]. As archaeologists, a focus on emotion *per se* will not get us anywhere, however; even with anthropological subjects it is difficult or impossible to identify the specific emotions that are presumed to underpin mortuary behaviour, and it should go without saying that identifying emotions archaeologically is in most cases impossible. We will simply have to assume that some complex interplay of emotions—particularly centred around the poles of sorrow and anger—was part of the very partial remains of mortuary behaviour that come down to us in the form of fear, grief and aggression.

We might expect hominoids to identify dangerous places, especially those associated with death, and to communicate them effectively. Among the Taï group, when the body of a chimpanzee who had died by falling out of the tree was located, a group of five chimpanzees ‘stayed in the trees near the body for nearly 5 hours, alarm-calling most of the time and making fear screams and aggressive pant hoots’; they were joined by ‘many others’. They spent 93% of this time in the trees looking down at the dead body, but a few eventually came down to the ground [9]. Given the dangers of predation on early hominins, one might expect locales such as the australopithecine accumulation of Swartkrans, South Africa, to have quickly become known places of death and to have become part of the communicative repertoire [11]. Apes, and apparently monkeys, have the capacity to grieve the loss of conspecifics [6]. This takes the form of a two-stage process, beginning with intense agitation (movement and vocalization) and leads to depression or despair (silent immobility). Among small-scale societies, expressions of grief are shown at most (but not all) funerals [4] and we can assume that this was a common constituent of mortuary activities over the course of human evolution.

In mortuary activity, cycles of violence and sex can be seen among chimpanzees [3–10] and in small-scale human societies where both are often rule bound [4], sorrow and anger are the predominant emotions being expressed, e.g. in mourning dances of war among the Nyakyusa of East Africa, which have a strong sexual component [4]. Among small-scale societies there is a strong link between death and its associated mortuary rituals and fertility, particularly to the group’s ability to appropriate nature [23] and ultimately to concepts of rebirth and creation [4]. Sexuality in small-scale societies is often associated with putrefaction, and seen as a cause of death; hence, it can also come to symbolize deaths that are ‘bad’ (see below) [23].

Why eat bits of the dead, especially the bodies of conspecifics? I have previously drawn attention to numerous examples of cannibalism among chimpanzees (often, but not exclusively, associated with infanticide) and to the ubiquity of stone tool cut marks indicative of butchery on the remains of several hominin taxa from the Late Pliocene to Upper Pleistocene, including crania of early *H. sapiens* [3]. While this may have arisen from the pole of anger in the cycles of violence and grief, clearly it could be adapted for other purposes. The evidence of predation, butchery and consumption of individuals among the *H. antecessor* populations of Atapuerca, Spain more than 800 000 years ago [24] has, for example, been interpreted as part of competitive strategies of range expansion [25]. One might further expect that as the body became an increasingly potent social symbol over the course of hominin evolution, so the strategy of cannibalism may have become more important in competitive contexts, as I discuss below.

A challenge for evolutionary thanatology is to elucidate how understandings gained from morbidity and its associated emotions were perpetuated in social groups. Such *remembrance* is central to the emergence of funerary activity. Again, the roots of remembrance could manifest chemically; African elephants show considerable interest in the remains of their own conspecifics, even if it cannot be demonstrated that they specifically recognize their own kin [26]. A social factor seems also to be at play, however; they are drawn specifically to skulls and tusks (ignoring postcranial bones) suggesting that their interest in the tusks of the dead derives specifically from their interest in the tusks of their group members in life. Both emotion and remembrance constitute the raw materials that may become elaborated, by extending reference to the dead and the expression of emotions over time, and ultimately by associating them with specific places.

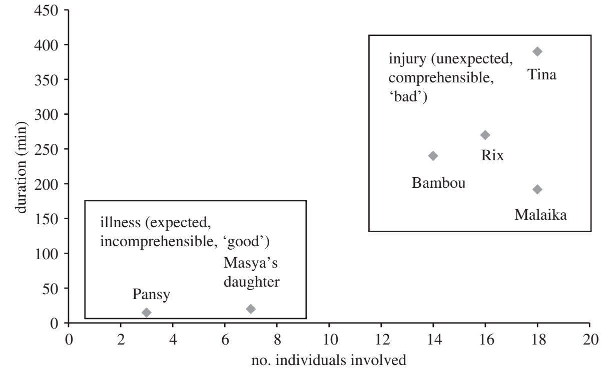

Figure 1. Duration and number of individuals observed in interaction with the dead among chimpanzees. Data: Rix, Gombe, Tanzania (Teleki [30]); Bambou and Tina, Taï, Ivory Coast (Boesch and Boesch-Achermann [10]); Pansy, Blair Drummond Safari Park, Scotland (Anderson *et al*. [7]); Malaika, Gombe (Stewart *et al*. [31]); Masya’s daughter, Chimfunshi Wildlife Orphanage, Zambia (Cronin *et al*. [32]: the infant was observed to be unhealthy from very early in life, thus the observers were not confident that she would survive and did not name her; K. Cronin 2012, personal communication). (Online version in colour.)

I have suggested elsewhere that as group size and complexity—and hence the social brain [27,28]—increased over the course of hominoid evolution, mortuary activity would constitute one of the package of social activities that came under selection to evolve, which could be recognized in terms of the relationship between group size and neocortical size [29]. Figure 1 plots data from the six most detailed published observations of activity around the newly dead bodies of infant chimpanzees (no such data being available for deceased adults in terms of the number of individuals apparently behaving exclusively in response to a new corpse, against the total amount of time that corpse-focused/affected activities were observed before the groups abandoning the corpse for). The data points are few and it is not possible on the basis of published data to establish what percentage of the total group the figures reflect; as such this may be modified or falsified over time, but there are two sets of observations and predictions that can be made from this. First, the greater the number of individuals ‘involved’ in the corpse-oriented activities, the more time the group spent in mortuary activity. Second, the dead individuals whose corpses received the most attention (the highest numbers of living individuals focused on them and the greatest total time spent doing so) were those whose deaths were from wounds, as opposed to illness. Illnesses may be inexplicable (there is nothing physical to investigate) although expected (predicted through behavioural changes and visible decline). By contrast, injuries are sudden and unpredictable (tree falls, leopard ambushes) yet the cause is visibly obvious. Hence one might predict first, that as hominoid and hominin groups became larger and more socially complex, mortuary activities in the broader sense would evolve as part of this, and second, that unpredicted but explainable deaths would be under selection for particular emphasis, i.e. further elaboration. It is tempting to link deaths by illness to 'good' (i.e. natural) deaths, and deaths by injury to 'bad', which I elaborate upon below.

Another issue for palaeoanthropology is documenting how a material aspect came to be incorporated into mortuary activity, and under what circumstances this became elaborated. Recently, evidence of the incorporation of material objects in chimpanzee morbidity has come to light, including the use of a twig to clean teeth of the deceased [1]. In five cases among the Taï chimpanzees, where individuals died in circumstances that did not leave any external signs to indicate the cause of death, groups members cut leafy branches, and without eating or otherwise engaging with them, allowed them to fall on the dead body, perhaps as an attempt to elicit a response from the dead [9]. Thus, while this need not reflect a concern to cover the corpse (although it may: if it is about eliciting a response, why not just hit it?), this indicates an interest in claustralization, which could function as a precursor to burial.

5. Rationalization: from morbidity to anticipation and denial

The process of rationalization includes attempts to understand the cause of death, mitigate for the emotional and social disruptions it causes, and ultimately anticipate and explain it. The morbidity observable in primates reflects a deep evolutionary role for the first two. At some point in hominoid or hominin evolution, emotionally based responses to death became complemented by *anticipation*, i.e. an expectation of death and perhaps a preparation for it or attempts to ward it off [33]. By contrast, most human groups strongly deny that death is an individual extinction [23], hence one might expect mechanisms of *denial* to form part of the rationalization process. Rationalization essentially transforms the core mortuary behaviours into socially repeated and, ultimately, rule-bound cultural activities. It may, therefore, provide a mechanism for growing complexity of face-to-face and transient behaviours which in theory at least should be reflected archaeologically.

The major transition reflected in the archaeological record, and arguably the major change that turned an effective primate set of mourning behaviours into a human set, is the extension of face-to-face, transient and peripersonal activity to ones that were anchored in the landscape, i.e. the association of places with the dead, and the function of the landscape in the process of remembrance [11]. Formally, this transition reflects the origins of *funerary* practices *sensu stricto*. Why would this happen, however, and under what circumstances? The difficulties of the living detaching themselves from the dead—particularly, in the case of mother–infant bonds—explains several observations of chimpanzee mothers carrying around the naturally mummified corpse of their dead infant [8] and in this sense a degree of spatial and temporal extension of the dead in the landscape forms the basis of further elaboration.

I hypothesize that the incorporation of places into mortuary activities became desirable, or even necessary, as the size and complexity of social groups increased, perhaps with archaic *Homo*. In groups where death required mortuary behaviours such as those discussed above, where the number of individuals required to participate in such behaviours is relatively large they may become too demanding on time, and hence difficult to resolve satisfactorily face-to-face and here-and-now. Hence a form of remembrance could be introduced, by associating the dead with recognized points in the landscape. To put this another way, they are deposited symbolically in the landscape, not simply left behind; they remain with the living, at least when these sites were revisited.

At this point, one might expect such landscapes of the dead to have become incorporated into social systems. Among modern humans, communities are ubiquitously constructed by reference to the dead [23]. Small-scale societies incorporate the dead into their living spaces, either below them (burial) or within them (structures), whether they are buried intact or as secondary collections of dry material. Conversely, they can delineate a particular space exclusive to the dead (cemeteries *sensu stricto* [3]), which often express the group's wider social order [23]. To a mobile hunter–gatherer, therefore, the landscape may be used to *incorporate* the dead in society, at least while groups (re)visit particular locales, or to *explain* or *justify* social order. Given the attention Palaeolithic groups inevitably paid to the temporal landscape—the periodic waxing and waning of resources over the course of the foraging year—it would not be surprising if the agency of the dead had similar, temporary and repeated manifestation, according to the natural order.

I have argued that the recovery of the remains of numerous individual hominins from caves that otherwise lack evidence of occupation indicates the deliberate deposition of the dead in natural fissures from at least 400 000 years ago [3]. Examples include a minimum number of individuals (MNI) of 28 assigned to *H. heidelbergensis* in the Sima de los Huesos at Atapuerca, Spain, approximately 400–50 000 years ago [34,35]; an MNI of 15 assigned to *H. naledi* in the Rising Star Cave, South Africa approx. 300 000 years ago, although the depositionary mechanisms here are at present unclear [36,37] and an MNI of eight Neanderthals including young adults, an infant, juvenile and adolescent in El Sidron, Spain, approximately 40 000 years ago [38]. These are accumulations of multiple individuals for which it is difficult to establish beyond doubt deliberate deposition as opposed to random sampling of humans at sinkholes through accidents, and it remains to be seen if this Middle Pleistocene phase of funerary caching as I have called it precedes the earliest burials, or whether the latter appear suddenly without this phase of natural deposition [39]. If they are deliberate accumulations, however, they would indicate a persistence of deposition of the dead at specific places, to which I shall return below.

From around 100 000 years ago we are on firmer ground, with a number of examples of burials for both *H. neanderthalensis* and early *H. sapiens* [3,39]. Establishing the credibility of presumed burials from Neanderthal and early *H. sapiens* (Middle Palaeolithic) archaeology can be difficult, at least when they were excavated before modern standards of excavation and recording. In some cases, corpses may have come to rest in natural (rather than deliberate) cuttings, such as the Neanderthal child from Roc de Marsal, France [40] or adult from Regourdou, France [41], although one cannot rule out that these questionable cases were deliberate burials. In several sites, however, the picture is clear, particularly where multiple burials (e.g.in the La Ferrassie rockshelter, Dordogne, France and Shanidar cave, Iraq) [42] indicate the repeated use of these occupation sites for the burial of both young and old, and the occasional association of the dead with stone tools, and in one case, the use of a rock engraved with cupules to mark an infant's grave pit [43,44]. Neanderthal mortuary practices were varied, not least of which because one cannot say that all of the dead were buried in all Neanderthal groups; where they were, all age ranges, from fetuses and infants to adults, received similar treatment, in materially simplistic, single inhumations in shallow graves [45,46]. The same seems to have applied for early *H. sapiens* around the same time, at least in the Near East, such as in Skhul and Qafzeh caves [46,47].

It may be no coincidence that at this time, human behaviour shifted in material emphasis from instrument-based culture to containers [48], part of which may have been a growing concern with containment of the corpse. Prior to that time, mortuary activity may have deployed only instruments (hands, the senses, stone tools for defleshing). Evidence of the defleshing of the body and cannibalism continues, however, among Neanderthals, for example, at Moula Guercy, France, and Krapina, Croatia [3,49–53]. One might say that it is with the Neanderthals that the extremes of mortuary treatment of the body emerge, i.e. fragmentation and containment. Does this indicate the existence of at least two distinct ways of thinking about the dead by this time?

Why funerary caching and burial? I have discussed the function of necroclaustralization above. In ants, if alarm/excitement is perpetuated long enough, it can stimulate ‘digging behaviour’, which probably derives from the act of rescuing workers when nests collapse [19]. It would of course be pushing interpretation to associate this digging with the eventual digging of graves—particularly as this activity is extremely rare in the animal and early human world (see below)—although it must be noted that very specific behavioural responses to death have very ancient origins. The deliberate construction of artificial fissures to contain the dead could, therefore, have emerged out of a wider behavioural concern with containers and enclosure; it may be no coincidence that the first containers for the living, in the form of dwelling structures, are noticeable (albeit rare) from this time. Cognitively, social perspectives on the origin of religious belief suggests that any links between mortuary activity and belief systems (such as afterlives) is contingent upon four orders of intention, and hence, to *H. sapiens* and *H. neanderthalensis* [11,27,28], and it is possible that rationalizing strategies from this time included concepts of after people [54], ultimately linked to landscapes, as peripersonal activities took on extrapersonal forms.

6. Cultural elaboration: burial, containment, stages of transition

Among human societies, mortuary activities are not isolated from wider social systems, and are often embedded in wider social practices as a form of *prestation*, i.e. a means of satisfying obligations [4]. The forms of social theatre observed among primates suggest that mortuary activity co-evolved in tandem with social systems perhaps throughout much of the primate order. The anthropology of mortuary activity provides complex *dramatis personae* of the corpse, its soul/spirit, and those who remain living, in this case, the mourners [4], which provides the raw materials for cultural elaboration over the course of the Palaeolithic. Although exceptions can always be found, several ubiquitous characteristics have been found anthropologically across the world, notably; the triad of colour symbolism whereby red represents power and life, white purity and fertility, and black decomposition and death [4]; archaeological intangibles such as the shaving of hair and covering of the body with ash; the association of noisemaking with the corpse (especially, the equation of percussion with the transitional stage of death—see below); and alternation of noisemaking with periods of profound silence [4]; and rituals that draw attention to the corpse or protect it from harm. Parallels with observations among chimpanzees are striking.

Primarily, the cross-cultural ubiquity of the *denial* that individual existence ceases with biological death suggests that this might be under the strongest selection for social and ritual elaboration. Most of the rituals associated with death in the modern world serve the purpose of *acting against* death by providing an alternative to it, notably by transforming the deceased into some form of an afterlife [55]. In modern humans, it is natural to believe in life after death, and specific conceptions of the afterlife will be coloured by social transmission [56]. Hence, the *emotions* expressed in mortuary contexts provide a source for *sentiment* that is in turn transformed into tangible *ritual* [4].

Among small-scale societies, the preparation of the dead for disposal, which entails close and often prolonged contact with the contaminating corpse, is strikingly similar among 57 representative groups recorded in the Human Relations Area Files [57]. As these activities function, in part, to confirm that death has occurred, they can be seen as a cultural elaboration of morbidity. A sense of agency is often ascribed to the deceased; even in the modern west, recently bereaved individuals commonly ascribe unexplained sights and sounds to their deceased loved ones. The visual exposure of the living to corpses that bear wounds, by investigation or otherwise, may therefore play a role in suppressing notions that the deceased has not quite left society, i.e. by confirming death [56]. In modern studies, viewing of a corpse that bears serious disruptions to the body envelope (mortal injuries) provides important evidence that the individual is dead, and hence reduces anxieties that the individual may still be found in the landscape [57,58]. Conversely, viewing of a corpse that is intact may not diminish the vigilance of dead agents.

The mitigation of fear and revulsion will also play a major defining role, manifest, for example, in practices of ‘scapegoating’ (ritual murder to atone for deleterious events) as has been suggested for some Upper Palaeolithic burials [21]; mitigation activities such as the cannibalism discussed above (among the Rossel Island *Kula* groups, for example, death was traditionally associated with cannibalism, a victim procured by a ‘sorceror’ who was assumed to have been the cause of the death) [59]; noise to drive off evil spirits; placatory offerings to the dead and so on.

Thirdly, funerary rites are often about life. The living left behind after the death of a close one become ‘social and psychological amputee(s)’ [4]. Prolonged interaction with corpses may accelerate grieving processes, serving to reorganize society in the light of the deceased’s altered relationship with it [57]. Mitigating rites will, therefore, emphasize the natural order, particularly in terms of the creation and maintenance of life, reminding individuals of the social order and the distribution of power within it. ‘Rituals are invariably caught up in relations of power’ and indeed ‘may make a show of power’ [4, p. 6]. Formalized links between social concepts of time (one might say, *order*) and death are common to small-scale societies, and notions of fertility and sexuality are often prominent in funerary practices; killing is seen as a rite of fertility and renewal [23]. The mortuary rituals of the Massim (the area of the *Kula* cycle in Papua New Guinea) are as significant for the perpetuation of daily life as the *Kula* cycle itself [60].

The concept of transition may have been central to the cultural evolution of funerary activity. Hertz famously observed that many societies do not see death as instantaneous, but rather see it occurring typically through three stages, a departure from the living, a transition in which the body decomposes and the spirit wanders, and a final arrival at a destination [61]. He observed that the fate of the body reflected the fate of the soul; decay of the former paralleling the formless, repulsive, homeless and dreadful soul; essentially a dichotomy between a 'wet' (decaying) stage usually associated with anger, danger and disgust, and a succeeding dry (bones) phase, only with which did the spirit finally arrive at its destination [4]. Victor Turner [62] noted how many societies make associations between decomposition of the body, and rotting, fermentation and similar processes of transformation of foodstuffs.

Archaeologically, the key here is Hertz's concept that societies *represent* death by manipulating the body; 'there are two jobs to be done; on the one hand a disaggregation of the individual from the collectivity, and on the other the re-establishment of society requiring a reallocation of the roles the deceased once occupied' [4, p. 4]. Van Gennep observed that rites of passage, of which funerary activities are examples, are concerned with transitions from one state to another [63]; his tripartite division of these into sequential phases of separation, liminality and reintegration characterizes a remarkably widespread number of rituals. Secondary burial—the deposition of the dry bones—and the funerary rituals which accompany this last phase, is widely connected to the concept of sacrifice, in that objects must be destroyed in this world in order that they may pass to the next, whether this be through sudden sacrifice or slow decomposition. 'Grave goods' are often deposited for this reason. The presence (and occasional colouring) of isolated human bones in the Mid Upper Palaeolithic (Pavlovian and Sunghirian) approximately 30 000 years ago onwards suggests the retention of importance of human remains after initial defleshing, possibly the human equivalent of chimpanzee mothers curating their dead infants. Secondary burials accompanied by grave goods are known from the same time (e.g. a young adult male at Brno II, Czech Republic), revealing the presence of at least two stages of funerary ritual; the processing of body parts, including cannibalism and the production of skull cups, is well known in Late Upper Palaeolithic (Magdalenian) Central and Western Europe [3,64]. It is tempting to see the latter as an attempt to instigate or accelerate the 'wet' phase of death.

We should be careful not to equate the archaeologically 'rich' burials of the Mid and Late Upper Palaeolithic with socially complex societies *per se*; while this may have been the case (and there are many grounds to assume this was the case), there is no anthropologically observable rule that richly furnished burials should correlate with individuals of high status or complex social organization. The Late Pleistocene remains of a child, a juvenile and young adult in the Galeria da Cisterna cave, Portugal were associated with shell ornaments, for example [65], and the deliberate selection of specific sizes of shells for use as ornaments worn by the corpse of a child buried in the La Madeleine rockshelter, Dordogne, France, was used to distinguish it from the larger shells accompanying adult burials; clearly these symbolized social distinctions between children and adults [66]. Further distinctions between the ornaments worn by the dead, and probably the way they were worn, are observable within and between sites such as the Aven des Iboussières, France, and Arene Candide Cave, Italy [67].

The elaborate social activities that constitute the funerary rites of the Ndembu of Zambia, for example, are masked by the simple act of burning the deceased's hut down and burying them simply in their clothing [62], and with elaborate funerary practices that span a year and a half, the Kaduwagan of the Trobriand Islands practice only simple burial in the centre of the village [68]. Archaeologists are necessarily focused on 'grave goods', and indeed as a window on the social individual, infants and adolescents provisioned with thousands of personal ornaments and primitive valuables such as mammoth ivory jewellery (e.g. Sungir 2 and 3, Russia; La Madeleine, France) may indicate personal possessions from life and hence, status, but the presence of goods in a grave need not *per se*. Studies of grieving mothers in the modern world suggest that filling the grave with mementoes is, along with the importance mothers' quality time with their dying and dead infants, an important part of detachment [69] rather than a statement about status. Archaeologists also assume burial indicates a state of permanency, although it need not be. Among the Ma'anyan of Borneo, burial in graveyards is simply a form of temporary storage before the dead are processed and receive further treatment [4]. Burials in Upper Palaeolithic Europe are exceptionally rare and patchily distributed in time and space [70], and probably relate to special cases rather than reflect the funerary norm [3].

There are several indications that Upper Palaeolithic burials were created in the context of social complexity, reflecting wider cosmological beliefs. Mid Upper Palaeolithic burials are known from campsites in the open air in the Czech Republic and Russia, and in the caves of Italy [3,70]; clearly a distinction was at work. Burials in caves often reflect a desire for secrecy [4], and although examples from Mid Upper Palaeolithic Italy occur in the context of occupation debris it may be that a similar concern was operating, in contrast to the incorporation of the dead into camp sites elsewhere at this time. A set of parallels between the depositional contexts of mostly male Mid Upper Palaeolithic burials and female humanoid (venus) figurines suggests the embeddedness of funerary activity in cosmological belief [71], and in this sense, it seems sensible to conclude that we are by now dealing with concepts of an afterlife, i.e. 'personal, imagined journeys into the unknown' as Gamble [54, p.160] suggested.

The clue as to how such culturally embedded funerary behaviour became increasingly elaborated may lie in pathology and causes of death. Many societies conceive of deaths as either good or bad. Good deaths—those which occur in accord with the progression of order—are seen as evidence of mastery of the otherwise arbitrariness of nature; conversely, bad deaths reflect an absence of such control [23]. The obvious archaeological correlate is that the latter are often accorded funerary rites distinct from the 'norm', e.g. suicides and the executed. Death during childbirth, for example, can be the subject of particularly strong revulsion [4]. The appropriate questions to ask of early burials are whether they reflect 'good' deaths that were to some extent normal or expected (e.g. old age) or 'bad' deaths that were exceptional or unexpected (e.g. during childbirth, violence); whether the very act of burial, or the actions and/or material culture associated with it reflect the social order (e.g. status, gender, age); whether the dead can be assumed to have continued to function in social networks; and whether there is a supernatural element to any of this. One of the notable features of Upper Palaeolithic burials is the relatively high frequency of pathologies observable on the deceased which had not lead to their death [3,72,73]. Death of the mother and/or child during or shortly after childbirth must have been relatively common, and several Mid and Late Upper Palaeolithic burials reflect this, such as the double burial of two newborn infants under a mammoth scapula and a separate burial of a slightly older child without such covering at Krems-Wachtberg, Austria [74] and the burial of a young adult female with fetus at Ostuni, Italy [75]. A suite of disabilities is evident among the dominant burial class at this time (young adult male); clearly, physical diversity, including disability, was not an obstacle to individual survival into adulthood. The restricted number of burials known suggests that it played a role in the form of funerary practice—perhaps even determining those rare circumstances where burial was required—from approximately 30 000 years ago. Specific examples of other 'bad' deaths can be found, such as the young adult, 'Il Principe' buried in Arene Candide cave, Liguria, Italy, who came to a violent end [3]. The single burial of an adult male and double burial of late juvenile/early adolescents at Sungir, Russia, constitutes the most elaborated provisioned Pleistocene burials known [76–79]. Pathologies indicative of both inherited disabilities and violent death provide a link to the varying funerary practices evidenced at Sungir, suggesting that by this time, specific funerary practice was conducted according to the dictates of individual biography, irrespective of age [78].

Binford's analysis of recent hunter–gatherers' beliefs about deaths provides support for this apparent association of burials with 'bad' deaths in the Upper Palaeolithic. Although his suggestion [80] that the archaeologically observable complexity of mortuary activity should relate to social complexity has been criticized, as many examples can be found where this is patently not the case and comparatively high status individuals can receive relatively simple and material poor disposal [4], he was able to forward some generalizations about belief [81], and how these correlate with social complexity, concluding that the more complex the group, the more death is regarded as *natural* (i.e. inevitable, expected), *with the exception* of the young, and young adults, i.e. individuals who have just begun life, and those in their prime. These are regarded as unnatural (which we might call 'bad'), and in his anthropological examples, it is these that receive the most elaborate funerary treatment. No surprise that it is young adults, and deaths during childbirth or at young age that dominate the Upper Palaeolithic sample.

7. Conclusion: a research agenda for human evolutionary thanatology

I am aware that I have drawn widely from the ethological and anthropological realm in order to establish the beginnings of a hominoid and hominin thanatology that we might use to understand how a specifically human set of funerary behaviour arose from a primate and simpler set of mortuary behaviours. Palaeolithic archaeology should provide the only means of testing hypotheses about the growing elaboration of chemical and emotional responses to death through the processes of rationalization and enculturation. Given the renewed interest in undertaking in the insect and animal world [12], should we archaeologists not try to nuance our understanding of early human morbidity and necrology, asking questions of relevance not only to human evolution but to the wider animal kingdom? We have interpreted the Palaeolithic record in relatively simplistic terms, notably looking for evidence of burial, a practice that was in fact remarkably rare, even taking issues of taphonomy and sampling into account. We have also tended to exaggerate its importance; we would do well to remember that early observations of insect necrophoresis lead to the conclusion that ants worshipped their dead and created cemeteries for them [20]. Instead, we need to ask exactly why cannibalism, curation of corpses, disposal of them in areas of 'discard', or burial, and the persistence of such practices were important, and what purpose they served to their social groups. If there is one practice that *is* special, and apparently unique to later *Homo,* I would argue that it is not burial *per se,* but the cultural delineation of specific areas for the disposal of the dead; the creation of landscapes of the dead.

The repeated use of persistent places in the foraging landscape intensified after 300 000 years ago, suggesting that social meaning and memory now constituted where and why particular locales were used [82,83]. It may be no coincidence that this occurred broadly at the same time as developments in the mortuary realm from which funerary practices arose. The earliest appearance of necroclaustralization, in the form of burials from approximately 120 000 years ago, and potentially funerary caching from approximately 400 000 years ago, perhaps formed part of this general evolution of 'landscapes of the mind' among Neanderthal and early *H. sapiens* groups [82], reflecting the growing importance of particular places in the foraging landscape whose natural affordances provided repeatedly exploitable opportunities which were remembered and re-used, and in turn, became important in the structuring of social life [83]. Parsimoniously, early funerary practices could have become incorporated into such socially meaningful use of places; disposal of the dead would, in such circumstances, provide another means to enculturate the landscape and imbue it with social memory, contributing to the 'enhanced patina of extended social life' evident from the Late Middle Pleistocene [82, pp. 1450–1451]. The more persistent humans became in particular locales, the more vigilant their prey became and hence, more difficult to hunt [84], and hence, the more social integration would be necessary for their successful exploitation. One might, therefore, view the evolution of mortuary behaviour as an integral part of a 'feedback loop' of social evolution based on ever more sophisticated mental maps.

If this notion is correct, the evolution of funerary commemoration from a core of mortuary behaviours would proceed from a peripersonal containment of the body, through the persistent use of specific locales for such simple containments, to the incorporation of such locales with others in wider social landscapes; a landscape of the dead as an integral part of the landscape of the living. Might this be the human development of mortuary activity? Rather than focusing on a 'did they bury their dead or not' question, or a simple equation of 'burial' with 'symbolism', or a presumed importance of 'grave goods', we do need to move our research agenda on. Research priorities for human evolutionary thanatology, aimed at bridging the gap between mortuary behaviours evident among higher primates and other animals on the one hand and modern culture on the other, could seek to nuance and define exactly how funerary practices coincided with, and contributed to, the development of human social landscapes, as purely peripersonal behaviour increasingly took on extrapersonal forms. Specific research questions arising from this could include the following.

- What are the limiting factors of peripersonal (face-to-face) mortuary behaviours, and when did these begin to be complemented by extrapersonal elements? Can one discern what factors stimulated the development of scale of mortuary activity, e.g. can one demonstrate or eliminate the hypothesis suggested above which correlates with increasing group size and social complexity?
- How much coincidence between the social development of persistent places in the foraging and mortuary realm are observable? Did these evolve simultaneously, perhaps in response to similar stimuli? Or were they distinct? At what point did funerary commemoration become a distinct manifestation of remembrance?
- Did a phase of Middle Pleistocene funerary caching precede burial as the earliest archaeologically observable manifestation of extrapersonal mortuary activity, or was Late Middle Pleistocene/early Upper Pleistocene burial its first evidence?
- To what extent was the cultural elaboration of mortuary/funerary practices during the Upper Palaeolithic linked to wider developments such as social inequality and cosmological belief systems? Did status play any role at all in the variability of funerary practice? Is a distinction between 'good' and 'bad' deaths discernible in the archaeological record and if so, when and why did it emerge?
- Is it possible—and if so at what point—to recognize a belief system underpinning mortuary/funerary practices? If so, does this reflect a denial of/action against death? Is the belief system prosaic or cosmological?
- How did developments in the mortuary realm reflect those in other areas, e.g. art and ritual? Are these explicable as responses to the same stimuli?

Is it possible to address these with the existing archaeological record? I am aware that it is easy to advance questions, but in palaeoanthropology difficult to answer them. Nevertheless, it should be possible. There is clearly a need for fieldwork to focus on caves and rockshelters where multiple examples of burials are known, both for Neanderthals (e.g. Amud, Dederiyeh, Shanidar, La Ferrassie) and *H. sapiens* (e.g. Skhul, Qafzeh). Notable ongoing projects include the re-investigations of Shanidar Cave in Iraqi Kurdistan [42] and La Ferrassie in the Dordogne [85], wherein modern techniques of micro-excavation and micro-stratigraphic analysis, and post-excavation analysis are proving invaluable in determining the nature of their burials, the relative timing of their deposition (and hence, re-use of these locales for funerary purposes), their wider associations such as grave markings, and their wider behavioural context. Additionally, focusing from wider perspectives on when social attachment is extended to the dead [86] and on the social functions of mortuary activities should provide more fertile soil for a reborn field of human evolutionary thanatology.

Data accessibility. This article has no additional data.

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Endnote

[1] I have based this on *Collins English Dictionary online* definitions. Mortuary (adjective) related to death or burial, from Latin mortuarius: *of the dead*. Funerary (adjective) relating to, or for, a funeral, burial or cremation, from Latin funerarius: *of a funeral*. https://www.collinsdictionary.com/dictionary/english/mortuary. https://www.collinsdictionary.com/dictionary/english/funerary.

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Changing relationship between the dead and the living in Japanese prehistory

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Research

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The aim of this paper is to propose a new insight on the changing burial practice by regarding it as a part of the cognitive system for maintaining complex social relationships. Development of concentrated burials and their transformation in Japanese prehistory are examined to present a specific case of the changing relationship between the dead and the living to highlight the significance of the dead in sociocultural evolution. The essential feature of the burial practices observed at Jomon sites is the centrality of the dead and their continuous presence in the kinship system. The mortuary practices discussed in this paper represent a close relationship between the dead and the living in the non-hierarchical complex society, in which the dead were not detached from the society, but kept at its core, as a materialized reference of kin networks.

This article is part of the theme issue 'Evolutionary thanatology: impacts of the dead on the living in humans and other animals'.

1. Introduction

The strong, long-lasting connection with the dead is a part of human uniqueness, but its manifestation varies according to the sociocultural situation. Archaeological evidence provides us with fascinating insights on how our treatment of the dead changes through time. Although the earliest evidence of intentional burial dates back to the Palaeolithic period [1], the number and the variety of burials significantly increase with the transition to more sedentary lifestyles after the last Ice Age. The development of the cemetery has been explained from a functional point of view as a means to legitimize the rights of a corporate group over crucial but restricted resources [2–4]. Pettitt straightforwardly describes that, at the end of the Pleistocene, what we recognize as 'normal' ways of thinking of the dead arise from 'agricultural' thinking, and resulted in formal cemeteries as territorial markers [1]. While the functional model seems to explain the formation of formal cemeteries, the variability in mortuary practices and forms of burial, and how it changes through time, should give us more clues to understand the nature of the critical transition of our species from mobile foragers to sedentary farmers, and how our relationship with the dead played a part in the process.

The aim of this paper is to propose a new insight on the changing burial practice by regarding it as a part of the cognitive system for maintaining complex social relationships. It has been argued that the large volume of the neocortex of the human brain is related to social group size [5–7]. Kinship is at the core of collaboration and social networking in human societies, but the recognition of the kin network is cognitively a hard task, especially when it needs to extend back to the past. When the idea of descent is introduced to add a diachronic dimension to social network, the dead members of the society need to be remembered. While the use of linguistic categorization and heuristic mental frameworks is a human universal that makes it possible to recognize kin relations [8,9], it is not easy to keep track of the deceased ancestors more than three generations ago. Construction of cemeteries in particular manners could be a creation of external symbolic storage

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or material anchor of cognition to support the long-term memory of social networks [10–13].

Archaeologically, formal cemeteries can be recognized as exclusive areas for burying the dead apart from the areas for domestic activities. Before the establishment of such exclusive cemeteries, however, early evidence of concentrated burials showed they tended to be closely related to settlements. In the Late Natufian to the Pre-Pottery Neolithic period in the Near East, bodies were buried under the house floors and their heads were often removed for additional ceremonies and placed in a cache within the settlement. Such practices have been interpreted as an emergence of the ancestor cult, whether it incorporated an emergence of social hierarchy or rather worked as a ritualistic system to limit the development and centralization of power and authority in early agricultural communities [14]. The concept of ancestor may be too broad to be used as an effective analytical tool for investigating the emergence of religion or social structure, but it still is an important viewpoint as a uniquely human cognition of kinship including dead members of the society. The purpose of this article is to examine the emergent stage of concentrated burials and their transformation in Japanese prehistory, to present a specific case of the changing relationship between the dead and the living to highlight the significance of the dead in sociocultural evolution.

Jomon refers to the cultures characterized by hunter–gatherer subsistence and pottery production which developed on the Japanese archipelago following the Palaeolithic period and preceding the agricultural Yayoi period [15–17]. Jomon culture can be characterized by hunter–gatherer subsistence and pottery production, although marked temporal and spatial variability is seen over more than 10 000 years [18] (table 1). While pottery appears as early as 15 000 calibrated before present (Cal BP), sedentary lifestyle develops only after the end of the Ice Age. During the Incipient and Initial Jomon periods, substantial settlements are rare, suggesting that mobile foraging lifestyles were dominant. It is when large settlements appear in the Early Jomon period that interesting relationships between the dead and the living can be visible in the layout of burials.

Table 1. Approximate dates (calibrated BP) for the six Jomon sub-periods.

sub-period	approximate age (cal. BP)
Final Jomon	3300–2800/2300
Late Jomon	4400–3300
Middle Jomon	5400–4400
Early Jomon	7000–5400
Initial Jomon	11 000–7000
Incipient Jomon	15 000–11 000

2. Living with the dead: burials at the centre of social construction

The essential feature of the burial practices observed at Jomon sites is the centrality of the dead and their continuous presence in the kinship system (figure 1). The feature is clearly recognizable at a number of ‘circular settlements’ that first appeared in eastern Japan during the latter half of the Early Jomon period and proliferated in the Middle Jomon period in the eastern part of the main island of Japan (figure 2). Circular settlements are large settlements with a circular layout of structures such as burials, storage pits, buildings and pit houses. The centre of a circular settlement is often found with no structures other than burials, encircled by residential space with pit houses and buildings. The size of the settlement varies from the largest ones about 150 m in diameter to the smallest about 70 m in diameter. More than 20 large circular settlement sites have been discovered in the Kanto and Chubu regions [19].

Large circular settlements with hundreds of structures are formed over a few hundred years as a result of repeated construction of burials and houses according to specific spatial rules. According to Taniguchi’s analysis using a Thiessen polygon method, large circular settlements in the Middle Jomon period are distributed evenly with a territory of about 54 km^2 each on average in the southwestern part of the Kanto region. The estimated size of the territories indicates that each Jomon group which left a circular settlement maintained a stable territory in the densely populated condition [20]. Close examination of the formation process of circular settlements revealed that the ‘circle’ is actually formed by two segments, each of which often consists of several subdivisions. It is highly probable that the layout of structures is defined by the kinship system with dual organization [19,21].

The strict rule governing people’s decisions on where to build a house and where to bury the dead is obvious in a number of circular settlement sites that have been fully excavated. The Nishida site in Iwate Prefecture is one of the most typical examples (figure 2). Dual structure is not clear in the overall layout of the structures, but two rows of 14 burial pits at the centre indicate a dual organization. The importance of the centre is evident in the radial alignment of all the burial pits and buildings around them. In the neatly aligned concentric spatial planning, the dead members of the society occupy the centre, surrounded by dug-standing pillar buildings, pit houses and storage pits. The burial pits seem to consist of eight groups, each of which may be divided into two. The subgroups of burials seem to correspond with the groupings of buildings on the outer side of the settlement [22].

Although bones are not preserved owing to the acidic nature of the soil, it has been assumed that the dead were placed in the grave with their head towards the outside of the settlement based on the slight inclination of the base of each burial pit, except for those in the central two rows whose heads were pointed towards the centre [22]. Conscious placement of the dead is similarly recognized at the Sannai Maruyama site in Aomori Prefecture. Although it is not a circular settlement, the Sannai Maruyama is one of the largest settlements in the Jomon period, occupied from the Early to the Middle Jomon period. At the site, infants were buried inside the settlement, but adults were buried on both sides of the road connected to the settlement. The inclination of the base of burial pits indicates that the heads of the interred individuals were pointed away from the road, so that the dead could look at the people coming into or going out of the settlement [23].

While the radial alignment is a unique feature of the Nishida site, (i) concentric distribution of different kinds of

Figure 1. The location of sites mentioned in the text.

structures with an open space or burials at the centre, and (ii) dual organization with subdivisions, are shared by many other circular settlements such as the Saikaibuchi site in Yamagata Prefecture, the Idaira site in Nagano Prefecture and the Kazahari 1 site in Aomori Prefecture. Based upon pottery chronology and associated radiocarbon dating, we know that these large circular settlements had been occupied for 200 to 300 years. Although houses and burials accumulated over a long period of time, it is evident that the basic spatial plan was set from the beginning of each settlement, and maintained through more than ten generations in some cases.

According to Koyama's population estimates based on the number of discovered sites, the population on the Japanese archipelago peaked during the Middle Jomon period [24,25]. It should be noted that circular settlements were formed in the most densely populated areas and period of Jomon.

3. Burials as a focus of ritualistic activities apart from settlements

At the end of the Middle Jomon, almost all large settlements were abandoned in eastern Japan, clearly suggesting a catastrophic social situation [18]. The relationship with dead ancestors changes its nature over the social fluctuation. Burials of ancestors were detached from settlements and established as large stone circles in northern Tohoku and Hokkaido regions in the Late Jomon period. While there are considerable variations in the form of such monumental sites, it has been recognized that features of settlements or houses in the previous period are inherited in their form.

The Oyu site in Akita Prefecture shows a striking similarity with circular settlements, although ritualistic aspects are more emphasized (figure 3). There are two large stone circles of almost identical size and structure about 130 m apart from each other. The two circles are named Manza and Nonakado stone circles, respectively. The diameter of the Manza stone circle, which is slightly bigger than Nonakado, is 46 m. Each stone circle consists of two concentric rings of stone alignments, each of which comprises a number of small stone clusters which are considered as burial markers. The two stone circles are aligned to the direction of either summer solstice sunset or winter solstice sunrise. There is no doubt that they were conscious about this astronomical alignment, as a 'sundial'-type stone cluster is set in both Manza and Nonakado stone circles between the outer and inner rings on the line that passes through the centre of the two stone circles.

Figure 2. Feature distribution at the Middle Jomon Nishida site, Iwate Prefecture (adapted from Kobayashi [42, fig. 29]. Different shades of the burial pits represent estimated grouping.

Based on the pottery chronology and stratigraphic information, the two large stone circles of Manza and Nonakado are considered to have been constructed around the same time in the early Late Jomon [26]. Although the dual structure is not clear in the distribution of small stone clusters at each stone circle, the construction of the two identical stone circles probably indicates that the representation of dual organization has become more intense. Several circular stone alignments in the north of the Manza stone circle are later additions in the middle Late Jomon period.

Although bones are not preserved at the Oyu site, excavations have found pits under the stone clusters that can be identified as burial pits. We can recognize both crowded and scarce parts in the distribution of small stone clusters in the ring. Such uneven distribution is similar to that of burial pits in circular settlements, and can be understood as a result of a strict rule of where to bury a person according to descent. While the concentric structure of the Oyu site is similar to that of the Nishida site in that burial place is encircled by the buildings, only five pit houses have been found from around the stone circles, suggesting that the site was not a part of sedentary settlement. After large settlements were abandoned at the end of the Middle Jomon period, people split into small groups and adopted mobile foraging lifestyles. The astronomical alignment of the structure may suggest that the site was a meeting place for the scattered groups that were connected through kinship to conduct rituals associated with the dead ancestors annually, possibly around the summer solstice [21].

4. Collective secondary burials as a symbol of social integration

Another direction of the transformation of mortuary practice is recognized in the formation of collective secondary burials in the Kanto region. Twelve cases have been found from eight shell midden sites. The construction of the collective secondary burials belongs to the early phase of the Late Jomon period, and can be situated at the starting period of a new settlement in each place [27,28]. As in the Tohoku region, large settlements that developed in the Middle Jomon period were mostly abandoned in the Kanto region by the end of the Middle Jomon, and their residents are considered to have adopted a more mobile life in small groups. Large settlements were newly established during the early Late Jomon period by reorganization of the once scattered small groups [29]. Most of the examples of collected secondary burials contain the bones of 5 to 18 individuals. The collected secondary burials are usually placed at the central position in a cemetery. Some cases are accompanied with post holes around them, suggesting that they were marked by roofed structures [27], and that the collected burial had a symbolic significance for the group.

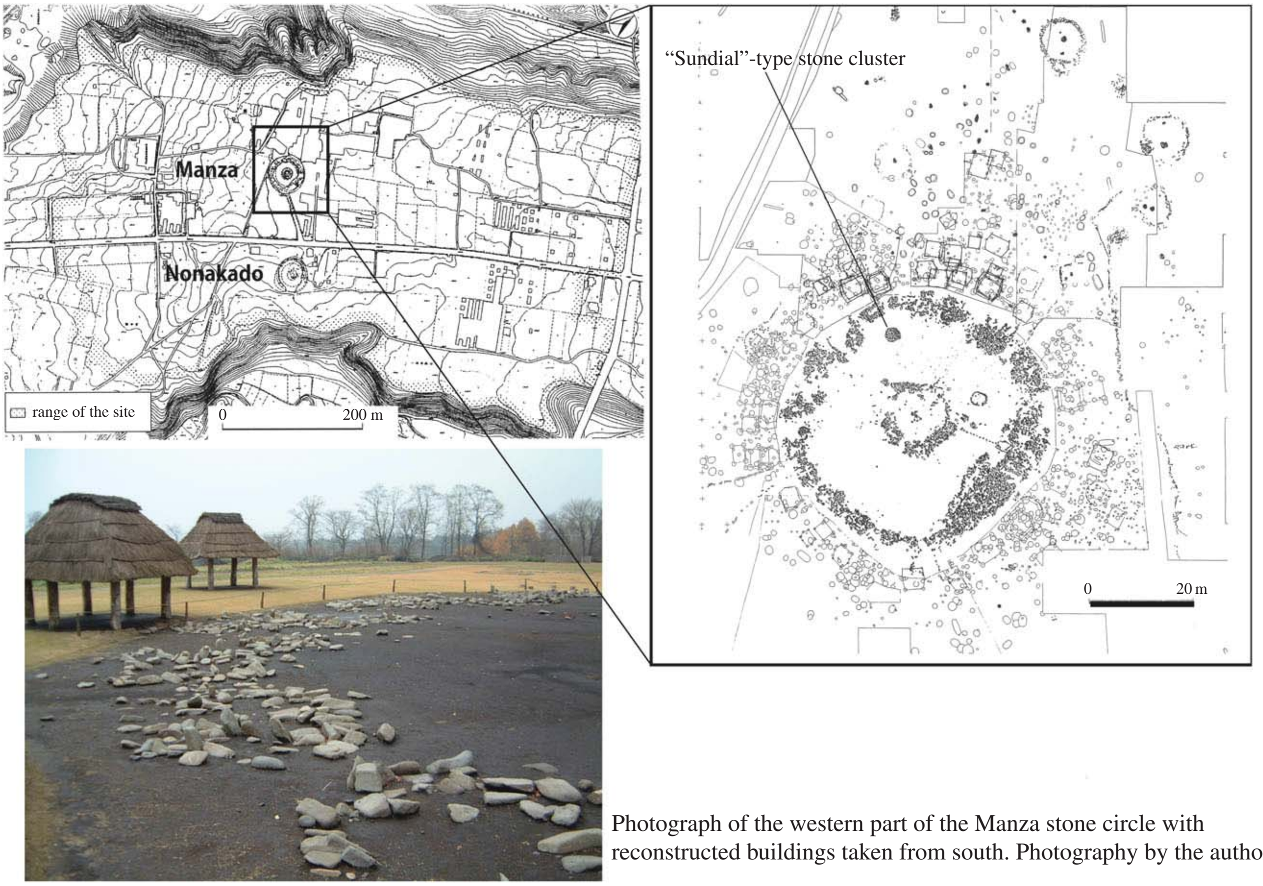
The most striking example of the collected secondary burials is pit A at the Nakazuma shell midden in Ibaraki Prefecture, which contained the bones of more than 100 individuals [30]. In a pit 2 m in diameter and 1.2 m in depth, long bones and skulls were carefully aligned in three or four layers (figure 4). As some of the skulls are accompanied by mandibles while others are not, we can assume that the period between death and the construction of the collected burial varied. The bones show little damage, which could be caused by the process of exhumation prior to reburial, suggesting that those who conducted the ritualistic reburial knew the exact place of the first inhumation, and probably who was buried where. Morphological analysis of the teeth and mitochondrial DNA analysis were conducted on the well-preserved bones of 29 individuals to show that 17 out of the 29 shared a common haplotype, indicating that the ancestors selected for reburial were selected by matrilineal descent [31,32]. Based on the evidence, we can infer that the Jomon people were conscious about where to bury their ancestors even after they abandoned the sedentary settlements at the end of the Middle Jomon period, and that information was transmitted across generations until they established a new settlement. Based on the pottery chronology, most settlements were abandoned in the Kasori E3 phase (4730–4540 Cal BP), followed by the Kasori E4 (4540–4490 Cal BP) and the Shomyoji phases (4490–4235 Cal BP) during which a number of short-lived settlements appeared. In the next Horinouchi phase (4235–3900 Cal BP), further relocation of settlements occurred while a small number of the existing settlements continued to develop [29]. Considering that most of the collective secondary burials appear in the Horinouchi phase, the period between the end of large settlements in the late Middle Jomon and the construction of collective burials in the early Late Jomon is estimated to be more than 200 years [33].

5. Discussion

In the examinations above, I focused on the three patterns of burial practices in the Jomon period. The first is the formation of a cemetery at the centre of the settlement when population and the level of sedentism significantly increased in the Middle Jomon period. The second and the third patterns emerged in the Late Jomon period after the catastrophic socio-demographic change at the end of the Middle Jomon period. The second is the construction of stone circles in the Tohoku region, which can be understood as a development of the central burial place of a circular settlement. The third is the construction of collective secondary burials in the Kanto region at the early stage of newly established settlements.

From the functional point of view, the first pattern fits into the scheme of ‘agricultural’ thinking, in that people were certainly concerned about their territories. Although the basic subsistence in the Jomon period was hunting, gathering and fishing, recent analysis of the impressions on the pottery revealed that cultivation of soybeans (*Glycine*) and azuki (*Vigna*) beans started in the Early Jomon and developed at least in the Chubu Mountain region during the Middle Jomon period [34]. The term ‘forest-based Neolithic’ has been coined to represent the Jomon societies in which intensive production of pottery and development of ground stone tools for plant food processing are observed [35]. It may be interpreted from a structural point of view that the domestic aspect became important when people were trying to build a new relationship with plants and animals, and this resulted in the incorporation of death in the realm of domus in order to evade its danger [36]. Apart from these frameworks, however, I want to focus on the importance of burial practice as a part of the cognitive system, especially as an external mnemonic system for long-term memory of social networks. In preliterate societies, keeping memory of kinship relationships for more than three generations is not easy, because direct contact with deceased ancestors is impossible. Therefore, a systematically organized cemetery should be a good reference.

An important point to note concerning the cemetery in a circular settlement is that the burials did not just accumulate near domestic space as a result of inadvertent repetition of



Photograph of the western part of the Manza stone circle with reconstructed buildings taken from south. Photography by the author.

Figure 3. The Late Jomon Oyu stone circles, Akita Prefecture (adapted from Akimoto [26] and Kazuno City Board of Education [43]).

burying the dead near residential places, but the alignments of burials, as well as that of the houses and other structures, were planned at the beginning of each settlement. The settlement and cemetery consist of a whole artificial environment that works as an efficient mnemonic system. As written information such as an inscription on a tombstone was not available, memory about who was buried where must have been activated frequently enough. Being both a living place and symbolic monument at the same time, a circular settlement could always revive and confirm the memory of ancestors in the residents.

Other differences such as gender and social statuses are not clearly represented in the mortuary practice. Burial goods are rare all through the Jomon period, and circular settlements are no exception. One jadeite pendant is the only burial good found from the Nishida site. No significant difference in the size and shape of burial pits can be recognized, either. It is probable to assume certain social differences between those who led the construction of large stone circles and the other members of the society who took part in the rituals performed there, but individual difference is not obvious in the attributes of burials. While it has been proposed that the Late and Final Jomon can be categorized as a transegalitarian society [37–39], social attributes other than descent are not clearly displayed at circular settlements in the Middle Jomon period. This is also true of the Oyu stone circles and the collective secondary burial at the Nakazuma shell midden in the Late Jomon period.

The difference between the second and the third patterns may reflect the difference in social strategy of the groups in the Tohoku and Kanto regions. People who built the stone circles tried to maintain the rigid kinship structure for social integration. At the Oyu site, as in the circular settlements, people do not lose their position in the society after death. They virtually remain a member of the society by physically occupying the designated place in the site. The groups in the Kanto region, on the other hand, intended to dissolve, or actively reorganize, the kin relations by putting the bones of ancestors together in the same pit. Collective secondary burials in the Late Jomon period such as that at the Nakazuma shell midden show the continuing importance of the bodies of the ancestors, but the position of each ancestor in the kinship structure is not clearly maintained anymore. This change may suggest that quasi-kin networks started to be emphasized when strict kin networks became ineffective owing to the shrinking population [40]. Prolonged consciousness of the bodies of the dead also seems to become weaker compared with the situation in the Middle Jomon. We may be able to see the emergence of a more abstract or collective concept of ancestors in this case.

Another characteristic point that is common to all three patterns is the prolonged consciousness about the bodies of the dead, even after they are buried and rot away under the ground. Careful arrangement of the bodies according to the rules shared by community members and transmitted across generations indicates that those who lived in the settlement could easily remember, or visualize in their mind, the exact place and position of each ancestor.

It should be noted that only a few outstanding sites are examined here out of a vast variation of mortuary sites of the Jomon period [15,16,41]. The selected sites, however, are not just extraordinary but rather typical examples of a

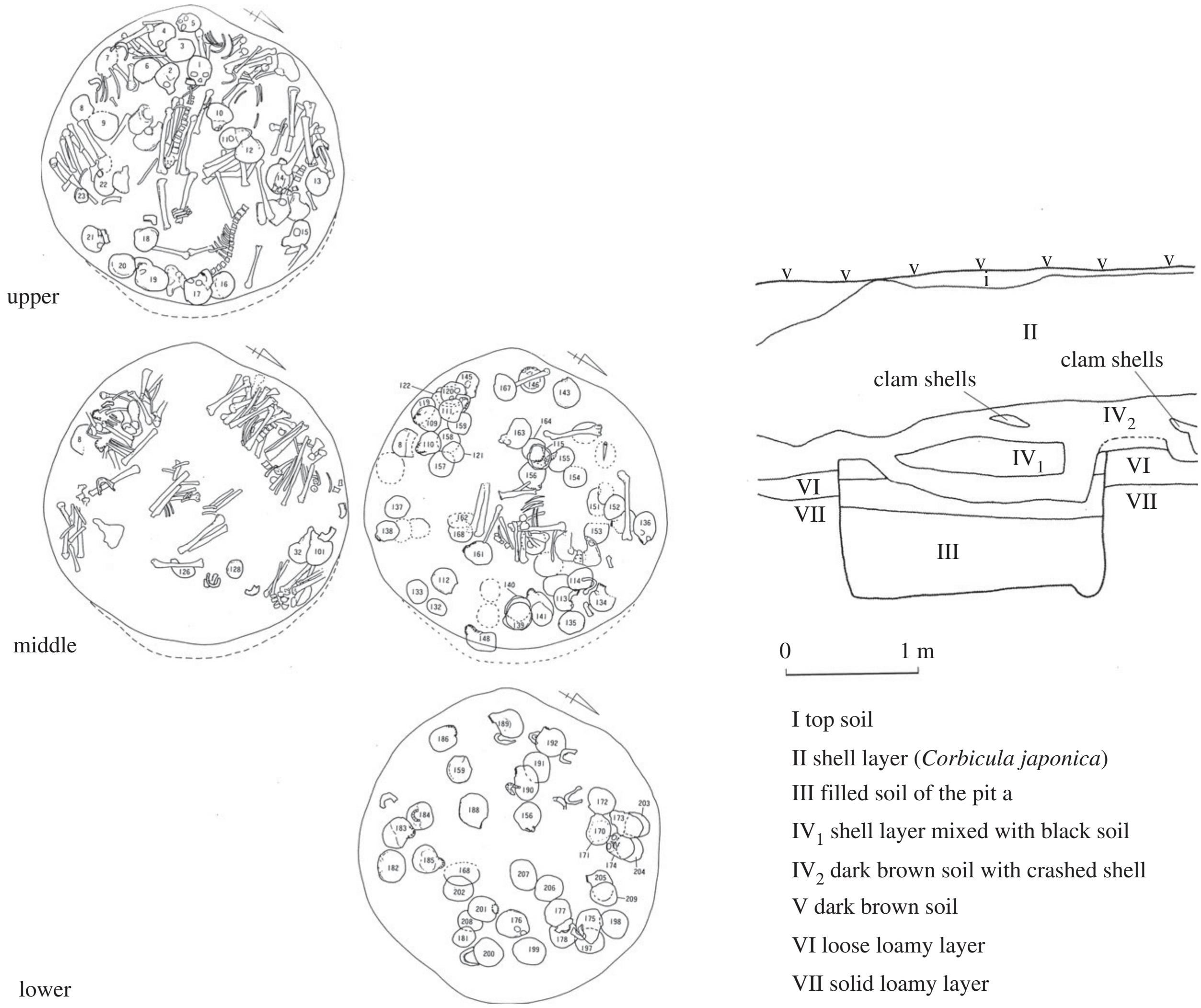


Figure 4. Collective secondary burial at the Late Jomon Nakazuma shell midden, Ibaraki Prefecture (adapted from Nakazuma kaizuka hakkutsu chosadan [30]).

widely shared cognitive tendency in the Jomon societies: a continuous existence of the dead in the social cognition of the living members of the society. The mortuary practices discussed in this paper represent a close relationship between the dead and the living in a non-hierarchical complex society, in which the dead were not detached from the society, but kept at its core, as a materialized reference of kin networks.

Data accessibility. This article has no additional data.

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Children's understanding of death: from biology to religion

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Young children construct a biological conception of death, recognizing that death terminates mental and bodily processes. Despite this recognition, many children are receptive to an alternative conception of death, which affirms that the deceased has an afterlife elsewhere. A plausible interpretation of children's receptivity to this alternative conception is that human beings, including young children, are naturally disposed to remember and keep in mind individuals to whom they are attached even when those individuals leave and are absent for extended periods. This disposition is reflected in the pervasive tendency to talk about death as a departure rather than a terminus. It also enables the living to sustain their ties to the dead, even if, in the case of death, the departure is permanent rather than temporary. Linguistic and developmental evidence for these claims is reviewed. Possible biological origins and implications for archaeological research are also discussed.

This article is part of the theme issue 'Evolutionary thanatology: impacts of the dead on the living in humans and other animals'.

1. Introduction

Psychological research on children's conception of death has focused on their emerging grasp of the biological nature of death, but more recently attention has also been paid to the way that many children and adults entertain an alternative conception. Despite acknowledging the termination of bodily and mental functions at death, they come to believe in some form of afterlife. I seek to explain humans' receptivity to that belief, especially given its apparently counterintuitive status. I argue that afterlife beliefs are supported by a wide-ranging human disposition to feel connected to, think about and talk about attachment figures, despite their physical absence.

2. Two conceptions of death

As they get older, children growing up in a variety of cultures realize that death inevitably comes to all living creatures and is an irreversible transformation [1]. The exact age at which they realize those biological facts varies but, barring cognitive pathology [2], children typically attain those insights by 10 years of age [3]. More recent research has focused on how children conceive the sequelae of death. I argue that many children, and adults, are inclined to adopt two parallel conceptions of death—a biological conception in which they think of the deceased as a dead corpse and an afterlife, or religious, conception in which they think of the deceased as someone who has departed this life but lives on elsewhere in some form.

Initial evidence for these parallel views was obtained by Harris & Giménez [4]. They presented 24 7-year-olds and 24 10-year-olds growing up in Madrid with two narratives about the death of a grandparent. In one narrative, the death was presented in a biomedical context. Thus, following the death of the grandparent, a doctor explained to a grandchild what had happened: 'Your grandfather is dead now'. In an otherwise similar narrative, also involving the death of a grandparent, the death was presented in an afterlife context. Following the death of the grandparent, a priest rather than a doctor explained to a grandchild what had

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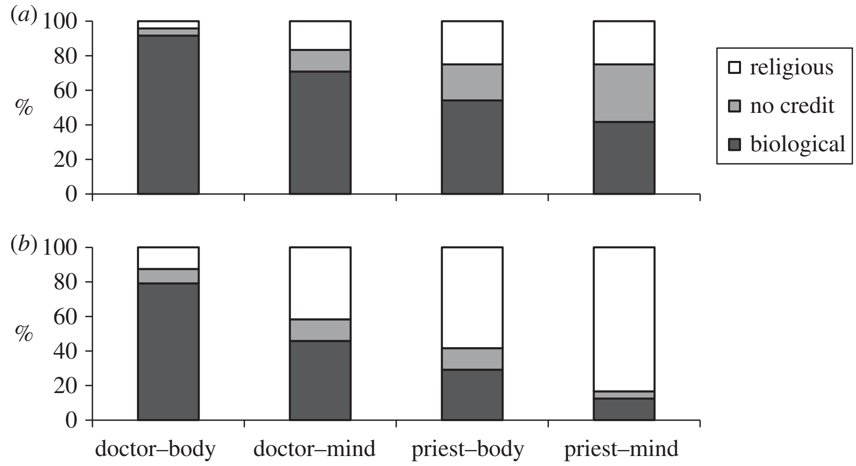

Figure 1. Percentage of younger children (*a*) and older children (*b*) credited with a religious stance, a biological stance or given no credit in response to four probes, based on Harris [3].

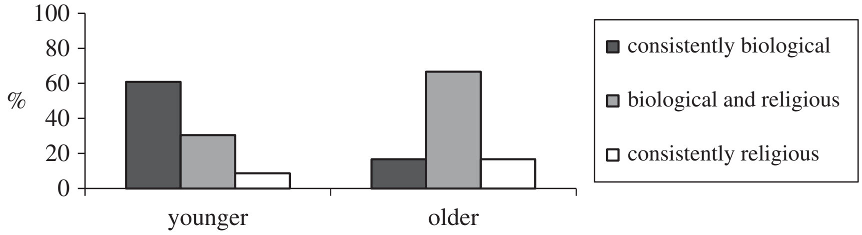

Figure 2. Percentage of 7- and 11-year-olds showing three patterns of responding across four probes, based on Harris [3].

happened: 'Your grandmother is with God now'. After answering questions about the continuation or cessation of particular bodily and mental processes, children were also asked two more generic questions: to say whether the body and the mind of the dead grandparent still functioned—or had ceased to function—and in either case, to explain their conclusion. These two generic questions were asked in the context of both the doctor and the priest narrative, yielding a total of four such probes.

When children claimed that either the body or the mind had ceased to function and went on to explain that cessation in biological terms (e.g. 'He has been eaten by worms; he has no body. He just has bones'; 'If he is dead, nothing can work'), they were credited with a biological stance. By contrast, when they claimed that the body or mind continued to function and went on to explain that continuation in religious terms (e.g. 'In Heaven everything can work even if she is dead'; 'The soul keeps working'), they were credited with a religious or afterlife stance. Finally, when children failed to offer an explanation for their claim regarding cessation or continuity, or offered an explanation that did not cohere with that claim, they were given no credit for either stance. Figure 1 shows for each of the four probes the percentage of 7-year-olds (*a*) and 11-year-olds (*b*) credited with a biological stance, a religious stance or given no credit.

Inspection of figure 1 shows that, as expected on the basis of statistical analyses of children's replies to the questions about cessation versus continuity of function after death as well as their explanations [4], both age groups were influenced by the narrative context. They were more likely to adopt a biological stance for the two doctor probes than for the two priest probes. Conversely, they were more likely to adopt a religious stance for two priest probes than for the two doctor probes. In addition, the religious stance increased between 7 and 11 years, whereas the biological stance declined. One possible interpretation of this age change is that the religious stance increasingly displaces the biological stance. However, even among the 11-year-olds, the religious stance was not overwhelmingly adopted. For example, when asked to think about the functioning of the body in the context of the doctor narrative, most 11-year-olds adopted a biological stance. A different interpretation of the age change is that children do increasingly adopt a religious stance but in parallel with a biological stance. To assess this possibility more directly, Harris & Giménez [4] looked at the consistency of children's replies across the four probes. Individual children were assigned to one of the three categories depending on the pattern of their answers across the four probes: (i) consistently gave biological replies; (ii) gave a mix of biological and religious replies; or (iii) consistently gave religious replies. Figure 2 shows the percentage of 7- and 11-year-olds falling into each of these three patterns of responding.

Figure 2 shows that the majority of 7-year-olds gave consistently biological replies, whereas the majority of 11-year-olds gave a mix of biological and religious replies. By implication, children do not abandon the biological stance as they get older. Instead, they increasingly adopt the religious stance alongside the biological stance.

The study conducted by Harris & Giménez [4] was based on children growing up in a distinctive and relatively homogeneous culture, notably Catholic Spain. Arguably, the tendency to adopt two distinct ways of thinking about death is restricted to communities with a commitment to Catholicism or to Christianity. The tendency to adopt the two stances might also diminish or disappear if children strive for greater consistency as they get older. Subsequent findings cast doubt on both of these arguments. They show that the tendency to adopt a dual stance towards death is not confined to Christian cultures and persists into adulthood. Astuti & Harris [5] conducted a study with children and adults of the Vezo community in Madagascar. As in Spain, participants listened to two narratives about death. One involved a death in a biomedical context, whereas the other included cues to the ancestral afterlife. (Note that the Vezo believe that the dead take up a new form of life among the ancestors, from where they are able to influence the lives of the living.) Following each narrative, participants were presented with questions about the impact of death on the cessation or continuity of bodily and mental processes. The pattern of responding echoed that found in Spain. Participants were more likely to argue for the cessation of living processes following the biomedical narrative as opposed to the afterlife narrative. Indeed, in the biomedical context, a substantial minority of children and adults argued consistently for the cessation of all living processes. Nevertheless, the majority made claims of both cessation and continuity. This mixed response pattern was especially frequent in the afterlife context.

A possible interpretation of such mixed responding is that participants subscribe to a form of dualism. They think of the body in biological terms, emphasizing its cessation of function at death, whereas they think of the mind in religious terms, emphasizing its continuity of function. However, this account offers no explanation for the pervasive impact of narrative. Inspection of figure 1, for example, reveals that the type of narrative impacted children's replies whether they were questioned about the body or the mind.

More recent findings confirm that many participants display both a biological and a religious stance not just when they think about the body compared with the mind but also when they think about various different bodily processes or about various different mental processes. Watson-Jones *et al.* [6] compared beliefs about death among children and adults in the city of Austin, Texas, with those of children and adults in the city of Lenakel, on the island of Tanna, part of the Melanesian archipelago of Vanuatu. As in the studies in Spain and Madagascar, participants were primed with a narrative about death that provided either a biomedical context or an afterlife context. Following each narrative, participants were asked questions about various biological processes (e.g. 'Do his eyes work or not?'; 'Does his heart beat or not?') as well as various psychological processes (e.g. 'Does he see things or not?'; 'Does he miss his children or not?') and to explain their claim of cessation or continuity for each process. In line with the findings in Spain and Madagascar, the stance that participants adopted was influenced by the narrative. They produced more cessation claims and more biological explanations following the biomedical narrative compared with the afterlife narrative. Conversely, they produced more continuity claims and more religious explanations following the afterlife narrative compared with the biomedical narrative. Nevertheless, participants drew on both types of explanation when explaining the fate of particular psychological processes or when explaining the fate of particular bodily processes. Thus, the tendency to adopt a biological or a religious stance cannot be ascribed to a dualistic division between body and mind. It is found when participants think about each component of dualism—the body and the mind.

Finally, it is important to note that although evidence for the adoption of both a biological and a religious stance towards death has come from diverse cultures, this conception is unlikely to be universal. In communities where the surrounding culture provides little or no support for afterlife beliefs, it is likely that children and adults will adopt a predominantly biological stance, irrespective of the narrative context. Indeed, in a cross-national study, Lane *et al*. [7] found an effect of narrative on judgements of continuity versus cessation among participants in the USA but not in China.

Summing up across these various studies, they confirm that, depending on the surrounding culture, children and adults will often come to entertain two parallel stances towards death, a biological stance and an afterlife or religious stance. The narrative context in which a death is described and the type of process that participants are asked to think about (bodily processes versus mental processes) affect the probability of their adopting one stance rather than the other. Nevertheless, participants are prone to draw on both within a given narrative context and even for different processes of the same type. They readily recruit, and switch between, the two stances.

3. Missing persons

The findings described so far can be interpreted in terms of the following framework. In the course of childhood, children arrive at an understanding of the biological nature of death. They come to realize that, when someone dies, a living person turns into an insensate and unresponsive corpse that will decay and be disposed of. At the same time, children have the ability to think of deceased individuals as continuing to exist in some form. As noted by several authors [8–10], thinking about a deceased person is, in key respects, akin to thinking about a living person who has left for an extended period of time. Indeed, from an early age, children's social and emotional life is predicated on their ability to mentally represent the continued existence of various attachment figures (i.e. carers, siblings and friends)—despite their prolonged physical absence. This ability to represent absent persons presumably means that children are receptive to claims that, no matter what the fate of the corpse, the deceased person continues to exist elsewhere. The exact nature of that existence and of that elsewhere may be ultimately unknowable but when supplied with relevant testimony by the surrounding culture, children will be led to construct a suitable mental representation, just as they might do for a country they have never visited or a phenomenon they have never observed [11].

Children have the ability to represent absent persons before they have a comprehensive understanding of the biological inevitability and finality of death. Thus, even toddlers can think and talk about an absent attachment figure or anticipate a future reunion [12]. Children's emerging understanding of death confronts them with the fact that a separation brought about by death, unlike everyday separations, will be permanent rather than temporary. Yet children's continuing representation of the deceased is likely to be based on their memory of interactions with the living person—what Boyer [13] describes as the person-file system—and not just on their memory or representation of the insensate corpse. When children receive testimony about the afterlife, they are effectively offered further support for their representation of the 'living person' as existing elsewhere. He or she has departed this world for the afterlife, be it with God, in the Kingdom of Heaven, or among the Ancestors.

This account explains why many children and adults shift back and forth between two different but parallel stances towards death. They can adopt a biological stance towards the dead corpse—it no longer functions and will decay but, concurrently, they can also adopt an afterlife stance towards the absent person. He or she is assumed to exercise various mental and bodily powers, commensurate with local, cultural beliefs about the nature of that afterlife.[1]

In the sections below, I explore several implications of this account. First, if death is seen as a departure and not just as a biological terminus, this should be reflected in the euphemistic metaphors adopted in everyday talk about death. Second, the bereaved, including children, should voice their continuing psychological ties to the dead person even while recognizing that the separation that death entails is permanent. Third, the conception of death observed in humans invites two interrelated questions about the conception of death displayed by non-human primates. First, do non-human primates arrive at a piecemeal, empirically based understanding of death or the more comprehensive grasp of total cessation found among children? Second, if non-human primates display behaviours akin to human grief—especially immediately after the death of an individual to whom they were attached—what is the cognitive basis for that grief? Finally, if ideas about the afterlife are founded on the cognitive disposition to keep the deceased in mind despite their permanent absence, is that disposition also manifested in the increasing prevalence of burial sites in the course of human—and Neanderthal—history?

4. Metaphorical talk about death

If death is readily conceptualized in terms of a departure that ends our contact with the deceased, we may expect to find that departure implicated in the metaphors used to talk about death. Indeed, Lakoff & Turner [14] note that references to death as departure are common in English, fitting into a broader cognitive scheme in which life is conceived as a journey where birth is arrival, life is being present here and death is departure (e.g. 'She passed away', 'He's gone', 'She's left us', 'He's no longer with us', 'She's been taken from us'). Death is often viewed as the crossing of a threshold. A dying person is described as 'slipping away'; a surgeon may 'bring him back' or 'lose him'. Crossing that threshold implies that the deceased has left for another destination. He or she has 'gone to a better place', 'gone to Heaven', 'gone to meet their Maker' or 'to join the Ancestors'. When the focus is not on the deceased but on the bereaved, they are described as 'left behind' and their experience is described in terms of a rupture in contact with the deceased, as in 'they lost their father'. Funereal rituals are represented as a leave-taking, an opportunity for the bereaved to say a 'last goodbye'.

The examples of metaphorical language described by Lakoff & Turner [14] are taken from English, including English poetry. However, subsequent analyses of a variety of other languages have confirmed that the metaphor of death as departure is found in Polish [15], Serbian [16], Spanish [17], Turkish [18], EkeGusii, a Bantu language of Western Kenya [19], Paiwan and Seediq, two Formosan languages and Mandarin [20]. It is unclear whether the metaphor is universal but evidently it is found in several unrelated languages.

Metaphorical talk about death might be restricted to adults. However, if Lakoff & Turner [14] are right in claiming that the metaphor of death as a departure is based on a relatively basic conceptual schema of life as a journey through the world with a final departure, we might also expect children to use that same metaphor. Silverman *et al*. [21] report findings supporting this speculation. They interviewed 125 children ranging from 6 to 17 years ($M = 11.6$ years) at four months, 1 year and 2 years after the death of a parent. Silverman *et al*. [21] focus on the content of children's replies, not on their use of metaphor. Nevertheless, the death as departure metaphor does appear in the answers that they quote, for example: '... I go to sleep fast so I won't think about his being gone' (7-year-old); 'He's not with me, and it hurts' (10-year-old); '... however, I don't want her to come back and be in such pain' (12-year-old).

5. Continuing ties to the dead

Traditionally, post-Freudian clinical analyses of grief have implied that it involves the 'work' of detachment. However, later empirical research has shown that grief is often accompanied by strategies that maintain rather than sever a psychological tie to the deceased. In an influential study of widows (age range = 25–65 years) interviewed several times in the first year of their bereavement, Parkes [22] reported that in the first month, all the widows were preoccupied with thoughts of their dead husband and after a year, such preoccupation was still evident in the majority (68%). In the first month, most widows (73%) reported memories involving clear visualizations of their dead husband as he had been when he was alive and most (81%) continued to do so after a year. Indeed, most widows (73%) had a sense of their husband being near them during the first month and just over half (55%) continued to have that sense one year later. Not surprisingly, over the course of this first year of bereavement, there was a strong correlation among these three measures of a continuing psychological connection to the dead husband. Indeed, nearly half the widows engaged in activities likely to stir or sustain such connections. Most (86%) treasured objects associated with their husbands even if many also avoided certain items such as clothing or photographs for fear of provoking pangs of grief. Nearly half re-visited old haunts or returned to the cemetery or the hospital. Similar findings emerged in a study of young widows (under 45 years) in Boston [23]. One year after their bereavement, two-thirds reported that they continued to think of their husband 'often' or 'a lot'. Many had the feeling that their husband was watching over them and reported deliberately invoking his presence when they were feeling depressed or unsure.

Reviewing these findings, Bowlby [24] proposed that an initial period of preoccupation and turmoil often gives way, not to detachment, but to the more comforting sense of a continuing psychological tie to the deceased. Recent longitudinal research has confirmed this pattern of sustained connection. In a large-scale study of widowhood, the majority of bereaved spouses reported thinking about their partner 'daily or almost daily' when interviewed six months after the loss. When re-interviewed 18 months after the loss, most reported thinking less often about their partner but they still did so 'two or three times a week' if not daily. At both time points, most spouses affirmed that thoughts and memories of their deceased partner had made them feel happy or at peace during the preceding months [25].

Do bereaved children also display a continuing psychological tie to dead attachment figures? Silverman and co-workers [21,26] interviewed bereaved children in the USA four months after the death of a parent. They found that most children (74%) said that their dead parent had gone to another place, typically Heaven. Children also talked about preserving their ties to the parent in various ways. Most said that they were still thinking about their dead parent several times a week (90%), thought that the dead parent was somehow watching them (81%) and kept something personal that belonged to their parent (77%), either in their room or on their person. The majority also said that they could talk about their dead parent with a family member (66%), had talked with friends (54%) and indeed reported speaking to the dead parent (57%). Despite the prevalence of these various strategies for maintaining ties with the dead parent, and even though half the children acknowledged having dreams in which the parent appeared to be alive, only a very small percentage (3%) reported that they could not believe that the death was real.

In summary, the findings reported by Silverman and co-workers [21,26] confirm that children think about and remain connected to a dead attachment figure while simultaneously acknowledging the reality of his or her death. By implication, many children cope with grief in the same manner as adults. They rarely deny the permanent loss that death brings about but nor do they become psychologically detached from the deceased parent.

6. Chimpanzees' reactions to death

In the context of the special issue, the proposals above invite two sets of questions about the way that non-human primates conceive, and respond to, death. First, how far do chimpanzees interpret a given death in biological terms as a permanent cessation of function? Second, how do their psychological ties to a deceased group member impact their reactions, both immediately and in the longer term?

Observational reports of chimpanzees discovering a corpse [27–29] provide a preliminary, albeit partial, answer to the first question. They initially react with agitation and alarm. A suite of behaviours ensues: close investigation of the corpse via peering or smelling; subdued, and sometimes prolonged, visual inspection with limited manual contact and striking the corpse or lifting the limbs, as if testing for agency or responsiveness. These reactions imply that an encounter with the corpse of a conspecific is viewed as a major and disturbing deviation from ordinary interaction, a deviation that leads to uncertainty and empirical probing. Still, it is unclear whether the cessation of activity is understood—even by senior members of the group—in light of a broader biological framework in which death is understood as the permanent termination of all living functions.

Arguably, the pattern of behaviour just described reflects the shock of discovery. Via their investigation and inspection, group members may be 'taking in' an unanticipated event. Indeed, Anderson *et al*. [30] report a different constellation of reactions to the relatively peaceful, and arguably foreseeable, death of Pansy, a female chimpanzee aged 50+ years, living in a Scottish Safari Park. Group members groomed the ailing female in the days and hours before her death. Immediately after the death, they engaged in close inspection (pulling at her shoulder and arm, attempting to open her mouth) but only for a minute or two. That night, group members displayed signs of disturbed sleep (as indexed by postural shifts). In the next few days, their behaviour was subdued and, with the exception of Pansy's daughter, they avoided sleeping in the nesting platform where the death had occurred for several days. Overall, this set of observations suggests that Pansy's death was not unexpected. Still, even in this case, it is not clear that the long-term implications were fully understood.

The preceding observations of chimpanzees' reactions to death also indicate that individual reactions vary depending on the prior relationship with the deceased. For example, Teleki [27] notes that Godi, a male adolescent belonging to the same subgroup as the deceased, was the most persistent in making a distinctive type of call (i.e. a Wraa call), showed the greatest interest in the corpse and became agitated when others approached it. Stewart *et al*. [28] report that Mambo, the daughter of the dead Malaika, watched her body more than other group members. Van Leeuwen *et al*. [29] describe how Pan, an older male who had had frequent interactions with the deceased Thomas, grabbed a branch and suddenly lunged at Thomas's corpse causing other individuals to scatter and scream. Pan also inspected the corpse more than any of the other adult males. Finally, the daughter of Pansy remained close to her body on the night of her death—unlike other group members [30]. These individualized patterns imply that some primate reactions to an unresponsive corpse are triggered not just by a disturbing departure from the ordinary pattern of living behaviour but also by the severing of a social or affective bond. Still, it remains to be seen whether non-human primates distinguish between the permanent loss of an attachment figure caused by death and the prolonged separation from an attachment figure that can be caused by physical absence.[2] Recall that the interviews with bereaved children suggest such a differentiation. They understood the permanence of death despite their continuing psychological ties to the dead parent.

7. The origins of burial practices

The evidence from non-human primates suggests that they experience a sense of loss and, arguably, some form of grief after the death of a group member. Still, it is important to note the limits of that grieving process. There is no evidence of any systematic effort to dispose of, or bury, the corpse and no evidence of active efforts to remain connected with the deceased, for example by regular and repeated visits to the site of death.

By contrast, among anatomically modern humans and Neanderthals, there is persuasive evidence for deliberate, albeit highly regionalized, burial practices, starting in the Middle Palaeolithic *ca* 120 000 years ago and becoming more systematic, and eventually more cemetery-like, in the course of the Upper Palaeolithic, from approximately 30 000 years ago [31]. Reviewing this record, Stiner [32] emphasizes one emerging feature of many burial sites, notably their location within, or close to, spaces that were important to the living. There is some evidence of earlier mass graves, but these can be conservatively viewed as disposal sites, given their location in inhospitable caves or crevices at some distance from areas bearing clear signs of regular habitation.

From a psychological perspective, a key question is what led to the increasing prevalence of such burial practices. It is unlikely that burial became more widespread simply because of technological progress. There is no obvious change in the tool-based demands of burial over the initial 100 000 years. Second, granted that burial practices became more prevalent long after the emergence of anatomically modern humans, it is unlikely that cortically based changes can account for the later appearing behavioural change in burial practices [33]. Admittedly, those cortical changes may have underpinned the emergence of relevant cognitive capacities—such as the capacity for planning or mental time travel—but we need to look elsewhere if we are to explain the eventual onset and historical trajectory of the burial practices.

In the light of the analysis offered earlier, notably the distinction between a biological and an afterlife conception of death, two lines of speculation are worth considering. First, in the course of the shift from the Middle to the Upper Palaeolithic, insight into the nature of death as a biological terminus may have become increasingly consolidated. For example, increased insight into the irrevocability of death might have motivated both anatomically modern humans and Neanderthals to bury and memorialize the dead. However, it is not obvious what would have driven such increased insight or indeed exactly why any such biological insight would have translated into more systematic burial practices.

A second line of speculation is more promising. As argued above, contemporary human adults and children maintain, and seek to maintain, their psychological ties to the deceased in various ways. Over an extended period, they often think about the deceased, talk about them and retain their possessions as keepsakes. Burial in close proximity to the living is consonant with the tendency to keep deceased individuals in mind rather than to dispose of their corpse and forget them. Indeed, the proximity of a grave is likely to serve as a reminder to the bereaved of the deceased. In addition, burial of kin or of group members in the same grave or in contiguous graves might symbolize for the living the restoration of severed ties between dead individuals. Such practices could have gradually produced a ratchet effect in which the proximity of burial sites helped to sustain memories of the dead among the living; and in turn, the accumulation of those memories, perhaps amplified by verbal recollection of the dead, provided a communal mental framework for the living to engage in the planning and execution of burials. Eventually, in the context of sustained burial practices, a group or community with a shallow collective memory of its ancestors might elaborate and deepen its awareness of successive, antecedent generations.[3]

8. Conclusion

Death is indubitably a biological event and it is important to ask how far children acquire a coherent understanding of its nature, especially its causes and its terminal consequences for all living functions. However, many children do not conceive death as an exclusively biological event. Especially when considering the social and emotional ties between the living and the deceased, they represent death as a separation. They are prone to represent that separation, not in narrowly biological terms as the termination of living functions, but rather in terms of a departure by the deceased to another place. In many cultures, religious testimony offers support for that representation. This parallel stance towards death invites questions about the degree to which it is present or absent in non-human primates and its emergence in the course of prehistory.

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Endnotes

[1] On this view, the human conception of death, whether as a biological event or as a departure, is primarily aimed at making sense of other people's deaths rather than our own. By implication, existential insecurity about our own personal mortality is a marginal rather than a central aspect of the human conception of death.

[2] In concrete terms, it is possible that non-human primates will behave similarly whether they register identifiable cues (e.g. a distinctive vocalization) that signal the return of an individual who has been temporarily absent or that signal the apparent return of an individual who is known to have died. By contrast, human beings, including children, would presumably be disturbed by any apparent 'return from the dead', given its inconsistency with their biological understanding.

[3] It is noteworthy that such a ratchet effect is not inevitable. For example, among some hunter–gatherer groups, disposal of the body barely goes beyond the practical need to dispose of a rotting corpse. Moreover, following a death, camp is generally abandoned thereby precluding the cumulative effect of successive burials in the same location [34].

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Sources of children's knowledge about death and dying

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Review

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In the last century, decreases in infant and child mortality, urbanization and increases in healthcare efficacy have reduced children's personal exposure to death and dying. So how do children acquire accurate conceptions of death in this context? In this paper, we discuss three sources of children's learning about death and dying, namely, direct experience of death, parental communication about death and portrayals of death in the media and the arts. We conclude with recommendations about how best to teach modern children about this aspect of life.

This article is part of the theme issue 'Evolutionary thanatology: impacts of the dead on the living in humans and other animals'.

1. Introduction

Over the last hundred years, improvements in public health and modern medicine have led to decreased mortality rates, particularly in children and young adults [1]. Prior to the twentieth century, death was most commonly experienced at home, following a short illness or as a result of workplace accidents [2]. The highest mortality rates were found in children and infants, but it was not uncommon for adults to die while still in the prime of life [1,2]. When a death occurred outside the home, the body was typically held in the home for traditional rituals (e.g. wakes) before burial or cremation [2,3]. Extended families lived in close proximity, so death was encountered and mourned by a close-knit community that included children.

Recent changes to family structures and compositions, and greater geographical mobility reducing contact with extended family has resulted in a significant decline in mourning rituals (for example, traditional Irish wakes at home [4]), particularly in Western societies [1–4]. This trend is also being increasingly experienced in many traditional cultures as a result of increasing globalization and a shift from traditional rites and ceremonies to more modern social norms (see, for example, Jacob *et al.* [5]). As a result, children, and even young adults, have become increasingly isolated from the realities of death in everyday life.

Coincidently, there have been significant changes to attitudes concerning how children should be raised [1] and this includes attitudes about exposing children to death and dying [6,7]. Overall there has been a marked shift in Western societies from the stance that death is a 'natural part of life' to an attitude of protecting children from the realities of death [6,7]. This attitude was documented by Miller *et al.* [7] in their interviews with Mid-Western American parents and teachers of 3- to 6-year-old children. These adults expressed the views that their children were cognitively and emotionally too immature to comprehend and cope with death, and thus should be actively shielded from its realities.

For researchers investigating children's death concepts, the protectionist trend is highly pertinent. It is increasingly difficult to carry out research because ethical review boards, education departments, individual teachers and parents often reject researchers' requests to investigate children's understanding of death. Yet it is essential to understand where and how modern children learn about death and dying both from a basic research perspective and as a basis for educational and clinical intervention. Here we examine three main sources of information about death and dying that children access: direct exposure to death, parental

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communication about death and depictions of death and dying in the media. We conclude with suggestions for further research and recommendations for how best to teach modern children about death and dying.

2. Assessing children's understanding of death

Death is a complex concept to grasp as it has interweaving biological, socio-cultural, spiritual and emotional elements. To assess children's understanding of death, researchers typically adopt a cognitive perspective focusing on children's recognition of death as a biological event [8–12]. In this tradition, a mature death concept is measured and defined in terms of several sub-concepts. While the terminology may vary from study to study, the most commonly assessed sub-concepts are:

(1) Irreversibility/permanence: the understanding that death is a permanent state from which there is no return to life;
(2) Inevitability/universality: the understanding that all living things must die eventually;
(3) Applicability: the understanding that only living things can die;
(4) Cessation: the understanding that all bodily processes cease to function upon death; and
(5) Causation: the understanding that death is ultimately caused by a breakdown of bodily functions [11].

Early researchers sometimes classified afterlife reasoning (e.g. asserting that 'the dead can think and feel') as evidence of immature irreversibility or cessation sub-concepts. However, in the last decade, research on the development of spiritual and/or religious beliefs about the afterlife (e.g. [13]) has confirmed that spiritual conceptions of death are developmentally distinct from biological [13–16] ones. Children's biological concepts of death are typically mastered first, and then spiritual elements are layered on top, leading to an adult pattern of sophisticated understanding of the biological reality of death coexisting with belief in an afterlife for the mind or soul [13–16]. This may explain why individual difference studies typically have found minimal effects of specific religious beliefs or levels of religiosity on children's biological understanding of death [17–19].

This review will focus on how children acquire a biological understanding of death. Research in this tradition indicates that the sub-concepts are acquired in a relatively consistent developmental pattern that follows the numbered list above. Irreversibility is almost always understood first, as early as age 3, and causation is acquired last, usually by age 8. This general pattern is evident even across diverse cultural groups [18,19]. Within this broadly normative pattern of acquisition, ecological and individual factors influence the order of acquisition for inevitability, applicability and cessation, as well as the developmental timetable for understanding death as a whole [8,9,11,12,20]. Hesitancy around investigating children's understanding of death means that experimental or training studies are almost non-existent. Therefore, most of what we know about how children learn about death comes from individual differences studies correlating subject or environmental variables with children's mastery of death sub-concepts. The most common variable included in such investigations is children's direct experience of death.

3. Direct experience of death

Intuitively, the maturity of children's death concepts should be associated with their first-hand experience. However, the data are inconsistent on this. Whereas many studies report that experience with death increases children's death understanding (see Speece & Brent [21] for a review), some report no association [10,22] or even a negative association [8]. One reason for the lack of consensus could be varying definitions of what 'experience' constitutes [23]. Experience of death is measured via child self-report, parent or teacher report, and can include one or more of: (a) death of an immediate family member or close friend, (b) death of an extended family member, acquaintance or family friend, or (c) death of a pet [8,9,24,25]. Additional variables such as closeness of the relationship, extent of physical exposure to the corpse, involvement in funerary rituals etc. are almost never included yet individual differences in these specific experiences are likely to be important to children's understanding. Another reason for the mixed findings may be that the association is age-dependent: it appears that direct experience predicts children's death concepts for children up to the age of 6 years [26], but not for older children.

Alternatively, the association between direct experience of death and children's death concepts may be mediated by parental communication. Parents report that an experience of death is one of the most significant factors influencing their decision to talk to their children about death [24,27]. As we discuss below, parental input appears to be a significant predictor of children's understanding.

Although exposure to death and/or corpses is arguably the most powerful source of learning about death [28], there may be other experiences that influence children's understanding of death indirectly. For example, children's concepts of death are developmentally intertwined with their concepts of life and the life cycle [20,29], such that learning about one automatically promotes development of the other [12]. Numerous studies indicate that contact with the natural world is positively associated with development of various biological concepts, many of which are conceptually related to death and dying (for a complete review, see Longbottom & Slaughter [30]). Thus it stands to reason that experience with cycles of nature and living animals also plays a role in children's understanding of death, although so far no research has been conducted to test this assumption.

4. Parental communication about death and dying

What children know and learn is grounded in what their parents teach them. This includes children's developing understanding of biology and the natural world [31], with numerous studies demonstrating the influence of parental communication on concepts such as natural life cycle changes and metamorphoses [32], genetic inheritance [33] and human–animal categorization [34,35].

Clinical psychologists and bereavement experts emphasize the importance of talking to children about death from an early age in an honest and informative way, and to portray death as a natural part of the life cycle (e.g. [36–38]). These same sources express concern that many parents do not discuss death in depth with their children until the issue is forced by the death of a close relative, friend or pet [8,10,34,35]. A survey of 270 American parents of 4–6-year-old children revealed that parents were least comfortable talking with their children about death, when compared with talking about other biological topics including reproduction, life processes, ageing and illness [39]. Although it should be noted that these parents' average response for discussing death fell between 'comfortable' and 'somewhat comfortable'. Another issue is that parents' communications about death can be misleading; the use of euphemisms ('she's passed on' or 'we lost her') can actually be detrimental to young children's understanding, because these forms of expression avoid the biological realities of death and may even imply that the dead can return.

Despite widespread consensus that parental communication is an important factor in children's development of a mature death concept, few studies to date have directly examined the links. One exception is Matalon [26], who examined communication about death in 68 middle- to upper-middle class parents from New York City with their 6- to 9-year-old children. Based on the recommendations of death education specialists, she devised a questionnaire to assess parents' tendency to engage in 'effective' communication about death. Matalon's definition of effective communication included: the 'parents' willingness, availability and comfort' when answering their children's questions about death and dying, their 'ability to share the unpleasant feelings' and uncertainties about death and their 'awareness of the need to prepare the child for the inevitable reality by using opportunities in nature.' Matalon [26] found that parents' self-reported frequency of this type of communication was significantly correlated with their children's sophisticated understanding of death. The study also revealed a significant negative association between parents' own death anxiety and their tendency to communicate effectively about death, suggesting that parents who were more death-anxious were more avoidant or more likely to resort to euphemisms [26]. It should be noted, however, that parents' questionnaire responses about how they talk to their children about death may not accurately represent what they say when the topic comes up. Hunter & Smith [9] found no significant correlation between children's death concepts and their parents' communication about death, when the latter was assessed by having parents write direct responses to a 5-year-old actor's audio-taped questions about death. This methodological difference could account for the contrasting findings, or, as the authors acknowledged, it may be that Hunter & Smith's [9] null findings could be attributed to their relatively small sample ($N = 37$) and restricted range of scores. Ultimately, the role of parental input about death should be explored with methodologies that capture what parents actually say to their children.

Explorations of parents' communication about death and dying highlight two factors that influence death concept development in Western populations. These are: (1) the age at which children are believed to be capable of understanding death, and therefore should be taught, and (2) the type of information parents provide their children. Given that what parents discuss with their children is influenced by the age of the child, this factor will be discussed first.

Early researchers examining the development of death concepts argued that children were incapable of understanding or even thinking about death before the age of 7, and that a mature death concept was not fully developed until 10 years of age [25,40]. These estimates were informed by Piagetian cognitive developmental theory, which assumed that children could not think about abstract concepts until middle childhood. As noted above, the modern approach assesses children's understanding of death as a biological, as opposed to abstract, concept. This shift has significantly revised the developmental timeline, with modern research indicating that most children acquire a complete death concept between 5 and 7 years of age, and many are capable of understanding some sub-concepts of death as young as age 3 [10–12,35]. Despite this updated approach and research findings, much of the popular press, as well as some researchers, continue to cite outdated research and adhere to Piaget's initial developmental ages. This may account for the variation in parents' observed beliefs about their children's capacity to understand death.

Research with Western educated parents indicates that the majority tend to fall into two groups with respect to their beliefs about children's ability and readiness to learn about and understand death. One group of parents aligns with recent research, citing ages of around 5 and 6 years and younger [7,20,25,41,42]. Others report that children are not cognitively or developmentally capable of thinking about death before 7 years of age, and do not fully comprehend before 10 years of age at least [41–43]. For example, Hendricks *et al.* [42] explored how American parents discussed sensitive topics with their children, and when they believed children were able to understand such topics. They found that, of a sample of 39 parents recruited online, 43% believed children were unable to understand death prior to 7 years of age, and 10% of those reported that a complete understanding of death was acquired after age 12. In the only study of its kind to date, Gaab *et al.* [44] compared New Zealander parents' perceptions of their children's understanding of death to the children's actual comprehension levels. After assessing the death concepts of 141 5- to 7-year-old children and surveying their parents, Gaab *et al.* [44] found that parents underestimated their children's understanding of all the sub-concepts of death to some degree, with parents' estimations of their children's understanding of death causality being the most conservative. Together, these studies suggest that parents may be unaware of the extent of their children's understanding of death. Beliefs about their children's conceptual underdevelopment, combined with hesitancy about the emotional implications of talking about death, may explain why many parents avoid the topic until circumstances demand it [10,24].

The content of parents' explanations is also revealing. These can be broadly divided into two categories: scientific facts and explanations, and religious, spiritual or emotional reassurance and comfort. Reassurance responses are explanations aimed at providing solace to the child, and can include religious, emotional, biological or spiritual information (e.g. continued existence after life, I won't die until I'm much older, or it's alright to feel sad [24,45]). Facts and explanations generally relate to the biological processes involved in death, although they can also relate to rites and rituals following death [24,45].

Providing children with the biological facts is obviously important for children's developing concepts of death. Gutiérrez *et al.* [45] explored the content of 60 American parents' self-reported conversations with their 3- to 6-year-old children as part of a wider study. In response to their children's questions about death, the majority of parents (79.2%) reported that they had incorporated facts and explanations relating to the biological nature of death. However, other survey studies suggest that not all parents provide these sorts of explanations. For example, Renaud *et al*. [27] surveyed Canadian parents of 2- to 5-year-old children about their conversations about death and what these conversations included. Seventy-five percent of parents reported that they had spoken at least once to their child about death. Of these, 36% reported that they had provided their child with a 'known' cause of death, and fewer than 20% reported that they explained the irreversibility of death. While many parents claim that their explanations include causes of death (when known) [24,45], this is the one piece of information children are most likely to ask about, or wish they were provided with in retrospect [46,47]. Coincidentally, causality of death is also the sub-concept that is mastered latest in development. This may mean that parents' causal explanations are not sufficiently informative, or may be pitched at the wrong level for children to absorb, or may be confused by parents' emotional reassurances.

It should be recognized that the true proportion of parents who do talk to their children about death may be overestimated in the research literature. It seems likely that parents who are more open to the idea of speaking about death with their children are also more likely to agree to participate in studies. When interviewing high school students, Stillion and Wass (1982, described in [47, p. 67]) found that 40% of American teenagers reported that death was never or rarely discussed at home when they were younger, while a further 26% reported that it had only been discussed when 'absolutely necessary'.

How parents communicate with their children about death and dying not only influences their children's understanding of death, but also how they in turn communicate about it throughout their lifetime. There is increasing evidence that how a parent communicates about death and dying with their child, particularly when addressing a personal experience, influences how death is subsequently discussed or approached by the child [46,47] and this influence extends into adulthood [4,7]. For example, Irizarry [46] found that Australian 8- to 12-year olds explained their grandparents' deaths using the explanations provided to them by their parents, even when they reported that they did not agree with, or understand, them. McGovern & Barry [4] found that Irish parents and teachers reported that their personal experience of death and bereavement was the most salient influence on their communications with children about death and dying. These findings suggest a perpetual transmission cycle of attitudes and conversations about death across generations.

The literature has identified several ways in which children construct an understanding of death in the absence of direct teaching from parents and other carers. One way in which children learn about death is by listening in on adults' conversations [28]. As Kurowska-Susdorf [48, p. 141] puts it, 'by overhearing adult conversations, [children] construct their own internal understanding using snippets of information'. A second way in which children formulate an understanding, particularly when insufficient information is provided, is by drawing on their own existing understanding of the world, or their imagination, to 'fill in the gaps,' or simply by making up their own stories to explain what happens (47, 5). For example, Irizarry [46, p. 46] observed a 10-year-old girl who pieced together overheard snippets and concluded that:

> 'The sleeping pills she [Grandma] had been given may not have been the correct ones because normal ones don't make someone die. My gran was talking about it. My grandma had a cold and had gone to the hospital. She didn't want to go to sleep and was given sleeping pills and then she died. My father said it was 'old age'.'

Similarly, Miller *et al*. [7] report instances of children integrating what they know about religion or biology to make sense of death. One example was a child who:

> 'asked her therapist if she thought her deceased mother would 'grow back when it gets back to summer time? . . . she might come back as a flower'. This child had witnessed her mother's coffin being lowered into the ground. Using her knowledge that seeds that are planted in the ground emerge as plants, she reasoned analogically that her mother would grow back. . . .This child seemed to draw on her existing understanding of biology to create a unique and comforting idea about her dead mother.' [7, p. 27].

Finally, children may assimilate information about death and dying from broader contexts, for example, by learning that important historical figures are dead. The following section considers one specific context, namely, the portrayal of death in the media.

5. Media portrayals of death and dying

In times past, one function of literature, particularly fairy tales and oral stories, was to help children to understand and develop a sense of meaning about the world they lived in [49]. While this role continues today, researchers acknowledge that for modern children, conveyors of these messages are more likely to be movies and television shows [6]. It is estimated that children under 8 years of age spend an average of 3 h per day consuming media, with the majority of that time dedicated to film and television [50,51]. Given its prevalence in children's lives, media is now recognized as a legitimate cultural purveyor of specific roles, values and ideals, equivalent in influence to traditional sources of learning such as schools and the family environment [52,53].

Sedney [6, p. 316] suggests that the media is an 'indirect [form of] death education' which can be just as powerful as directed forms of learning. There is evidence that exposure to media portrayals of real-life traumas (such as terrorist attacks) can produce symptoms of post-traumatic stress disorder in children [54,55]. However, as yet there is surprisingly little research addressing how exposure to death in the media relates to children's death concepts.

Among adults, media portrayals of death have been found to influence attitudes towards, and concepts about, death (e.g. [56,57]). In one of the few research studies to address the role of media exposure in children's learning about death, Gutiérrez *et al*. [45] asked American parents of 3- to 6-year olds about what prompted their children's questions about death and dying. Sixty-seven per cent of the parents reported that their children had asked questions about a death portrayed in the media, most commonly in books and films. Similarly, Renauld *et al*. [27] found that a majority of parents they surveyed reported that their children were first exposed to death in the media. These parents also reported that their earliest conversations with children about death were most commonly about a media portrayal, followed by death of a pet and death of grandparents [27]. These findings suggest that media portrayals of death may be as important as direct experience in exposing children to death and dying, and stimulating parental communication on the topic.

Although not characteristic of all mainstream media representations of death, many films and books for children contain confusing, unrealistic and potentially harmful information about death and bereavement [6,49,52,58]. Sedney [6] argues that children may internalize the unrealistic messages about death being provided by popular media, and these inaccurate ideas may impact on their developing understanding of death and their attitudes towards it. Distorted portrayals of the permanence of death and protagonists' grief responses following a death are most common. For example, Tenzek & Nickels [52] examined the prevalence and characteristics of death portrayals in 57 Disney and Pixar films. They found that at least one death occurred in 84.2% of the movies. Of those deaths, 31.6% were portrayed as reversible (either physically or by characters returning as spirits). They also observed that, when characters reacted to these deaths, 63.2% of those reactions were portrayed as either positive or lacking in emotion. Tenzek & Nickels [52] point out that these unrealistic portrayals can be confusing to young children, but propose that parents and educators may use them to frame conversations with children about the realities of death.

Alongside concerns about unrealistic and inaccurate depictions of death and grief in the mainstream media, there is also recognition that carefully crafted media portrayals can have a positive influence on children's understanding of death [6,52,58,59]. For example, there is a small children's literature on death education, aimed at providing facts about death and suggesting ways to cope and normalize grief [59]. Clinicians and educators recognize the value of these books both in promoting children's understanding of the realities of death and in stimulating communication between children and their parents [59]. In the USA, a now-famous episode of the children's television show *Mister Rogers' neighbourhood* focused on the death of a goldfish [60,61]. This episode 'dealt with death in a low-anxiety situation' [60, p. 183] and was explicit in providing factual information about the death sub-concepts of irreversibility, universality and cessation. The producers received numerous letters from parents and children expressing thanks for the programme and providing examples of how the programme helped them deal with the realities of death [60]. The programme was repeated several times over the next few years. More recently, an episode of the *Sesame Street* television show, entitled 'Farewell Mr Hooper' centred around the death of a popular (human) character in the show [62]. The episode portrays frank and factual discussions about death and grief. Shortly after the 2012 Sandy Hook massacre in the USA, the episode went viral as parents sought a way to help explain death and dying to their children [63]. Despite being released decades ago, the episodes of Mr. Rogers and *Sesame Street* are still accessed today, and demonstrate that media can provide a positive resource for children's developing death concepts.

However, it must be acknowledged that what topics are addressed, and how they are portrayed in the media, are governed by social norms and beliefs about what society deems 'appropriate' for children. This has been evident in public reactions to two noteworthy portrayals of death in media for children. The first is E. B. White's classic storybook *Charlotte's web* [64], which was criticized for its ending in which the main character dies [59]. White's publisher initially told White to modify the ending so that Charlotte survived, but White refused [59]. After its release, the book was controversial with reviewers claiming that the death was 'not an appropriate subject for children'. Despite this, *Charlotte's web* remains a best-seller for young children [7] and has since been remade for film. More recently, Disney was criticized for *The lion king* movie's depiction of lead character Mufasa's death. Critics argued that the film was too violent and scary for young children, with the death deemed to be inappropriate [65]. Again despite the protestations, *The lion king* remains one of the highest grossing and popular Disney films of all time. It should be noted that the initial critical reviews of *The lion king* eventually gave way to praise for its realistic and honest depiction of grief and for its portrayal of death as part of the 'cycle of life' [6,66].

These examples suggest that there is an appetite in society for realistic media portrayals of death and dying, and highlight the potential for media to play an important role in children's developing concepts of death. This is a ripe area for further research. For instance, there is as yet no research examining how death portrayals in video games relate to children's developing death concepts, which is surprising given the widespread recognition that many video games portray death as impermanent.

6. Conclusion and recommendations

Modern children have limited access to realistic information about death and dying. Alongside socio-cultural trends that have removed death from everyday life, many adults endorse attitudes of shielding children from the reality of death. Furthermore, it appears that parents tend to underestimate what their children know about death, and often discuss the topic using euphemisms that actually contradict the biological facts. While media exposure is an increasing influence on children's learning, there is no research to date investigating how media portrayals influence children's developing death concepts.

Drawing together the limited evidence reviewed above, and the advice of bereavement experts and clinicians, the following tentative recommendations about how to teach modern children about death and dying can be made:

Parents, educators and other influential adults should ensure that young children have exposure to nature and animals, as these sorts of experiences promote children's understanding of biological concepts [30].

Death education should be frank and honest, but it does not have to be head-on. Research shows that understanding life and understanding death are intertwined; so providing children with biological information about the life cycle and how the body works may have a positive influence on their understanding of death [12,38].

Adults should be aware of the potential to confuse children when their communication contains a mix of factual information and euphemisms. Furthermore, parents should bear in mind that their communications about death affect both their children's emerging understanding and how their children will approach the topic in their turn.

Media portrayals that address death frankly (e.g. Mister Rogers, *Lion king*) may be valuable resources for teaching children the realities of death. At the same time, parents should be on the lookout to counteract beliefs and attitudes that might arise from children's exposure to inaccurate media portrayals of death.

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Speaking of death

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As a human-specific trait, language offers a unique window on human cognition. Grammatical constraints on the ways we speak about events, for instance, have long been thought to reveal the representational formats that our minds impose on the ways that we think about events. In recent research, verbs that name events of death have stood out as key counterexamples to standard theories of the grammatical constraints on possible verbs. The special status of these thanatological verbs raises two important questions: why, given the vast number of verbs in any language, is it that verbs of death hold this special status, and what do they tell us about the restrictions on the representational format for possible verbs? This paper reexamines the evidence coming from verbs of death, confirming that they are counterexamples to standard theories, but that their behaviour suggests a more revealing constraint on our mental representations—that our minds impose strict restrictions on the format of asserted meaning. Thus, the constraints on linguistic representation and the human mind offer a unique perspective on the mental representations of thanatological phenomena.

This article is part of the theme issue 'Evolutionary thanatology: impacts of the dead on the living in humans and other animals'.

1. Introduction

Do the ways we speak about events of death reveal anything special about how we think about events of death? Studies on verbs and verb meanings have been seen as core to our understanding about how we mentally represent events. Decades of research have worked to isolate how different aspects of events are encoded in grammatically relevant meaning components across different parts of a sentence, with the verb acting as a key locus of event information. These studies have furthermore demonstrated that there are substantive constraints on what meanings can be packaged into a single verbal concept.

The main focus of this paper is how verbs can be separated into those that encode the manner in which an event process unfolds and those that encode the result of an event having unfolded, and what constraints exist between these two meaning components. Verbs like those in (1) encode the manner in which the process of an event unfolds, for instance as a process of something being screamed or someone being scrubbed or rocked. Other verbs like those in (2) encode the results of an event, for instance an event resulting in something being repeated or someone becoming clean or arriving. These encoded meanings are those that are lexically entailed by the verbal concept; that is, the verb *scream* always entails a manner (of screaming) while the verb *repeat* always entails a result (of something being repeated).

(1) a. Kevin screamed the lyrics.
b. Laura scrubbed Billy.
c. Willy was (gently) rocked.
(2) a. Kevin repeated the lyrics.
b. Laura cleaned Billy.
c. Willy arrived.

This categorization of verbs into manner versus result is one that cuts across our more naturally intuitive semantic verb classes. The verbs *scream* and *repeat* are drawn from a wider semantic class of verbs that name events of speech given in

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(3). The verbs *scrub* and *clean* are only a couple of the verbs that name events of changes of state given in (4). The verbs *rock* and *arrive* come from a class of verbs that name events of motion given in (5). Within each of these classes, we can identify subclasses of verbs that encode either the manner of the event, those in (a), or the result of the event, those in (b).

(3) SPEECH VERBS
  a. *Manner*: babble, bellow, chant, cry, grumble, holler, mumble, mutter, roar, scream, shout, sing, snap, stammer, whisper, yell . . .
  b. *Result*: admit, announce, blurt, claim, convey, declare, mention, proclaim, propose, remark, repeat, report, say, state . . .
(4) CHANGE OF STATE VERBS
  a. *Manner*: bash, dust, hammer, hit, kick, polish, pound, pour, scour, rub, scrub, strike, sweep, tamp, tap, wash, wipe . . .
  b. *Result*: break, chip, clean, crack, dissolve, divide, drain, empty, freeze, melt, pop, remove, rip, shatter, sink, splinter, tear . . .
(5) MOTION VERBS
  a. *Manner*: crawl, dance, gallop, glide, jump, limp, meander, rock, roll, run, saunter, slither, spin, swim, swing, taxi, wade, walk . . .
  b. *Result*: approach, arrive, ascend, come, depart, descend, enter, exit, fall, flee, go, increase, leave, near, recede, return, rise . . .

Thus, it seems that manner and result are basic building blocks of verb meanings apart from a verb's semantic field, and an investigation of these basic meaning components of verbal concepts may give us insight into our underlying mental representations for events. As such, if there is anything special about how we think about events of death, an examination of our verbal concepts for events of death in terms of manner and result might be a good place to start.

At first blush, the class of verbs we use to speak about typical events surrounding death seem no different from other verbal classes. There are verbs like those in (6) that encode an event process, for instance of shooting or stabbing, and there are others like those in (7) that encode an event result, such as in being killed or dying.

(6) a. Laura shot Billy.
  b. Willy was (viciously) stabbed.
(7) a. Laura killed Billy.
  b. Willy died.

Thus in both our more mundane everyday discussions of events and of those events that seem more critical to human preservation, a complementary pattern emerges. Verbs like those in (1) and (6) encode the manner of an event, directly telling us how an event unfolds, but not what the result of that event unfolding is. Other verbs like those in (2) and (7) encode the result of an event, directly telling us what the result of an event unfolding is, but not how that event unfolds.

To investigate these distinctions more systematically, linguistic research draws on naturally occurring examples found in corpora and native speaker judgements of the interpretations and acceptability of constructed examples. For example, native speakers permit sentences with manner verbs to occur with an additional predicate that encodes the result of the event, often expressed by an adjective or a prepositional phrase, as in (8), but reject similar sentences with result verbs, as in (9).[1]

(8) a. Kevin screamed the lyrics to life.
  b. Laura scrubbed Billy dirt-free.
  c. Willy was rocked to sleep.
(9) a. *Kevin repeated the lyrics to life.
  b. *Laura cleaned Billy dirt-free.
  c. *Willy arrived to sleep.

This same pattern of native speaker judgements is attested with verbs related to death. Resultative predicates are permitted with manner verbs like *shoot* and *stab* in (10), but rejected with result verbs like *kill* and *die* in (11).

(10) a. Laura shot Billy dead.
  b. Willy was stabbed to death.
(11) a. *Laura killed Billy dead.
  b. *Willy died to death.

This complementary pattern between manner and result verbs has been attested again and again across a variety of languages, suggesting that the mental representation of any verb in any natural language is formatted such that it encodes only a manner meaning or a result meaning. This constraint on the representational format of our verbal concepts, dubbed manner/result complementarity as given in (12), has been proposed and defended by Levin & Rappaport Hovav [1–3]. In this paper, I take manner/result complementarity to be an empirically testable claim about the limits of what meanings we can bundle together and store in our mental lexicon for any single verbal concept.

(12) *Manner/result complementarity*: Manner and result meaning components are in complementary distribution: a verb lexicalizes only one. Levin & Rappaport Hovav [4, p. 50]

Investigating potential counterexamples to manner/result complementarity has been important in advancing our understanding of the representational format of possible verbs and the events they name. From the evidence seen so far, it would seem then that there is not much that is special about death when it comes to our verbal concepts. The verbs in (6) and (7) conform to manner/result complementarity as closely as their mundane cousins.

However, closer inspection reveals that events of death may hold a special status when it comes to the ways we can package verbal meanings together. Unlike the more mundane events of everyday life, some verbs related to events of death, like those in (13a) and (13b), appear to encode both a manner and a result in apparent violation of manner/result complementarity [5]. The verb *crucify* denotes both the manner in which a particular event process unfolds—that is, as a process in which an individual is affixed to and left up on a cross—along with the result of that event unfolding, which at least at first blush appears to be a result of death. The same holds for the verb *disembowel*, where the manner is now one in which the organs of the gastrointestinal track are removed through an incision in the belly, and the result seems again to be one of death.

(13) a. St. Andrew was crucified.
    i. Manner: crucification
    ii. Result: death

b. Dutch executioners disemboweled Balthasar Gérard.
   i. Manner: disembowelment
   ii. Result: death

Although such verbs appear to have a clear manner meaning component—indeed it is the manner of the event that changes between (13a) and (13b)—we can tell that the result meaning component is encoded by attempting to add a result predicate to these sentences. As shown in (14), both *crucify* and *disembowel* reject the addition of the result of death, similar to the result verbs in (11) and unlike the manner verbs in (10).

(14) a. *St. Andrew was crucified dead.
b. *Dutch executioners disemboweled Balthasar Gérard to death.

Verbs like *crucify* and *disembowel* are not alone. Beavers & Koontz-Garboden [5] propose that there is a class of these verbs given in (15), which I will call *manner of death* verbs.[2]

(15) MANNER OF DEATH VERBS (to be revised): asphyxiate, behead, crucify, hang, decapitate, disembowel, drown, electrocute, eviscerate, gas, guillotine, gut, immolate, impale, poison, quarter, smother, strangle, . . .

The behaviour of this class of verbs is important as it reveals that certain events of death are somehow marked in human thought, licensing them to bypass the manner/result complementarity constraint that limits our more mundane verbal concepts. In this rest of this paper, I will argue that these verbs reveal how it is that a manner and a result meaning component can be bundled together in a single verbal concept and reflect on why a result of death, as opposed to other result meanings, can accompany a manner meaning. Section 2 unpacks our currently intuitive notions of manner and result meaning and §3 further investigates the manner and result meanings of *manner of death* verbs specifically, suggesting a revision to the class of *manner of death* verbs in (15). Having isolated those *manner of death* verbs that truly encode both manner and result meanings, §4 demonstrates that the manner and result meanings are encoded at distinct levels of meaning. Section 5 discusses the consequences of this paper for our understanding of how verbs encode meaning and why results of death are special. Section 6 concludes.

2. Manner and result in verbal concepts

Before turning our attention to a deeper investigation of *manner of death* verbs, we should be clear about what distinguishes manner and result meanings and how we can make such distinctions. Rappaport Hovav & Levin [7] propose that manner meanings are distinguished from result meanings by the kinds of event of change they represent: manner meanings are a type of non-scalar change and result meanings are a type of scalar change.

In this theory, a scale is formalized to be ‘a set of degrees—points or intervals indicating measurement values—on a particular dimension (e.g. height, temperature, cost, alive/dead), with an associated ordering relation’ and a scalar change is ‘a change in value of this attribute (i.e. dimension) in a particular direction along the scale, with the direction specified by the ordering relation’ [7, p. 28].[3]

Applying this theory, the result meaning of a result verb like *clean* is encoded as a unidirectional change in a value of cleanliness. When we say that *Laura cleaned Billy*, what we mean is that the degree of Billy’s cleanliness increased as a result of the event. The manner meaning of a manner verb like *scrub*, however, is not encoded as some unidirectional change in a value of some dimension. Scrubbing is a set of complex actions that need not occur in any particular order and have no underlying dimension. When we say that *Laura scrubbed Billy*, what we mean is that a complex series of unordered actions of scrubbing occurred to Billy.

As noted above, there are a variety of linguistic diagnostics that track this difference between manner and result verbs. Here, I focus on four diagnostics: denial of result, denial of manner, implicit direct objects, and non-subcategorized direct objects using *scrub* as a canonical manner verb and *break* as a canonical result verb.

Because manner verbs encode only the specific manner of an event and not some specific result, even strongly implied results of the event can be denied by the speaker. In (16a), the potential result of scrubbing, e.g. that the bathtub becomes cleaner, can be denied. Attempting to deny the result of a result verb is markedly odd, as shown in (16b). This is taken as evidence that result verbs encode results.

(16) a. Cinderella scrubbed the bathtub, but it didn’t get any cleaner.
b. *Harrison Ford broke his leg, but it didn’t become broken.

Attempting to deny the manner of an event reveals the opposite pattern. As result verbs only encode the result of an event and not some specific manner, even strongly implied manners for the event can be denied by the speaker. In (17b), the potential manner of breaking, e.g. that of falling, can be denied. Attempting to deny the manner of a manner verb, however, is judged to be unacceptable, as shown in (17a). This is taken as evidence that manner verbs encode manner.[4]

(17) a. *Cinderella scrubbed the bathtub, but not by scrubbing.
b. Harrison Ford broke his leg, but not by falling.

Perhaps more interestingly, manner and result verbs differ in the way they relate to direct objects, demonstrating how native speakers tie their knowledge of verbal meanings to grammatical relations. Native speakers tacitly know that manner verbs allow them to leave the direct object implicit. In (18a), there must be some object that Cinderella is scrubbing, but the speaker is not required to tell us what it is. Result verbs, however, require native speakers to explicitly mention a direct object. In (18b), the speaker is obligated by their mental grammar to explicitly say what it was that Harrison Ford broke.

(18) a. Cinderella scrubbed (all morning).
b. *Harrison Ford broke (all morning).

Native speakers also tacitly know that manner verbs can also occur with so-called non-subcategorized objects, i.e. direct objects that are selected by some predicate other than the predicate of the verb. This can be seen in the interpretive difference between (19a) and (19b). In (19a), Cinderella may not be scrubbing her fingers; instead, her fingers could be in a raw state because of the scrubbing she was doing to some implicit object. This interpretation is distinct from

(19b) in which Cinderella must be scrubbing her fingers (though we do not know what state her fingers end up in due to this scrubbing). Result verbs again differ in this respect and cannot occur with non-subcategorized objects. The example in (20a) cannot be interpreted as Harrison Ford's leg becoming bloodied because he broke some unspecified thing, and thus is considered unacceptable to native speakers.

(19) a. Cinderella scrubbed her fingers raw.
b. Cinderella scrubbed her fingers.

(20) a. *Harrison Ford broke his leg bloody.
b. Harrison Ford broke his leg.

These diagnostics distinguish between manner and result verbs, and in particular can be used to demonstrate when a verbal concept encodes a manner or a result meaning. In the next section, we will apply these diagnostics to *manner of death* verbs to uncover those verbal concepts of events of death that transcend manner/result complementarity and deserve further attention.

3. *Manner of death* verbs

As introduced above, *manner of death* verbs are verbs that appear to name both the manner in which an event of death occurs and the result of that event, namely, death.[5] Beavers & Koontz-Garboden [5] offer the first thorough investigation of *manner of death* verbs and provide evidence that these verbs encode both a manner and a result component in their verbal concepts. Intuitively, these verbs express that a particular manner of action happened to an individual and that the action resulted in the death of that individual. For example, (21) expresses that drowning/hanging/electrocution/crucifixion happened to Shane and that Shane died.

(21) Shady drowned/hanged/electrocuted/crucified Shane.
a. Manner: drowning/hanging/electrocution/crucifixion
b. Result: death

In this section, I apply the diagnostics introduced in the previous section, demonstrating that *manner of death* verbs encode both manner and result components in their verbal concepts.

(a) Result in *manner of death* verbs

Most mundane verbs appear to wear their manner or result meaning component 'on their sleeve', so to speak; indeed, we think of them as naming either the manner or the result of an event. The verb *scrub* names an event with the particular manner of scrubbing, and the verb *break* names an event with the particular result of breaking. Therefore, application of denial of result or denial of manner diagnostics was straightforward, and repetition of the same lexical item ensured that we were targeting a precise manner/result.

For *manner of death* verbs, the precise meaning of their manner component is fairly clear,[6] but the meaning of their result component is more debatable since it is not encoded on the surface. As a first approximation, the result meaning component seems to be whatever the result meaning component of *kill* or *die* is, and indeed, applying these to a variety of *manner of death* verbs in (22), native speakers report the same contradictory interpretations reported for (16b).

(22) a. *The revolutionaries guillotined King Louis XVI, but he wasn't killed.
b. *Herennius decapitated Cicero, but he wasn't killed.
c. *Geoffrey of Shrewsbury quartered Dafydd ap Gruffydd, but he didn't die.
d. *Thích Quảng Dúc immolated himself, but he didn't die.
e. *Terrorists beheaded Daniel Pearl, but he wasn't dead.

Of course, such judgments could arise from our knowledge of the world. Having one's head removed or one's body cut into four pieces seems like a sure way to end up dead. However, certain special contexts like those in (23) allow the result of death itself to be delayed or to not obtain at all.

(23) a. The executioner guillotined the man's arm off, but he lived.
b. Jason decapitated the hydra, but it continued to fight.
c. The research quartered the starfish, and it grew into four little starfish.
d. The asbestos monster immolated itself, but it did not die.
e. The farmer beheaded the chicken, but it continued to run around the yard.

The examples in (23) suggest caution when interpreting the denial of result evidence in (22). When it comes to understanding whether *manner of death* verbs are true counterexamples to manner/result complementarity, Beavers & Koontz-Garboden [5, p. 338] argue that the exact meaning of a *manner of death* verb's result component is not important, only that it has some result component because some result does obtain. For instance, the verb *guillotine* may not always entail death, but does entail the loss of a body part (typically the head), and therefore a result. Similarly *crucify* requires at least a change of location result, since crucification requires one 'being hung upright in a particular configuration'. Indeed, this type of argument can also be made for *decapitate* and *behead* in (23) as both verbs entail the resulting loss of a head. A case can also be made that the result of *quarter* in (23) is the creation of four pieces. Less clear is *immolate* in (23) where immolation may be argued to cause no necessary change to an asbestos monster. Indeed, these arguments seem to be heavily reliant on particular world knowledge, something we may not want our analysis to rely upon.

These arguments, however, must be considered carefully, as they may threaten any coherent notion of a lexically entailed result meaning. As we push the result meaning further and further from something intuitively verb specific, all kinds of unintended but potential result meanings might be at issue. Consider some of the 'hard-core' manner verbs which, when pushed, certainly obtain some kind of result. The verb *nibble*, for instance, in (24a) entails some resulting consumption or 'biting off', thus resulting in an irreversible change in the apple along some scale. Similarly, the verb *wipe* in (24b) entails some resulting surface contact, thus there is a result of contact between the table and Mary (or the instrument that Mary uses). To my mind, these results all meet the definition of result as a scalar change given in Rappaport Hovav & Levin [7] and thus present potential problems for a clear delineation of manner and result meanings. Indeed, determining whether there is a result component and what that component actually is is a non-trival process.

(24) a. *The squirrel nibbled at the apple, but the apple remained whole.
b. *Mary wiped the table, but no contact with the table resulted.

In attempting to address such worries when it comes to denial of result diagnostics, Beavers & Koontz-Garboden [5, p. 337] propose a more general test aimed at detecting 'some single, non-verb-specific inference for all result verbs', which I will call the *nothing different* test. They report that application of the *nothing different* test does not create a contradiction with canonical mundane manner verbs, shown in (25), but does create a contradiction with canonical mundane result verbs, show in (26).[7] A floor can be swept with no change in the floor resulting, but if a vase is broken then there has been a change to the vase.

(25) a. Tracy just swept the floor, but nothing is different about it.
b. Bob just yelled, but nothing is different about him.
(26) a. *Shane just broke the vase, but nothing is different about it.
b. *Shane just destroyed his house, but nothing is different about it.

But the *nothing different* test may not be as clear cut as Beavers & Koontz-Garboden [5] would like it to be. Consider again the case of canonical mundane manner verbs like *nibble*. If the squirrel nibbles at the apple even a little bit, then some little bit of the apple is no longer there, and it is not the case that 'nothing is different about it'. Similarly for *wipe*, if Mary wipes the table, then some contact with the table must be made, and again it is not the case that 'nothing is different about it' as it has now had contact with something. Instead, what seems to be the case in all of these instances is that there is no relevant result such that that result is encoded into these manner verbs. That the apple is minimally consumed in a nibbling event, or that contact with the table is made in a wiping event isn't a relevant or salient result from our human perspective.

(27) a. ??The squirrel nibbled at the apple, but nothing is different about it.
b. ??Mary wiped the table, but nothing is different about it.

Husband [10] suggests a different approach to detecting the result component of *manner of death* verbs, following a more general restriction on result predicates noted by Tenny [11]: only one result is possible per (complex) event. We can see this constraint on display in (28) in which verbs that clearly result in death, namely *kill* and *die* are judged to be incompatible with the resultative *to death*.[8]

(28) a. *North Korea killed two civilians to death.
b. *Kurt Cobain died to death.

Interestingly, some *manner of death* verbs seem to allow the resultative *to death* as seen in (29), while other *manner of death* verbs are, as expected, unacceptable with the resultative *to death* as seen in (30).

(29) a. The state of Florida electrocuted Ted Bundy to death.
b. Joe Delaney drowned to death.
c. Richard Montague was strangled to death.
d. Michael Hutchence asphyxiated himself to death.
e. Napoleon was poisoned to death.
(30) a. *The revolutionaries guillotined King Louis XVI to death.
b. *Herennius decapitated Cicero to death.
c. *Geoffrey quartered Dafydd ap Gruffydd to death.
d. *Thích Quảng Dúc immolated himself to death.
e. *Terrorists beheaded Daniel Pearl to death.

This suggests that *manner of death* verbs as listed in (15) in fact form two separate classes. The class of *manner of death* verbs in (30) appear to encode a result meaning component, thus blocking the addition of a second resultative with the same meaning like the undisputed result verbs *kill* and *die* in (28). The other class of *manner of death* verbs in (29), however, do not seem to encode a result meaning component. Because this latter group doesn't appear to encode a result meaning component, the addition of a resultative with the meaning *to death* is acceptable.

An examination of naturally occurring examples in the Google Books corpus with and without *to death* reveals a similar picture in a comparison of (31) and (32). Verbal uses were isolated with *was*, *were*, or *been Ved* both with and without *to death*, search numbers were summed together, and the percentage of *to death* uses are given in the final column. The *manner of death* verbs in (31) uniformly have a relative high co-occurrence with *to death* except for *drown*, while those in (32) are all relatively low in their concurrence with *to death*, with some exceptions for *crucify*, *guillotine* and *impale*. These exceptions conflict with speaker judgments, suggesting that other features of these particular cases should be explored in future research. Overall though, naturally occurring examples corroborate the use of the *to death* diagnostic to identify two separate classes of *manner of death* verbs.

	verb	was/were/ been Ved	was/were/ been Ved to death	%
(11)	asphyxiate	29 540	179	0.606%
	hang	1 620 000	4150	0.256%
	drown	2 750 000	710	0.026%
	electrocute	73 400	879	1.198%
	gas	87 900	4266	4.853%
	poison	665 300	5443	0.818%
	smother	151 800	5850	3.854%
	strangle	203 900	15 020	7.366%
(12)	behead	679 500	9	0.001%
	crucify	1 165 200	772	0.066%
	decapitate	110 100	2	0.002%
	disembowel	29 920	0	0.000%
	eviscerate	23 340	1	0.004%
	guillotine	64 700	83	0.128%
	gut	125 800	4	0.003%
	immolate	26 780	0	0.000%
	impale	64 500	64	0.099%
	quarter	382 100	2	0.001%

Why might some supposed *manner of death* verbs occur with *to death* resultatives? If we examine the set of *manner of* *death* verbs that occur in (29) and (31), they are the kinds of incidents that are, in fact, known to be survivable. An individual can be electrocuted, for instance, by being struck by lightning, and yet survive to tell the tale. There are also cases of individuals being hanged, only to be cut down and revived before dying. Therefore, the events that these verbs name are not true manners of death, but instead are simply events with a manner that can, at times, lead to death. As such, these verbs are more like the manner verbs *shot* and *stab* in (6).

The *to death* diagnostic acts as a strong test for true *manner of death* verbs. To the extent that native speakers find the combination of a *manner of death* verb unacceptable with *to death*, there is good reason to claim that that verb encodes a result. To that end, a revised list of *manner of death* verbs is given in (33).[9]

(33) Manner of Death Verbs (revised): behead, crucify, decapitate, disembowel, eviscerate, guillotine, gut, immolate, impale, quarter, . . .

Turning to other diagnostics, native speaker intuitions about the grammar of *manner of death* verbs are also revealing. Like more mundane result verbs, *manner of death* verbs do not allow implicit direct objects. As the examples in (34) demonstrate, the individual who is being guillotined or quartered or beheaded must be overtly mentioned. This is further evidence that *manner of death* verbs encode a result as part of their verbal concept.

(34) a. *The revolutionaries guillotined.
b. *Herennius decapitated.
c. *Geoffrey of Shrewsbury quartered.
d. *Thích Quảng Dúc immolated.
e. *Terrorists beheaded.

The inability to occur with non-subcategorized objects also favours the encoding of a result meaning component in *manner of death* verbs. The examples in (35) demonstrate that the object of *manner of death* verbs cannot be selected by a predicate that is not the verb. Thus, while is it sensible to think that decapitation is a good way to silence one's enemies or that self-immolation is the ultimate of compassionate acts to resist religious intolerance, a speaker can not express this using (35b) or (35d).

(35) a. *The revolutionaries guillotined King Louis XVI off the throne.
b. *Herennius decapitated Cicero silent.
c. *Geoffrey of Shrewsbury quartered Dafydd ap Gruffydd into exile.
d. *Thích Quảng Dúc immolated himself compassionate.
e. *Terrorists beheaded Daniel Pearl kidnapped.

(b) Manner in *manner of death* verbs

Having established more clearly the result component found in the more restricted set of *manner of death* verbs in (33), a second challenge arises concerning the status of the manner component of these verbal concepts. In a careful exploration of the purported *manner of death* verb *drown*, Rappaport Hovav [16] argues that some *manner of death* verbs may, in fact, simply be result verbs that lack a manner. For *drown*, she argues that it encodes only a result, i.e. that someone/something becomes submerged, often in water. Although the verb *drown* was already removed from the list of *manner of death* verbs in (33), other verbs on this list may also be threatened. For instance, as noted above, the verbs *decapitate* and *behead* entail the loss of a head, and these entailed meanings might, in fact, simply be results as they appear to encode a scalar change from having to not having a head. Similarly, *quarter* may too only encode a scalar result that something/someone is separated into four pieces. Stronger evidence therefore is needed to secure the manner component of *manner of death* verbs.

An initial diagnostic for the presence of a manner meaning in a verbal concept involves denial of the manner meaning. As noted above, the manner component of *manner of death* verbs is often fairly clear, allowing the denial of manner test to be more straightforwardly applied and interpreted. As *manner of death* verbs differ from one another specifically in the manner in which the event they name unfolds, it is unsurprising that attempts to deny their named manner, shown in (36), results in contradiction. For those *manner of death* verbs where the manner meaning can be spelled out in more detail, denial of the subprocesses of the manner meaning are also contradictory, as in (37). These denial diagnostics are initial evidence that *manner of death* verbs encode a manner component as part of their verbal concept.

(36) a. *Geoffrey of Shrewsbury quartered Dafydd ap Gruffydd, but not by quartering him.
b. *Terrorists beheaded Daniel Pearl, but not by beheading him.

(37) a. *The revolutionaries guillotined King Louis XVI, but not by releasing the rope and letting the blade drop.
b. *Herennius decapitated Cicero, but not by striking several times with a sword at his neck.
c. *Thích Quảng Dúc immolated himself, but not by setting himself on fire.

Beavers & Koontz-Garboden [5] suggest other diagnostics to identify and isolate the manner component of a verbal concept. One diagnostic involves the relationship between a verb and its subject. Result verbs place few requirements on their subjects, allow human agents like John, instruments like a hammer, or natural forces like an earthquake to be subjects, as shown in (38). Manner verbs, however, place more requirements on their subjects, so human agents like John can appear as subject, but not instruments like a stiff brush or natural forces like an earthquake, as shown in (39).

(38) a. John broke/shattered the vase (with a hammer).
b. The hammer broke/shattered the vase.
c. The earthquake broke/shattered the vase.

(39) a. John scrubbed/wiped the floor (with a stiff brush).
b. ??The stiff brush scrubbed/wiped the floor.
c. ??The earthquake scrubbed/wiped the floor.

Importantly, it is not that instruments cannot appear with manner verbs. A comparison of (39a) and (39b) demonstrates that this restriction is more specifically related to instruments being subjects. Additionally, as Beavers & Koontz-Garboden [5] note, natural forces are not omitted from manner verbs simply because they could not plausibly function as a direct cause for scrubbing/wiping. If a wet towel were on the floor at the time of an earthquake, it could be moved around by the earthquake, thereby scrubbing/wiping the floor. However, even with this scenario in mind, (39c) is judged to be odd. Instead, manner verbs like *scrub* and *wipe* appear to encode a meaning that involves a specific method of applying an instrument to a patient.

Turning to *manner of death* verbs, these also appear to place strict requirements on their subjects, allowing agents like revolutionaries, but not instruments like a rusty blade or natural forces like a heavy wind. Again in these cases, a comparison of (40a) and (40b) shows that the instrument can appear with the verb, just not as its subject, and for natural forces in (40c), a direct cause is plausible, but it fails to make these cases acceptable.

(40) a. The revolutionaries guillotined King Louis XVI (with a rusty blade).
b. ??The rusty blade guillotined King Louis XVI.
c. ??A heavy wind guillotined King Louis XVI (by loosening the blade).

A second diagnostic they deploy involves distinguishing the temporal duration of the manner component from the temporal duration of the result component. When an event requires a complex process to unfold, the complexity of this set of processes requires a non-trivial interval of time to elapse. Because of this requirement, complex meanings are temporally durative.

Temporal durativity can be diagnosed with a *took time* test [17]. In particular, a durative 'during 5 min' interpretation of *take 5 min* can occur with a complex event. Simple events only allow for a punctual 'after 5 min' interpretation to occur. For manner verbs, *take 5 min* can only be interpreted as 'after 5 min' for a simple manner action like *blink* in (41a), but is ambiguous between an 'after 5 min' or 'during 5 min' interpretation for a complex manner action like *run* in (41b). For result verbs, Beavers [15] furthermore demonstrates that *take 5 min* can only be interpreted as 'after 5 min' for a simple two-point scalar change result like *break* in (42a), but is ambiguous between an 'after 5 min' or 'during 5 min' interpretation for a complex multi-point scalar change result like *clean* in (42b).[10] Therefore, to use this test to isolate a manner meaning for a possible verbal concept encoding both manner and result meanings, we need to know both whether the manner of the verbal concept is simple or complex and whether the result of the verbal concept is simple or complex.

(41) a. It took John 5 min to blink. ('after' only)
b. It took John 5 min to run. ('after' or 'during')
(42) a. It took John 5 min to break the vase. ('after' only)
b. It took John 5 min to clean the vase. ('after' or 'during')

For *manner of death* verbs, the result component ultimately represents a simple two-point scale: not dead or dead.[11] Because of this, we would expect a *take time* test to only permit an 'after' interpretation if these verbs merely encoded this simple result. However, some *manner of death* verbs also permit a 'during' interpretation, and this interpretation must be linked to a complex manner.[12] Beavers & Koontz-Garboden [5] observe that the verb *crucify* in (43a) can have a durative interpretation in addition to an 'after' interpretation. On its durative interpretation, the complex non-scalar event process encoded in the manner meaning of *crucify* is highlighted: an individual is tied/nailed down, hoisted upright and then monitored until death. Similarly, a durative interpretation of *disembowel* highlights a distinct complex non-scalar event process, requiring a horizontal incision to the belly, removal of the gastrointestinal track though the incision and monitoring until death.

(43) a. It took Aegeas' men three days to crucify St. Andrew . . .
after three days: because that is how long it took for St. Andrew to die.
during three days: because that is how long it took to tie St. Andrew down, hoist him up and wait for his death.
b. It took executioners several hours to disembowel Gérad . . .
after several hours: because that is how long it took Gérad to die.
during several hours: because that is how long it took to make an incision in Gérad's belly, remove his intestines and wait for him to expire.

Importantly for both *crucify* and *disembowel*, the complex manner highlighted by the durative interpretation is idiosyncratic to the particular verb, suggesting that these complex manners must be specifically encoded in these particular verbal concepts.

Taken together, the diagnostics reviewed above along with others developed and applied in Beavers & Koontz-Garboden [5] strongly support the argument that *manner of death* verbs are counterexamples to manner/result complementarity. Moreover, the status of *manner of death* verbs as counterexamples to what is otherwise a well-supported constraint on verbal meaning suggests that *manner of death* events are somehow specially marked in human thought. In the next section, however, I will outline a key distinction between the manner and result components of *manner of death* verbs.

4. Assertion, presupposition and *manner of death* verbs

In defiance of manner/result complementarity, *manner of death* verbs encode both a manner and a result meaning component. However, the idea of encoding that we have been using up to this point has been somewhat unspecified and has treated meaning as a single unified phenomenon. However, research in semantics and pragmatics has found that the variety of meanings that are composed together in a single sentence are often not of a single type. Instead, sentence meaning can be split apart on several different levels of meaning. One question to ask is whether lexical meanings (i.e. the meaning components of verbs) can be similarly split apart into multiple types, each possibly encoded on a different level. Here, I will focus on two types of meaning: meaning that is asserted, and meaning that is presupposed.

Asserted meaning is the meaning of a sentence that is directly expressed. It is often what is taken to be the at-issue or new content of a sentence that is foregrounded by the speaker. Presupposed meaning, on the other hand, is the meaning of a sentence that is more indirectly expressed. It is often taken to be meaning that is not-at-issue and may be backgrounded as part of what speakers take to be uncontroversial and not contested, i.e. the common ground between speakers.

Consider the case of a sentence with the aspectual verb *stop* given in (44), which bears two meanings given in (44a) and (44b). These two meanings have different status. The meaning in (44a) is the meaning that is asserted by the speaker. This meaning is what is said to be at-issue, bringing in new information to the unfolding discourse. The meaning in (44b), however, is something that the speaker is taking for granted, that is, the speaker presupposes that smoking used to occur.

(44) John stopped smoking
  a. Assertion: John does not smoke now.
  b. Presupposition: John used to smoke.

As with the distinction between manner and result meanings discussed above, perhaps the clearest way to distinguish assertion from presupposition is by way of their behaviour with respect to certain linguistic diagnostics. The classic diagnostics for identifying asserted versus presupposed meanings are their behaviour with questions and negation: assertions can be directly questioned and negated; presuppositions cannot [18].

When a yes/no question is asked of (44) as in (45), native speakers take the question being asked to only be about (44a), whether or not John smokes now. The question cannot be asking about (44b), whether or not John used to smoke. Intuitively, it would be very misleading for a speaker to ask (45) if, in fact, John has never smoked. Instead, the proposition that John used to smoke in (44b) is taken to be common ground. Thus, a response to the question that attempts to deny that any smoking ever occurred seems like an unacceptable continuation of the discourse.

(45) Speaker A: Did John stop smoking?
  a. Speaker B: No, John still smokes. (Assertion)
  b. Speaker B: *No, John has never smoked! (Presupposition)

Similarly, negation of (44) as in (46) cannot negate (44b), that John used to smoke, but only (44a), that John doesn't smoke now. As with questions, a continuation of the discourse that attempts to argue that no smoking ever took place is unacceptable.[13]

(46) Speaker A: John did not stop smoking.
  a. Speaker B: Wrong. He did stop smoking. (Assertion)
  b. Speaker B: *Wrong. He has never smoked! (Presupposition)

Thus, presuppositions have a special status when it comes to sentence-level meaning operators like questions and negation. Because they cannot be the targets of these sentence-level meaning operators, presupposed meanings are said to project outside of the scope of questions and negation. Assertions lack this property, and are thus targeted by questions and negation.

Given this difference in the status of asserted compared to presupposed meaning and the possibility that different meaning components could be encoded on different levels of meaning, it is important to establish what types of meaning the manner and result meaning components of *manner of death* verbs are.

Beginning with the manner component of *manner of death* verbs, the discourses given in (47) are evidence that the manner component of *manner of death* verbs does not project out of questions. When Speaker A asks a yes/no question, Speaker A is asking about the manner in which the individual died. This can be seen in that the responses by Speaker B, which may affirm the manner or deny it and propose a different manner, are acceptable continuations for discourse.

(47) a. Speaker A: Was King Louis XVI guillotined?
  Speaker B: Yes, he was killed by a guillotine.
  b. Speaker A: Was Cicero decapitated?
  Speaker B: No, he was stabbed.
  c. Speaker A: Was Dafydd ap Gruffydd quartered?
  Speaker B: Yes, he was cut up into four pieces.
  d. Speaker A: Did Thích Quảng Dúc immolate himself?
  Speaker B: Yes, he set himself on fire.
  e. Speaker A: Did terrorists behead Daniel Pearl?
  Speaker B: No, he was shot in the back of the head.

The manner component of *manner of death* verbs also does not project out of negation, as seen in the discourses given in (48). When a speaker negates these sentences, he is negating the particular manner being asserted by the verb. Proposing a different manner in light of this negation is, thus, acceptable when continuing a discourse.

(48) a. King Louis XVI was not guillotined. He was strangled to death!
  b. Cicero was not decapitated. He was stabbed!
  c. Dafydd ap Gruffydd wasn't quartered. He was drawn and hung.
  d. Thích Quảng Dúc didn't immolate himself. He died in his sleep.
  e. Terrorists didn't beheaded Daniel Pearl. He was killed by firing squad.

Turning to the result component of *manner of death* verbs, the discourses given in (49) are evidence that the result component of *manner of death* verbs projects out of questions. By asking a yes/no question, Speaker A is not questioning whether the individual died. This can be seen in that the responses by Speaker B, which affirm or deny that the individual's death are unacceptable continuations for discourse.

(49) a. Speaker A: Was King Louis XVI guillotined?
  Speaker B: *No, he did not die.
  b. Speaker A: Was Cicero decapitated?
  Speaker B: *No, he did not die.
  c. Speaker A: Was Dafydd ap Gruffydd quartered?
  Speaker B: *Yes, he was killed.
  d. Speaker A: Did Thích Quảng Dúc immolate himself?
  Speaker B: *No, he did not die.
  e. Speaker A: Did terrorists behead Daniel Pearl?
  Speaker B: *Yes, he died.

The result component of *manner of death* verbs also projects out of negation, as seen in the discourses given in (50). When a speaker negates these sentences, he cannot be directly negating the individual's death. Thus, expressing that the individual continued to live immediately after negating the *manner of death* verb sentence is unacceptable when continuing a discourse.

(50) a. King Louis XVI wasn't guillotined. *He remained King of France for years.
  b. Cicero wasn't decapitated. *He led the revolution against Caesar.
  c. Dafydd ap Gruffydd wasn't quartered. *He escaped to France.

d. Thích Quảng Dúc didn't immolate himself. *He's alive in Vietnam.
e. Terrorists didn't behead Daniel Pearl. *He's an active journalist in the Middle East.

Evidence from questions and negation point to differences in the manner and result meanings encoded in *manner of death* verbs. The manner component is an assertion; the result component is a presupposition. Importantly, both assertions and presuppositions are lexical entailments, i.e. meanings that must be encoded in a verbal concept [19]. As such, *manner of death* verbs remain counterexamples for the original specification of manner/result complementarity given in (12). The distinction between the levels of meaning of each of these components, however, suggests an important difference in the way they are encoded within a single verbal concept.

5. Manner/result complementarity and the special status of death

The previous two sections have demonstrated that *manner of death* verbs encode both manner and result meaning components and that these components reside at different levels of meaning: the manner component is asserted, and the result component is presupposed. Given this analysis, two issues remain to be addressed. The first issue concerns the status of manner/result complementarity as a constraint on verbal meanings. As *manner of death* verbs are counterexamples to manner/result complementarity as presented in (12), how should we think about possible constraints on verbal meanings? The second issue concerns the seemingly special status of death. Why is it that results of death can be accommodated into complex verbal concepts when other types of results fail to do so? I'll address each of these in turn.

(a) Complementarity of assertions

Considering the implications of *manner of death* verbs as counterexamples to manner/result complementarity, one tempting avenue is to abandon any hard grammatical constraint on verbal concepts. However, the fact that the manner and result components of *manner of death* verbs reside on different levels of meaning suggests an alternative pathway. Complementarity may be a hard constraint after all, but perhaps it is a constraint only on certain levels of meanings.

Widening our view somewhat, *manner of death* verbs are not the only verbs that have some kind of complex verbal concept. Consider the classic case of a verb like *regret* in (51) when compared with *dream* in (52). In addition to their more overt meanings (disappointment and dreaming, respectively), both verbs take propositions like *he smoked* as complements, but the status they give to their propositions is distinct. The verb *regret* requires its proposition to be a fact, something true of the real world, while *dream* has no such requirement. Saying (51) assumed the proposition *he smoked* to be true. Therefore, we say that *regret* is a factive verb.

(51) Sam regrets that he smoked.
a. Assertion: Sam is disappointed that he smoked.
b. Presupposition: Sam has smoked.
(52) Sam dreamed that he smoked.
a. Assertion: Sam had a dream that he smoked.
b. Presupposition: ~~Sam has smoked~~.

Furthermore, we can demonstrate that the disappointment meaning and factive meaning carried by *regret* reside on different levels of meaning. If a speaker asks a yes/no question of (51), as in (53), the speaker is asking about Sam's disappointment, not about the underlying fact of his smoking. Similarly, if the speaker negates (51), as in (54), they are negating Sam's disappointment, not the underlying fact of his smoking. Also, attempts to carry on the discourse by directly addressing the factive meaning are considered unacceptable to speakers. Therefore, the factive meaning of *regret* is encoded as a presupposition because it projects out of questions and negation.

(53) Does Sam regret having smoked?
a. No, he isn't disappointed that he smoked. (Assertion)
b. *No, he didn't smoke. (Presupposition)
(54) Sam doesn't regret having smoked.
a. He enjoyed smoking a lot. (Assertion)
b. *He didn't smoke at all! (Presupposition)

A different case comes from the treatment of the verb *acquiesce* in (55), which also has at least two components to its meaning: an acceptance meaning and a reluctance meaning. This suggests that *acquiesce* also encodes a complex underlying verbal concept.

(55) Bill acquiesced to our demands.
a. Assertion: Bill accepted our demands.
b. Presupposition: Bill was reluctant to accept our demands.

As with *regret*, only one of these two meaning components is asserted. A speaker questioning (55) as in (56) can only be directly asking about Bill's acceptance of the demands, not about Bill's willingness to accept the demands. The same pattern is revealed by a speaker negating (55) as in (57), with negation only able to target Bill's acceptance of the demands, not his reluctance to accept them.

(56) Did Bill acquiesce to our demands?
a. No, Bill did not accept our demands. (Assertion)
b. *No, it was easy for Bill to accept our demands. (Presupposition)
(57) Bill did not acquiesce to our demands.
a. He did not accept a single one. (Assertion)
b. *He found it easy to accept our demands. (Presupposition)

Looking beyond verbs for the moment, the much discussed noun *bachelor* is known to have many components to its meaning. To appropriately apply *bachelor* to an individual, that individual needs to be someone who is unmarried, human, male, of marrying age, not previously divorced, and not restricted from marriage. When we probe each of these meanings, we find that speakers presuppose most of these attributes. The only component that is asserted is the unmarried meaning component. As seen in dialogues with questions in (58) and negation in (59), all other components (human, male, of-marrying-age, not-divorced, and possibility-of-marriage) are found to be presupposed (P. Jacobson 2010, personal communication).

(58) Is Jessie a bachelor?
a. No, he's married to Clare.
b. *No, he's a humpback whale!
c. *No, Jessie's a girl!
d. *No, he's a 5 year old!

e. *No, he's a divorcée!
f. *No, he's a catholic priest!

(59) Jessie's not a bachelor
a. He's married to Clare.
b. *He's a humpback whale!
c. *Jessie's a girl!
d. *He's a 5 year old!
e. *He's a divorcée!
f. *He's a catholic priest!

The generalization behind these examples and those concerning *manner of death* verbs is that complex lexical concepts assert only one component of their meaning, with other meaning components forming some kind of presupposition. In the light of these observations, a revision to the initial hypothesis as it pertains to manner/result complementarity in verbal meaning is proposed in (60), which restricts complementarity to the assertive level of meaning.

(60) *Manner/result complementarity* (*revised*): Manner and result meaning components are in complementary distribution with respect to the asserted level of meaning: a verb can assert only one.

This revised version of manner/result complementarity raises several questions that I would like to briefly explore. First, given (60), we would expect to find classes of verbs that assert their result and presuppose their manner, though at present no cases are known to me.[14] While this possibly suggests a further refinement of manner/result complementarity, another potential explanation comes from event structure differences between manners and results. Verbs asserting a result and presupposing a manner may be unattested because of the way our grammar encodes different event structure components: manner verbs are modifiers of event structure, whereas result verbs are arguments of event structure [20]. Modifiers and arguments have a different status in the grammar more generally. By way of explication, modifiers like the adverb *yesterday* in (61) are always optional elements. They are not inferred when omitted and are not covert, so speakers do not infer *yesterday* in (61b) or (61d) where *yesterday* is absent. Arguments like *something* in (61), however, can in certain cases be inferred when omitted and may be covert. So speakers can infer that something was eaten in (61c) and (61d) even though *something* is absent.

(61) a. John ate something yesterday.
b. John ate something.
c. John ate yesterday.
d. John ate.

Because the presence of a modifier is always optional and, thus, unpredictable, it may take on a more central role in meaning. This difference may interact with the process of verb learning, blocking certain meaning combinations from easily arising. While not currently worked out in detail, consider the following sketch of a theory of this interaction. When learning the meanings of a verb with a modifier and a result meaning, the modifier meaning of the verb must be asserted because modifiers are grammatically unpredictable. With its asserted meaning filled, the result meaning of the verb must be presupposed because of manner/result complementarity, and can be presupposed given its status as an argument.

Another potential issue concerns the limits, if any, on the number of presuppositions a word can encode. Given attested examples like *bachelor*, it seems that the number of presuppositions a lexical item can have may be potentially large. Indeed, even if the attested upper bound were discovered to be five, as found with *bachelor*, it would seem that this limit would to be more of an issue concerning the limits of human learning, memory and attention than a hard constraint coming from our mental grammars. Such a division of labour between our memory and attentional systems and our mental grammars is reminiscent of other arguments for the competence/performance distinction [21]. While our grammatical competence specifies no constraint on the content of a word's presupposition, permitting an unlimited number of meaning components at that level of meaning, the number that is attested in natural language is the result of the limits of the memory and attentional capacity of the performance systems that we use to acquire, comprehend and produce language.

Finally, there is a wider question as to why languages seem to have very few verbal concepts that encode both a manner and a result component. One possibility, again drawing on preferences related to human memory and attention, is that native speakers may tacitly prefer to minimize the number of meaning components encoded in a verb given the morphology of their language.[15] While English is relatively poor morphologically, we may see evidence of this in Dutch where some *manner of death* verbs require a verbal prefix that combines with a verb stem to create a result interpretation, as given in (62).[16]

(62)				
a.	*ont-hoofden*	'decapitate/behead'	*hoofden*	'head'
b.	*ver-drinken*	'drown'	*drinken*	'drink'
c.	*ver-stikken*	'asphyxiate'	*stikken*	'choke'

Arsenijevič [23, p. 5] makes similar observations about verbal prefixes in Serbo-Croatian. He proposes that this prefix tells speakers that 'the strangling event took place in its full extent, with its characteristic phase transition of Marija switching from being alive to being dead.'

(63) a. Jovan je gušio Mariju.
Jovan AUX strangle Marija
'Jovan was strangling Marija.'
b. Jovan je u-gušio Mariju.
Jovan AUX in-strangle Marija
'Jovan strangled Marija (to death!).'

As these morphologically rich languages can encode results through a verbal affix, constructing a verbal concept expressing both a manner and a result without using a verbal prefix may be dispreferred. Of course, the addition of a result meaning by verbal prefix may change the status of the result meaning itself from one that is presupposed by the speaker to one that is now asserted, and understanding the extent of such differences requires further cross-linguistic evidence and exploration.

(b) The special status of death

Why is it that, of all the results that we humans witness and encode in our languages, events that result in death appear to stand out? Indeed, aside from the class of *manner of death* verbs discussed here, other examples of violations of manner/result complementarity are in rather short supply.[17] The potentially unique and certainly exceptional status of the result of death in *manner of death* verbs raises some important questions: what is required for an additional meaning component to be accommodated in a verbal concept, and why are results of death able to meet these requirements?

At least two requirements appear to be at play. First, the meaning component must be important and prominent to human interest. Second, the component must satisfy the constraints of our mental grammars. On the first, additional meaning components clearly need to be salient to human thought to be accommodated into a more complex verbal concept. If a meaning component is not salient, then it is highly unlikely to become encoded in a verbal concept, simply again because of the limits on human memory and attention in place during word learning. Salience is very vague requirement, but consider another case where a similar notion appears to be at play, the rather muddled realm of implicit arguments of verbs. Take the verb *steal*, for example. Native speakers know that every event of stealing requires a thief, a victim, and some loot. They also know that events of stealing must take place at a particular time. Speakers are not required to explicitly mention all of these arguments. Given (64b) to (64d), we can see that speakers can leave the victim, the time or both implicit. However, when left unmentioned, the status of some arguments seems more salient compared to others. In (64d) the victim and the time of the stealing event remain implicit, and yet it is intuitively clear that the implicit victim of the event is far more salient in our minds than the implicit time of the event, even though both arguments are entailed by the event itself.

(64) a. Valerio Viccei stole £60 million from Knightsbridge Safe Deposit Centre on 12 July 1987.
b. Valerio Viccei stole £60 million on 12 July 1987.
c. Valerio Viccei stole £60 million from Knightsbridge Safe Deposit Centre.
d. Valerio Viccei stole £60 million.

Williams [28, p. 85] proposes that arguments that are either required overtly or implied by a verb make up a mental representation he calls a *sketch*, similar to earlier ideas found in Fillmore [29,30], Langacker [31] and many others. In his terms, a sketch ‘provides a psychological perspective on things that satisfy the predicate, perhaps engaged by default when one thinks of a thing as a satisfier of the predicate’. Thus the verbal concept of *steal* engages the notion of a victim by default as part of a stealing event, but not the notion of a time that resides elsewhere.

In a similar way, the verbal concepts for *manner of death* verbs also engage with a result of death by default and seem to be part of a *manner of death* verb’s sketch.[18] Native speakers know that every event named by a *manner of death* verb results in death by default, and this result of death is certainly salient enough in our minds when we think of events of beheading, guillotining or immolation to, for instance, block *to death* resultative, as seen in (30). Importantly, it is not a grammatical requirement that *manner of death* verbs exist in natural language. Instead, it is this functionalist element of prominence to human interest that highlights the result of death component and enables it to be accommodated into a *manner of death* verbal concept.

Where grammatical requirements play an important role, however, is in the treatment of how these additional meaning components are incorporated into a complex verbal concept. This is the second requirement that any additional meaning component must also be able to satisfy our grammatical restrictions on lexical encoding. Our mental grammar gives us the resources to format a lexicon, but as with any format, certain constraints must be met. For *manner of death* verbs to overtly name, and thus assert, the manner of an event, manner/result complementarity as revised in (60) required us to either background any other prominent meaning component as a presupposition or abandon the attempt to incorporate it. We can see both of these routes being taken by verbs that name events that often result in death. As noted in §3, events named by verbs like *electrocute*, *drown*, *strangle* or even *hang* are, in fact, potentially survivable, thus even for those cases where death does occur, we do not accommodate a presupposed result of death into their verbal concepts. But for events named by true *manner of death* verbs given in (33), a result of death appears unavoidable.[19] To meet manner/result complementarity, the result of death component is accommodated as a presupposition in these verbal concepts. Adding the result component in this way satisfies the manner/result complementarity constraint.

Thus it appears that both the formal constraints of our mental grammars and the functionalist pressures related to broader human interests and concerns conspire to give us the lexicons that we have. Our verbs are required to satisfy certain constraints on their formats that, by hypothesis, are dictated by manner/result complementarity in (60), and within those constraints, we encode the meanings that capture our attention and are prominent to our interests. Results of death certainly rise to the necessary level of importance in *manner of death* verbs, suggesting that results of death hold a special status in human thought.

6. Conclusion

A close inspection of the verbal concepts that name events surrounding death has revealed some of the exceptional ways that we think about events of death, providing a unique perspective on our mental representations of thanatological phenomena. The discovery of *manner of death* verbs as a special verbal class that violates the long-held manner/result complementarity constraint on verbal meaning suggests that results of death hold a special status in human thought and interest. In this paper, we have examined the manner and result components of *manner of death* verbs, finding that they are, indeed, encoded by these verbal concepts. Given that these verbs appear to name manners, the fact that results of death are also encoded was surprising and can be seen as further evidence that human cognition treats events of death as prominent and highly salient. Having a highly salient result but also needing to name a manner, *manner of death* verbs bypass the manner/result complementarity enforced by our mental grammar and constraints on learnability, encoding these meaning components on different levels of meaning. The asserted meaning of *manner of death* verbs encodes their named manner, while presupposing the prominent result of death meaning component. Results of death, it seems, are of such an exceptional status to our minds that we presuppose them when talking about the manners of events that result in death.

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Endnotes

[1] Standard linguistic practice is to star (*) sentences that native speakers judge to be unacceptable and use ? and ?? to indicate judgments of degraded acceptability.

[2] Other verbs that may belong in this class include (ia), which require intentional action as a manner and result in death (on *murder* and *slay* specifically, see Jimenez [6]). These verbs are distinct from other death-related verbs, like those in (ib), which relate to the magnitude of the result of death.

(i) a. Agentive Manner of Death Verbs: *assassinate*, *butcher*, *dispatch*, *execute*, *massacre*, *murder*, *sacrifice*, *slay*, …
  b. Magnitude of Death Verbs: *annihilate*, *decimate*, *eradicate*, *exterminate*, *extirpate*, *obliterate*, *slaughter*, …

[3] This theory of scales is thoroughly discussed in Kennedy & McNally [8] and applied to events of scalar change in Kennedy & Levin [9].

[4] One might ask if (17a) is unacceptable because of a straightforward contradiction: an event of scrubbing simply seems to require a process of scrubbing to occur. However, simply denying that any contact occurred with the bathtub as in (ia) or altering the manner of the event as in (ib) seems unacceptable to native speakers.

(i) a. *Cinderella scrubbed the bathtub, but nothing came in contact with the bathtub.
  b. *Cinderella scrubbed the bathtub by waving a magic wand.

[5] On the scalar theory of events of change, the result of death meaning is represented by a relatively simple two-point scale of *alive/not-alive* (or *not-dead/dead*) [7].

[6] Determining the precise primitive components of meaning is a particularly difficult issue that I side-step throughout this paper. Manner meanings and result meanings have intuitive differences, but knowing what a particular manner meaning or result meaning is is not always, or even often, clear. Consider the manner verbs *saunter* and *walk*. Since sauntering seems like a more elaborate type of walking and both seem to require moving, we could ask whether the manner meaning of *saunter* contains *walk* or even *move* as part of its meaning. Interestingly, with respect to presupposition diagnostics of questions in (i) and negation in (ii), *saunter* and *walk* share the same status as assertions, whereas *move* behaves like a presupposition. This suggests that the manner components of *saunter* and *walk* are on the same level of meaning and compete with each other even though one seems to intuitively contain the other, while the meaning component *move*, which is intuitively contained in both, is some kind of presuppositional component for both *saunter* and *walk*.

(i) Did Sally saunter/walk down the street?
  a. No, Sally walked/sauntered down the street.
  b. *No, Sally moved down the street.

(ii) Sally didn't saunter/walk down the street.
  a. She walked/sauntered down the street.
  b. *She moved down the street.

[7] Beavers & Koontz-Garboden [5] include *just* in the initial clause of these sentences to highlight that any result of change due to the event is not undone by the additional passage of time.

[8] The distribution of *to death* resultatives was noted in passing in Levin [12] as part of the distinction between her *murder* and *poison* verb classes, and investigated in more depth by Boas [13], Wechsler [14], and Beavers [15]. Importantly, other factors of event structure aside from the presence of a verbal result component can affect the acceptability of *to death*, so care must be taken when applying this diagnostic.

Beavers & Koontz-Garboden [5, p. 341] suggest that the resultative *to death* with *manner of death* verbs is acceptable as redundantly expressing the resulting state of death, though they only investigate this with the verb *electrocute*. The wider investigation of *to death* resultatives with *manner of death* verbs reported in (30) and (29) reveals a more nuanced picture.

[9] To emphasize, native speakers may disagree about which verbs should or should not appear in (33), but this is not an insurmountable problem. Instead, this merely suggests that different speakers, even of the same language, may show variation in their knowledge of different verbs. Instead, what is important is that there is a class of *manner of death* verbs that passes the diagnostics laid out in this section. That set, whatever it might be for any particular native speaker, constitutes evidence against manner/result complementarity and demonstrates the special status held by death in human thought.

[10] A further ambiguity within the 'after' interpretation of a *take time* test depends on whether the event starts or completes after the given time interval. The examples in (41) have a 'start time' interpretation while a 'time to completion' interpretation is more natural for those in (42).

[11] As noted above, the exact meaning of the result component may be more particular to the verbal concept, for instance, the loss of a head for *decapitate* and *behead*, but these results are still represented by a simple two-point scale, e.g. head or no head.

[12] Other *manner of death* verbs may not have a 'during' interpretation for a *take time* test because they encode a simple manner action, such as a single 'chopping' to remove a head for *behead*, *decapitate*, and, perhaps, *guillotine*.

[13] Speakers can raise an objection to a presupposition though a variety of linguistic means, perhaps the most famous being *Hey, wait a minute!* which challenges a presupposition. When used by a speaker, judgements about the goodness of a continuation are reversed from (45) and (46); it becomes very odd to continue to talk about the assertion.

(i) Speaker A: Did John stop smoking?
  a. Speaker B: *Hey wait a minute! John still smokes. (Assertion)
  b. Speaker B: Hey wait a minute! John hasn't ever smoked! (Presupposition)

(ii) Speaker A: John didn't stop smoking.
  a. Speaker B: *Hey wait a minute! He still smokes. (Assertion)
  b. Speaker B: Hey wait a minute! He hasn't ever smoked! (Presupposition)

[14] The other two verb classes which Beavers & Koontz-Garboden [5] cite as expressing both a manner and a result are *throw* verbs and *cooking* verbs.

Briefly, *throw* verbs, while expressing a manner, do not appear to entail a change-of-location result when the location is broad enough to actually include throwing events given our world knowledge. For instance, in (i), the ball's location begins and ends with the football team, and the contradiction diagnostic used in Beavers & Koontz-Garboden [5] fails to reveal a contradiction.

(i) The football team threw/tossed/flipped the ball to each other (and it is not somewhere else).

Cooking verbs fare much better, appearing to have both a manner component expressing the way something is cooked and a result component expressing that something was cooked. However, here, like *manner of death* verbs, the manner component is asserted, as seen in (iia) and (iiia), and the result component is presupposed, as seen in (iib) and (iiib).

(ii) Did Shane poach the egg?
  a. No, Shane boiled it.
  b. #No, Shane didn't cook the egg.

(iii) Shane didn't poach the egg.
  a. He fried the egg.
  b. #He didn't cook it.

Thus neither of these two cases gives us a verb asserting a result and presupposing a manner.

[15] While the suggestion here is for a performance preference on the packaging of meanings given the surface morphology of a language, it may ultimately be that our grammars constrain the amount of meaning that can be encoded in a single linguistic element even when such a decomposition isn't surface-obvious in a language's morphology. The *No Containment Condition* (NCC) proposed by Dunbar & Wellwood [22] represents a recent suggestion in this direction, and to the extent that they are correct (and that the NCC operates on both assertive and presuppositional levels of meaning), even apparently morphologically simple *manner of death* verbs may contain two morphemes underlyingly, similar to recent arguments in Rappaport Hovav [16]. Certainly further research is required to understand the scope and limits of the NCC and its relationship with manner/result complementarity.

[16] The verb *wurgen* ‘strangle’, however, does not require this prefix, and additionally, the verb pair *op-hangen* ‘hang’/*hangen* ‘hang’ seem to both be used in cases of hanging (though they may differ in the case of hanging a portrait versus hanging a person).

[17] See endnote 14 concerning *cooking* verbs as a potential case. Other challenges to manner/result complementarity can be found in Férez [24], Zlatev & Yangklang [25], and Goldberg [26]. See Levin & Rappaport Hovav [4,27]) for arguments against these challenges.

[18] Another interesting case of implicit arguments comes from distinctions between two types of so-called instrument denominal verbs like *tape* and *hammer* [32,33]. The verb *tape* requires a fairly specific subclass of instruments to be used (requiring something with a sticky side), while those for the verb *hammer* are fairly free. In both cases, mention of a piece of tape in (ia) or a hammer in (ib) is, however, felt to be redundant as an instrument.

(i) a. John taped the picture to the wall (with a mailing label/??a pushpin/??a piece of tape).
b. John hammered the nail into the wall (with a metal rod/his shoe/??a hammer).

Some *manner of death* verbs like *behead* also appear to license implicit instrument arguments, such as *a sword* in (iib). Others, like *guillotine*, are quite specific about the instrument that is employed, and indeed, mention of a guillotine as an instrument is felt to be redundant in (iia).

(ii) a. The rebels guillotined the traitor king (with *a guillotine).
b. The rebels beheaded the traitor king (with a sword).

[19] Though seemingly unavoidable, the examples in (23) suggest that results of death do not always apply. For the theory being developed here, speakers may be able to suspend or cancel the result of death presupposition as they are able to suspend and cancel other presuppositions like that of (44), shown in (i).

(i) John has stopped smoking, if he ever even smoked in the first place.

What conditions are required for suspension or cancellation of a presupposition go beyond this paper and are left for future research.

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The lure of death: suicide and human evolution

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At some point in evolutionary history, human beings came to understand, as no non-human animals do, that death brings to an end a person's bodily and mental presence in the world. A potentially devastating consequence was that individuals, seeking to escape physical or mental pain, might choose to kill themselves.

This article is part of the theme issue 'Evolutionary thanatology: impacts of the dead on the living in humans and other animals'.

Research

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1. Introduction

A late Roman ivory casket, in the British Museum, shows in sculpted relief two contrasting examples of humans who knowingly brought death on themselves (figure 1): Jesus, who had no desire to stop living, but who believed his death would benefit all mankind; Judas, who had no thought of benefiting others, but who wanted to end his own intolerable guilt.

Suicide used to be called self-murder, *felo de se*. In an evolutionary context, the term murder is not inappropriate. Human beings have always been murderers, killers of other living beings. First, of course, killers of animal prey for meat, but also killers of other men and women. While not every ancient human would have had first-hand experience of assassination, everyone would have known and talked about it. Then, at some point, the idea must have dawned. Here's how the psychiatrist, Erwin Stengel has put it: 'At some stage of evolution man must have discovered that he can kill not only animals and fellow-men but also himself. It can be assumed that life has never since been the same to him' [1, p. 37].

The purpose of this paper is to consider just how radically life changed. I argue that the human mind must have had to evolve to a critical level of sophistication before anyone could arrive at the idea that 'I can kill myself'. However, from then on, suicide would never have been far from people's thoughts. When times were hard, some individuals would have been bound to see death as an attractive option. Yet killing themselves would usually—if not always—have been a maladaptive act. I explore how this played out historically, and what remedies, if any, were available.

2. 'I can kill myself'

It's simple to say, it's a discovery made by every growing human, but the thought of killing oneself will usually have complex layers. Clearly, it has to begin with imagining the act: you have to have a picture of how it can be done. Stengel implies that early humans acquired this from observing how animals and fellow-humans could be killed. But this hardly seems probable. The fact is most of the ways you might observe to be effective for killing another—be it with teeth or claws or fists or clubs—would not be feasible ways for you to kill yourself. Instead, for most of human history (until the advent of modern murder weapons such as guns), a more likely model for suicide will have been accidental death: falling from a cliff, drowning in a lake and bleeding to death from a cut. By imagining yourself in the victim's place, you would see that what happened to him or her by accident could happen to you by your own intent. You might still want confirmation that it can really be done. But, for

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Figure 1. Panel from an ivory casket: the Crucifixion of Christ. Late Roman, AD 420–430. Copyright © The Trustees of the British Museum. All rights reserved. (Online version in colour.)

this, you might not have to look far. In a typical human community, where suicide is already prevalent, you will have heard tell of others who have successfully killed themselves. Humans as a species are notoriously imitative. Perhaps, every suicide is at some level a 'copy-cat suicide' (which I'll return to later in the paper.)

But, now, to go deeper: when you think 'I can kill myself', who is this 'self' and what do you imagine will result from 'killing' it? Again, Stengel implies that early humans would have understood the inevitable consequences of self-killing from observing the killing of others. Bodily death, however caused, has effects that anyone can see and take on board. There's the obvious bodily decay. But the most salient change is in the dead person's role as an actor in the physical or social world. They will not be coming back. This is a fact of death that non-human animals with complex social lives can also understand up to a point. Frans de Waal describes how, when a group of chimpanzees in the Arnhem Zoo were shown a video film of the alpha-male, Nickie, who had died by drowning 2 years earlier, his erstwhile rivals panicked as if they had seen a ghost [2, p. 214]. By applying this to your own case, you would realize that you yourself once dead will no longer participate directly in the lives of others.

But we must go deeper still. For there is, of course, another meaning of 'self', and hence, the probability that self-killing will have a still more significant result. When your body dies, what happens to your mind? Once you are no longer an actor in the public realm, can you no longer be a thinker or feeler in the private one? This is not of course something you or anyone else can discover from direct observation. But it is perhaps something you can deduce from circumstantial evidence. As a human, with a 'theory of mind,' you expect to be able to infer another person's mental state from their outward behaviour. When, now, you observe that an individual's body no longer behaves in any way at all—it neither acts spontaneously nor reacts to your probes—you have very good reason to suppose there is no longer anyone at home inside. True, absence of evidence is not entirely reliable as evidence of absence. But, in fact, you yourself have had plenty of direct experience of your own mind going absent at a time of pseudo-death. When you fall asleep, and your body becomes motionless and unresponsive, you know for a fact that your mind temporarily vanishes. You may remember how as a child you cried yourself to sleep and found blessed relief in the ensuing oblivion.

Thus, kill yourself, and the result will be that in every important respect you will have removed yourself from the world. Like the parrot in the famous Monty Python sketch, once dead, you will have ceased to be; you will be an ex-human being.

3. The path to suicide

So, to return to Stengel, 'at some stage of evolution', humans made this momentous discovery. I hesitate to put a date on it. But given the cognitive skills required—counterfactual reasoning, mental simulation, time travel and theory of mind—I'd say no one would have been able to make the discovery until *ca* 100 000 years ago. Soon after that, however, just about everyone was able to make it. And since then 'life has never been the same'.

The question is what the practical impact would have been. There seems no reason to doubt that the thought of self-killing would soon enough have been translated into action. Some of those who discovered they could kill themselves would have chosen to kill themselves. Suicide leaves no trace in the archaeological record. But modern day statistics presumably throw light on past history [3,4]. Today no fewer than 1.4% of all deaths worldwide are attributed to suicide, making it the world's leading cause of violent death. Across the world more people—some 800 000 yr^{-1}—die from suicide than all wars and homicides combined. Many more make the attempt. In total, 2.7% of the world's population have tried to take their own lives. Even more plan it. Fourteen per cent, of report, have had suicidal ideation at some stage.

These figures are enough to make any demographer sit up and wonder. How could self-destructive behaviour on this scale have been persisting at such a high frequency? What does this suggest about the effects—good or bad—of suicide on human fitness? Common sense would say that self-killing must be the ultimately disadvantageous act, a sure path to genetic oblivion. But maybe this is wrong. Could suicide be biologically adaptive after all?

As I implied at the outset, there would seem to be two broad classes of suicide, distinguished by their motivation: those concerned with benefiting other humans and those concerned with benefiting primarily the one who dies. We can call these, as Émile Durkheim did (but without necessarily buying into his theoretical framework), 'altruistic' and 'egoistic' suicide. I want to suggest they can be distinguished at another level: they correspond to the two different conceptions people have of what their death will immediately achieve.

When someone kills themself in order to remove their bodily person from the world, it would seem quite plausible that they believe the knock-on effects will improve things for others. Jesus dies on the cross in the hope that by this public sacrifice he can bring about the salvation of all mankind. Or, for a more straightforward example, Captain Oates stumbles out from his cabin to die in the snow in the hope that, by relieving other members of Scott's polar expedition from the burden of supporting him, he can give them a better chance of survival.

This is altruistic suicide. Could it be biologically adaptive? It clearly could be if it does, in fact, benefit the subject's kin or social group. In one of the earliest statements of the principle of kin selection, Haldane is reported to have said 'I would gladly give up my life for two brothers or eight cousins' [5, p. 496]. Humans do not, like social insects, have a propensity for specific acts of suicide hardwired into their brains. But humans are nonetheless genetically primed with feelings of love and obligation for family and friends. Many theorists accept that this could partly explain why humans are willing to sacrifice themselves for the common good—in times of famine, or plague or war. It might also help explain cases of apparent 'suicidal generosity', as when individuals choose to die—or even submit to being ritually killed—when they have become too old and decrepit to carry on. By relinquishing their bodies in such circumstances, they could certainly be adding to their inclusive fitness. So, there might indeed be positive selection for psychological traits that abet the decision [6].

What, however, when someone kills themselves in order to remove their *own mind* from the world? Then, it is in no way plausible that they are thinking of benefiting others. The much more likely motive must be that they believe they themselves will be better off as a result. Thus, Judas Iscariot hangs himself because he cannot live with his internal sense of shame. An Indian chieftain's daughter jumps to her death from a cliff rather than marry a man she does not love. A businessman drowns himself when his company fails.

This is egoistic suicide. And it's in many ways the opposite of altruistic. Far from wanting to help others, these self-killers are thinking primarily of personal escape. They either don't care about the effect on others, or sometimes even intend some kind of vengeance. And, whether they intend it or not, the effects on family and friends are often devastating.

Now, from an evolutionary viewpoint, here's the problem. Across the world the great majority of suicides are egoistical. Anthropologist Charles MacDonald, reviewing the motives for suicide, concludes: 'A cross-cultural comparison shows that grief over, and conflict between closely related people, together with sheer physical pain and discomfort, cause or promote suicide more often than any other circumstances' [7, p. 427]. 'The victims simply want to go. They don't mean to change things . . . The suicide wants to stop hurting' [8, p. 221]. Edwin Schneidman, from a clinician's perspective, observes that the common goal of suicide is cessation of consciousness. He writes: 'the idea of cessation—that you can be free of all your problems, get out of this mess, cancel your debts, release yourself from this anguish, stop this disease is the turning point in the suicide drama' [9, p. 13].

Could this type of suicide possibly be adaptive? Surely no amount of special pleading could make it so. Many of those who do it are young. Across the world, it is the second most common cause of death in teenagers. If these young people had not died by their own hand, they would almost certainly have got over the hurt and gone on to make a success of their lives. At a stroke, they have ruined their own fitness and that of related individuals too. At the level of biology, egoistic suicide is clearly a mistake, a path to genetic extinction.

4. Self-euthanasia

So, what's going on? How can it be that so many continue to die this way? The authors I've just quoted point to the obvious explanation. Yes, it is indeed a biological mistake. But it is precisely because humans rise above biology that they can make this mistake. For, at a rational psychological level, it is not a mistake at all. Humans like all animals have an instinctive drive to escape from pain, emotional as much as bodily. When they experience 'psychache', as Schniedman calls it [10], when they feel sad, jealous, unloved or inadequate; they will do whatever it takes to make these feelings go away. But for humans, unlike animals, the question of how to escape has been left open to reason. Given their insight that killing themselves will put an end to their suffering, suicide can seem to provide a perfectly rational solution: a reliable method of *self-euthanasia*. Nothing hurts less than being dead.

Moreover, when other possible escape routes would involve time and effort, suicide can seem to provide a solution that is quick and easy too. It may, as I noted above, require intelligence to think of it, but its realization can be simplicity itself. It requires no special expertise to leap from a cliff, to drink poison or to slit one's wrists. In parts of Asia, people are known to 'hang' themselves simply by kneeling and leaning into the rope [8, p. 208].

Susan Sontag has written 'How thin the line between the will to live and the will to die. How about a hole . . . a really deep hole, which you put in a public place, for general use. In Manhattan, say, at the corner of Seventieth and Fifth. A sign beside the hole reads: 4 PM–8PM/MON WED & FRI/SUICIDE PERMITTED. Just that. A sign. Why, surely people would jump who had hardly thought of it before' [11, p. 116]. And indeed, real suicides are often unplanned and impulsive. A survey of 306 Chinese patients who had been hospitalized following a suicide attempt found that 35% had contemplated suicide for less than 10 min and 54% for less than 2 h [12].

Schneidman's term psychache may suggest major distress. But the precipitating causes for impulsive suicide can actually be astonishingly trivial. A recent review in *Science* about suicide in otherwise normal people opens with this example: 'A young mother and loyal wife, Mrs Y showed none of the standard risk factors for suicide. Villagers said she exuded happiness and voiced few complaints. But when a neighbor publicly accused Mrs Y of stealing eggs from her henhouse, the shame was unbearable. Mrs Y rushed home and downed a bottle of pesticide' [12]. In 2016, Jacintha Saldhana, a nurse in charge of the Duchess of Cambridge in a London hospital, hanged herself, a day after accepting a hoax telephone call from a radio station. In the new world of social media, it is all too common for a schoolgirl to overdose on sleeping pills because she is being bullied on Facebook.

So, people kill themselves 'when they want to go': sometimes after careful reflection, sometimes on the spur of the moment, sometimes for profound reasons and sometimes for shallow ones. Hamlet asks 'who would bear the whips and scorns of time, the oppressor's wrong, the proud man's contumely, the pangs of despised love, the law's delay, the insolence of office, and the spurns that patient merit of the unworthy takes, when he himself could his quietus make with a bare bodkin?' The answer is, evidently, by no means everyone.

The trouble is everyone has moments of despair. It is a grand, if tragic, truth about the human condition that—just because humans have so much higher ambition than other animals—hurting is bound to be a part of life. The poet Cesare Pavese said it explicitly, 'everyone has a good reason for suicide' [13, p. 99]. The philosopher Wittgenstein once told a friend that 'all his life there had hardly been a day in which he had not thought suicide a possibility' [14, p. 155]. More typically, among today's American high school students, 60% say they have considered killing themselves and 14% have thought about it seriously in the last year [15]. George Santayana spoke for too many, when he wrote: ‘That life is worth living is the most necessary of assumptions and, were it not assumed, the most impossible of conclusions’ [16].

5. Fear of death?

We have to stop to consider. Humans have *evolved* to this point: a point where a significant number live near the threshold of a self-generated catastrophe. Surely, this cannot be where evolution has rested? If the threat is as great as I've suggested, would not natural selection have come up with ways of countering it? Why have humans not evolved to have better innate defences against suicide built into their minds?

There is, of course, one level of defence we might expect to have been there from the beginning. This is a natural *fear of death*. Geoffrey Miller has written: ‘There is no way to escape the hardwired fears and reactions that motivate humans to avoid death. Suffocate me, and I'll struggle. Shoot me, and I'll scream. The brain stem and amygdala will always do their job of struggling to preserve one's life at any cost’ ([17]). Ernest Becker has famously said ‘the fear of death haunts the human animal like nothing else’ ([18, p. xvii]). If, as these authors imply, the fear of death is an evolutionarily ancient animal fear, then presumably it would always have provided an important last-ditch barrier to human suicide. In fact, its existence ought to mean that the thought ‘I can kill myself’ must usually be something of an empty boast.

I have to say I am sceptical. And not just because people do, in fact, kill themselves, sometimes almost casually. I think there is actually precious little other evidence that humans have a naturally evolved fear of death. I don't disagree, of course, with Miller that humans have hardwired fears that motivate them to avoid situations that could put them at risk of dying—pain, anoxia and so on. They do instinctively recoil from pain and thus will certainly do what they can to avoid a painful death. That's why, for example, many people when terminally ill will choose—if only they are allowed to—to be ‘put to sleep’ rather than to endure the agonies of cancer. For the same reason, those intent on suicide will take precautions to prevent instinctive fears thwarting their attempt. A case in point is David Kelly, the scientist who exposed the British Government's lies about Iraq's weapons of mass destruction. He took 29 tablets of the painkiller co-proxamol before he slit his wrists.

So, no question, people often fear *dying in pain*. As Woody Allen said, they don't want to be there when it happens. However, if and when death is inevitable, but likely to come easily, all the evidence suggests that people generally take it remarkably calmly. The German photographer, Walter Schels, has made photos of people in the terminal stages of illness, shortly before they died, and the day after. The 26 sitters for these portraits were asked how they felt about dying. They had mixed emotions: sadness, relief and resignation. But not one of them showed fear. Annoyance was more like it. One of them, Klara, remarked: ‘I'd only just bought myself a new fridge-freezer. If I'd only known’ [19, p. 106].

Ah, some theorists say, but the lack of overt fear is due to some form of *denial*. When humans contemplate death, they do become scared momentarily, but then according to ‘Terror Management Theory’ they immediately suppress it [20]. Or they deny the truth of the facts that would otherwise cause them to be scared [21]. But I believe there is a more straightforward explanation. This is that fear of death simply does not exist, as an evolved adaptation, either in humans or in any other animals.

How could that be? Why wouldn't such a useful fear have evolved, especially once humans discovered death's fuller meaning? I suggest the answer is that the ancient fear system was simply blind-sided by the discovery. There had never before been occasion to respond to any such nebulous concept as the ‘idea of death’, and now it presented special difficulties. How was natural selection to get to grips with a hypothetical state of *not being*? True, there are lesser states of notness that humans have had no trouble adapting to. They can and do have a natural fear of not being fed, not being warm, not being loved. But not being at all, not existing? This was just too elusive a concept.

I look at it this way. It's a general principle of evolution that any behaviour that can be *learned* by an individual through extended practice can be adopted by selection and become innate. So, for example, people can readily learn to fear not being fed, by experiencing famine a few times. They can learn to fear not being loved, by experiencing abandonment. And so on. What's more, they can learn such fears vicariously, by sharing what others have been through. In these cases, selection could quite well have followed in learning's path. But death is different. No one could learn to fear death through practice: ‘Hey, I've just visited the other side. I'm not going *there again*!’ Nor will there be anyone else whose experience they could draw on.

This said, we should not assume that human suicide was destined to remain unopposed. If nature was unable to arrange things so that people instinctively feared dying by their own hands, then perhaps human culture could step in to arrange it. Or, as a completely different strategy, perhaps the threat of suicide could be answered by developing a new-found appetite for staying alive. I'll consider in a moment how culture may indeed have weighed in to supplement biology.

6. The suicide meme

But first, let's take a further look at the size of the problem our ancestors faced, for we have not yet revealed the full scale of it. At the critical juncture in prehistory, when the understanding of self-killing first surfaced, just how vulnerable would early humans have been? As far as I know, no palaeo-anthropologist has ever thought to ask. But I'd say we should assume the worst. To start with at least, people would have had no kind of immunity to suicidal thoughts. In which case it's realistic to imagine a scenario where suicide would have spread like measles in an unprotected population. And, indeed, measles is an alarmingly apposite analogy, because, as contemporary evidence shows, even today the suicide ‘meme’ is highly infectious. It jumps all too easily from one mind to another.

As Durkheim noted: ‘Suicide is very contagious . . . There is the well-known story of the fifteen patients who hung themselves in swift succession in 1772 from the same hook in a dark passage of the hospital’ [22, p. 97]. I suggested earlier that almost all suicides may be copy-cats. But suicide contagion is something more: copying with positive feedback. It has been dubbed the ‘Werther effect’ after the hero of Goethe's novel, *The sorrows of young Werther*, who kills himself after falling hopelessly in love with a married woman [23]. Following its publication in 1774, there were hundreds of imitative deaths across Germany.

Recent research has confirmed just how strong the effect is [24]. Every time a celebrity suicide is given exposure in newspaper or TV, the copy-cats follow. It is estimated that Marilyn Monroe's death, in August 1962, was responsible for 200 extra suicides within a month. After a popular South Korean actress hung herself in 2008, suicides jumped 66% that month, with young hanging victims accounting for most of the increase [12].

But 66%, that's nothing. There are still parts of the world today where rates of suicide are 10 times the average elsewhere, apparently as the result of local chain reactions. MacDonald's research, among the generally contented people on the island of Palawan in the Philippines, found evidence of waves of suicide spreading through small villages. In a recent study, Jollant & MacDonald undertook a psychological autopsy of the individual victims to try to uncover predisposing factors [25]. It turned out that much the most significant risk factor was having had a close relative die from suicide. MacDonald comments: 'The child grows up accustomed to the idea. He/she sees or hears about elders, uncles, aunts, older cousins, and friends' parents killing themselves . . . Thus suicide becomes an accepted model of behaviour, an option open to the individual' [8, p. 264]. Note how the thought 'I can kill myself' can then take on an added meaning: 'I can', not only in the sense that it is practicable, but that it is permissible.

What can have happened on Palawan to get the chain reaction started? MacDonald believes that suicide was at a 'normal' level until early last century some kind of disaster struck—a cholera epidemic, a slave raid—that wrecked the villagers' lives. This caused a surge in suicides, and the wave has been propagating ever since.

So, to ask it again, how prevalent might suicide have been among our ancestors? Suppose it's true that they first became at risk *ca* 100 000 years ago. To begin with, the incidence might have remained relatively low. However, once humans left Africa, living conditions were set to become increasingly harsh. In the icy climate of central Europe 50 000 years ago, with people battling the elements and in murderous competition with their neighbours, there would have been plenty of occasion for short-term despair. If then the rate of suicide reached a critical level, it could have become epidemic. Who knows, but that suicide threatened the very survival of whole populations. There have been several genetic bottlenecks in human history, suggesting that populations crashed almost to nothing. These have been attributed to factors such as internecine strife, volcanic winter or disease. But, perhaps, the real cause was this worm inside the human mind.

7. Cultural barriers

Still, here we all are today. Against the odds, our ancestors as a species evidently managed to pull through. Given that natural anti-suicide defences were absent or slow to evolve, what else could have brought the epidemic under control? Presumably, the best hope of developing timely and transferable defences must have been human culture. Here, I have to say, the picture is complicated and not well researched. But at least some of the more recent cultural barriers to suicide are in plain view [26].

In historical times, religious authorities have repeatedly issued anathemas against suicide. Mediaeval Christianity decreed it to be a mortal sin. Self-murderers would not be given decent burial, but rather be buried at a crossroads with a stake through the heart. In all modern states, until recently, suicide and attempted suicide have been considered to be crimes under the common law. The successful perpetrator's possessions could be confiscated, and the unsuccessful one imprisoned. In some places, the party supposed to have provoked the suicide—by spurning a love-suit, say—could also face a penalty. In the UK, attempted suicide was not decriminalized until 1961. In the 10 years pre-1961 nearly 6000 people were prosecuted, of whom 5400 were found guilty, and imprisoned or fined. It was common practice in the 1950s to have a policeman sitting at the bedside of an unconscious patient in A and E, waiting to interview them.

There have also been attempts to limit the spread of the suicide meme by limiting exposure to it. In Europe, after the effect of Goethe's book became apparent, it was soon banned in several countries. In Germany, it was even forbidden to dress like Young Werther in blue coat and yellow trousers. In most countries today, there are strict guidelines for the Press intended to play down the reporting of suicide—to keep it off the front page and avoid sensational headlines.

These are deliberate measures, with suicide directly in their sight. But there are also cultural practices that can work to deter suicide without targeting it so deliberately. One obvious and important way is by instilling beliefs that are incompatible with the premise that can make suicide so appealing to someone who wants to escape: namely, the belief—the hope—that death will bring about mental oblivion. The world over, humans have invented systems of religious belief that explicitly promulgate the idea of the *mind continuing after death*. What's more, the Abrahamic religions, in particular, make a point of threatening that the afterlife for sinners, and suicides especially, will be an unpleasant one.

Now, even though humans may not be set up by nature to fear the nothingness of death, they can quite easily be set up by culture to fear the somethingness of an afterlife. The threat of hell fire can certainly set the amygdala ringing. But it needn't be so specific as fire. It could be just the threat of strangeness, the unknown. Think of Hamlet, contemplating suicide:

> But that the dread of something after death,
> The undiscover'd country from whose bourn
> No traveller returns, puzzles the will
> And makes us rather bear those ills we have
> Than fly to others that we know not of.

I'm not suggesting that the idea of a horrible afterlife was ever invented specifically to deter suicide. But if, as is surely the case, it has consistently worked to this effect, this is presumably a reason why it has taken such a hold. Some humans undoubtedly owe their lives to it.

It's evident how culture has found ways to weigh in against suicide on several levels. The measures are by and large negative ones. They are clearly not wholly effective. But there's no question they can and do work as a deterrent. The fact that suicide rates are lower in Muslim countries, for example, presumably has something to do with Muslim teachings about hell. As the exception that proves the rule, the villagers of Palawan are reported to have largely lost any faith in an afterlife [8].

But does deterrence have to be the only strategy? Wouldn't we expect more positive methods to have evolved as well?

In place of punishment or censorship or threats, why not oppose a destructive mind virus with a redemptive one?

The English priest Chad Varah founded the Samaritans in 1954, a group dedicated to talking suicides down, simply with words of reassurance. The message 'There is hope', posted on the bridge or beside the railway track, may seem to verge on the banal. But, in fact, this is the one message that human society might long ago have discovered it can give with confidence. Research shows that in nine cases out of 10, the hurt isn't going to last. Daniel Gilbert, author of the book *Stumbling on Happiness*, advises: 'Few of us can accurately gauge how we will feel tomorrow or next week . . . We expect to feel devastated if our spouse leaves us or if we get passed over for a big promotion at work. But when things like that do happen, it's soon, "She never was right for me", or "I actually need more free time for my family". People. . . mistakenly expect such blows to be much more devastating than they turn out to be' [27].

The lesson is simple: 'Don't jump now, because it's not what your future self would choose'. Have humans had to wait for a Harvard psychologist to tell them this? Thankfully, not. The message is implicit—presumably for a good reason—in much of the hand-me-down wisdom of our folk cultures: the stories, songs, proverbs and so on, that are there to remind people if ever they doubt it that life is worth living after all.

8. Sensory consciousness

What does make life worth living? The poet Byron wrote 'The great object of life is sensation, to feel that we exist even though in pain' [28, p. 28]. I suggested earlier that, in the course of history, suicide might have been countered by some newly evolved appetite for staying alive. Humans collectively might have come up with some knock-down philosophical argument to chase away Santayana's scepticism. Maybe so, though we have yet to see it. But how much more promising, at the level of the individual, if natural selection acting on human genes could have found an answer internal to the self. Could mere—mere?—*sensory consciousness* have been refashioned in the course of human evolution just so as to make people pause before they seek oblivion?

'There's night and day, brother, both sweet things; sun, moon, and stars, brother, all sweet things; there's likewise the wind on the heath.' The words are from Lavengro, the autobiographical novel of the Victorian adventurer George Borrow. As Borrow tells it, he has been reading Goethe. He's toying with the idea of suicide. He gets into conversation with a Romany gypsy, Jasper, whom he has befriended on his travels. 'What is your opinion of death?' says Borrow, as he sits down beside him. 'Life is sweet, brother, who would wish to die?' 'I would wish to die', says Borrow. 'You talk like a fool', says Jasper. 'Wish to die indeed! There's the wind on the heath, brother; if I could only feel that, I would gladly live for ever' [29, p. 180].

It strikes a deeply human chord. We *get* it. But stop to consider just how unexpected this is. How come these sweet things—'the sun, moon and stars', 'the wind on the heath'—can be reasons not to kill ourselves? How come we humans are so awestruck by sensory experience [30]?

The phenomenal quality of consciousness is widely regarded as a mystery. I've argued in my book *Soul dust* [31] that its very mysteriousness is an adaptive feature. The seemingly magical qualities of sensation—the redness of red, the saltiness of salt and the paininess of pain—have been specifically designed by natural selection to impress us with their inexplicable out-of-the-world properties. Human consciousness on this level exists as a biological adaptation precisely to 'change the value we place on our own existence' [32].

I've been taken to task by critics for suggesting that any biologically evolved organism could need a reason to live over and above the imperatives of life itself. But human beings are not *any* organism. They are the first to have had to wonder whether it's all worthwhile. We've seen in this paper the dark side. If there's a bright side, it may be that humans have come to live—perforce—in a strikingly beautiful world.

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Competing interests. I declare I do not have any competing interest.

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The integrated motivational–volitional model of suicidal behaviour

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Review

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Suicide is a major public health concern accounting for 800 000 deaths globally each year. Although there have been many advances in understanding suicide risk in recent decades, our ability to predict suicide is no better now than it was 50 years ago. There are many potential explanations for this lack of progress, but the absence, until recently, of comprehensive theoretical models that predict the emergence of suicidal ideation distinct from the transition between suicidal ideation and suicide attempts/suicide is key to this lack of progress. The current article presents the integrated motivational–volitional (IMV) model of suicidal behaviour, one such theoretical model. We propose that defeat and entrapment drive the emergence of suicidal ideation and that a group of factors, entitled volitional moderators (VMs), govern the transition from suicidal ideation to suicidal behaviour. According to the IMV model, VMs include access to the means of suicide, exposure to suicidal behaviour, capability for suicide (fearlessness about death and increased physical pain tolerance), planning, impulsivity, mental imagery and past suicidal behaviour. In this article, we describe the theoretical origins of the IMV model, the key premises underpinning the model, empirical tests of the model and future research directions.

This article is part of the theme issue 'Evolutionary thanatology: impacts of the dead on the living in humans and other animals'.

1. Introduction

Suicide is a major public health concern with at least 800 000 people dying by suicide each year across the globe and at least 20 times that number attempting suicide [1]. The pathways to suicide are complex, with suicide being the end product of an interplay of biological, clinical, psychological, social, cultural risk and protective factors [2–4]. Although knowledge of risk factors for suicide has grown markedly in recent decades [4], our ability to predict suicide is no better now than it was 50 years ago [5]. There are many reasons why the field of suicide research has not enhanced its predictive ability; key candidates include the low base rate of suicidal behaviour, as well as the fact that risk factors are often assessed in isolation and in a static rather than in a dynamic fashion [5]. In addition, until relatively, recently, there was a paucity of comprehensive theoretical frameworks that have attempted to understand the emergence of suicidal ideation and the transition from thinking about suicide to attempting suicide/dying by suicide [6].

In the present paper, we focus on one such predominant framework, the integrated motivational–volitional (IMV, [6]) model of suicidal behaviour; we describe its theoretical origins, the key premises underpinning the model, empirical tests of the model and future research directions. In brief, the IMV model is a tri-partite model that describes the biopsychosocial context in which suicidal ideation and behaviour may emerge (pre-motivational phase), the factors that lead to the emergence of suicidal ideation (motivational phase) and the factors that govern the transition from suicidal ideation to

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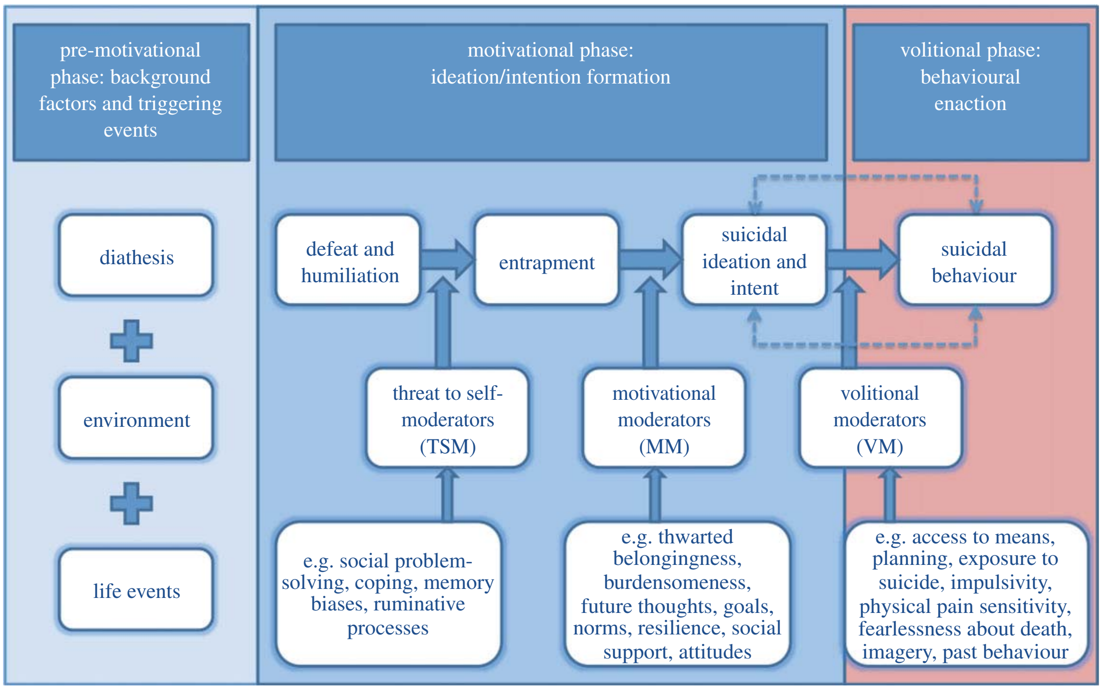

Figure 1. The IMV model of suicidal behaviour.

suicide attempts/death by suicide (volitional phase). This is the most detailed specification of the model to date, which includes some refinements since its original exposition in 2011 (figure 1).

2. Theoretical origins and conceptual rationale

The guiding principle that led to the development of the IMV model was the desire to synthesize the extant evidence into a detailed theoretical framework that could make predictions about the factors that lead people to think about suicide and those factors which govern whether people act on their thoughts, i.e. attempt suicide/die by suicide. Until Joiner proposed his interpersonal theory of suicide (IPT) [7], for the most part, the theoretical literature [8–11] did not account for the distinction between the prediction of ideation versus enaction. In this regard, the IMV model is a second-generation model, which, alongside the IPT [7,12] and the three-step theory of suicide (3ST) [13], is a theoretical perspective which explains the suicidal process consistent with the ideation-to-action framework [14]. These more recent models specifically hypothesize that the factors leading to the development of suicidal thinking are distinct from those that govern behavioural enaction, i.e. attempting or dying by suicide.

As detailed elsewhere [6,15], four distinct theoretical perspectives were particularly important in the IMV model's development [9,11,16,17]. First, the backdrop to the IMV model is the diathesis–stress model [9], which recognizes that individual vulnerabilities confer elevated risk for developing suicidal ideation when activated by the presence of stressors. Examples of these vulnerabilities are personality characteristics, such as high socially prescribed perfectionism, or socio-environmental factors, e.g. socio-economic deprivation [4,18]. Combined with acute or chronic life stressors, these vulnerability factors increase the likelihood that an individual will experience an adverse psychological reaction to stress. This forms the basis of the pre-motivational phase of the IMV model, which includes background vulnerability factors.

Second, the theory of planned behaviour (TPB) [16] influenced the development of the IMV model as it contends that the strongest immediate predictor of behaviour is an individual's intention or motivation to carry out the behaviour. Crucially, the TPB delineates distinct phases of intention formation and behavioural engagement (enactment).

Central to the motivational phase of the IMV model is the relationship between defeat and humiliation, and entrapment, leading to suicidal ideation; key variables within Williams' cry of pain theory of suicide [11]. These elements are drawn from a concept known as 'arrested flight', which was adopted from evolutionary psychology and originally used to explain behavioural states observed in individuals with depression. Arrested flight describes the experience of feeling as though one has been brought down (defeated) and has no prospect of escape or rescue (entrapment) [19]. These concepts characterize well the 'tunnel vision' often observed in individuals experiencing suicidal distress, whereby suicide becomes the only perceived escape route. Humiliation also features within the cry of pain theory, but has received little substantive attention relative to defeat and entrapment.

The final theoretical perspective drawn upon within the IMV model is the differential activation hypothesis [20,21], which posits that when an individual experiences distress, an association is formed between the feeling of distress and, in this case, suicidal ideation. With each subsequent episode of distress, the pathway from distress to suicidal cognitions becomes more established and, therefore, more easily activated; negative mood also potentiates a bias towards negative information, termed 'cognitive reactivity' [22]. Even once an individual is no longer acutely distressed, these pathways lie dormant until triggered by a negative mood state or stress.

3. Key premises underpinning the motivational–volitional model of suicidal behaviour

The IMV model is a three-phase biopsychosocial framework (figure 1 and table 1) that delineates the final common pathway

Table 1. Key premises of the IMV model of suicidal behaviour.

	premise
1	Vulnerability factors combined with stressful life events (including early life adversity) provide the backdrop for the development of suicidal ideation.
2	The presence of pre-motivational vulnerability factors (e.g. socially prescribed perfectionism) increases the sensitivity to signals of defeat.
3	Defeat/humiliation and entrapment are the key drivers for the emergence of suicidal ideation.
4	Entrapment is the bridge between defeat and suicidal ideation.
5	Volitional-phase factors govern the transition from ideation/intent to suicidal behaviour.
6	Individuals with a suicide attempt or self-harm history will exhibit higher levels of motivational and volitional-phase variables than those without a history.
7	Distress is higher in those who engage in repeated suicidal behaviour and over time, and intention is translated into behaviour with increasing rapidity.

to suicidal ideation and behaviour. As noted above, the pre-motivational phase describes the biopsychosocial context, identifying vulnerability factors and triggering negative events. The motivational and volitional phases are operationalized at two different levels. From a higher-order perspective, the core constructs of defeat/humiliation, entrapment, suicidal ideation and suicidal behaviour form the backbone of the model and span both phases. These core constructs have the potential to be influenced by lower order moderators, with the latter defined as factors that facilitate or impede the transition within a phase (threat to self and motivational-phase moderators) or across the phases of the model (volitional-phase moderators). The key premises of the model are summarized in table 1.

(a) The pre-motivational phase: background factors and triggering events

The pre-motivational phase is comprised of a diathesis–environment–life events triad [2–4]. Diatheses take the form of biological, genetic or cognitive vulnerability factors or individual differences characteristics that increase risk of suicide. For example, decreased serotonergic neurotransmission is one such vulnerability factor for suicidal behaviour [23]. Socially prescribed perfectionism, defined as unrealistically high expectations that we believe significant others have of us [24], is another individual difference vulnerability factor that has been consistently associated with suicide risk [25,26]. According to the IMV model, socially prescribed perfectionism is hypothesized to increase the likelihood that an individual feels defeated when an interpersonal crisis occurs (heightened sensitivity to negative signals in the environment). Indeed, higher levels of perfectionism are also associated with sensitivity to emotional pain [27], another factor within the pre-motivational phase.

Understanding the social and environmental context of suicide risk has a long history [28]. More recent evidence highlights the socio-economic inequality of suicide [18] and the impact of rapid societal changes, such as economic recessions [29]. Early life adversity is also an unequivocal suicide risk factor, with evidence that it is associated with epigenetic changes in genes, cortisol (dys)regulation as well as with the (disrupted) formation of attachment relationships [2,30]. However, negative life events experienced at any stage in life confer risk [31,32].

The overarching premise of the IMV model is that the pre-motivational factors have their effect on suicide risk through their influence on the constructs within the motivational and volitional phases.

(b) The motivational phase: emergence of suicidal ideation

Consistent with Williams' cry of pain hypothesis [11], in this phase, we focus on the psychological processes that lead to the emergence of suicidal ideation and intent. Although we acknowledge that suicidal ideation and intent are blurred but, arguably distinct constructs, at this stage there is insufficient evidence to specify whether it is useful to add another phase, which explains the movement from ideation to intent. In essence, we posit that appraisals of defeat and/or humiliation from which there is no perceived escape—a sense of entrapment—are the proximal predictors of suicidal ideation. As introduced above, sensitivity to signals of defeat may be affected by a range of factors, including socially prescribed perfectionism, pessimism and negative affect. Entrapment can be internal or external in nature; the former is concerned with being trapped by pain triggered by internal thoughts and feelings, whereas external entrapment relates to the motivation to escape from events or experiences in the outside world [19]. Feelings of entrapment are likely to give rise to agitation. Entrapment is distinct from hopelessness which is a pervasive sense of pessimism for the future [33].

The emergence of suicidal ideation is the outcome of a process beginning with feelings of defeat and humiliation. Defeat or humiliation may also be characterized by social rejection and loss, two frequently reported precipitants of suicidal distress [2,34–36]. However, entrapment is not an inevitable consequence of feeling defeated or humiliated. According to the IMV model, the presence or absence of threat to self-moderators (TSMs) renders it more or less likely that defeat leads to entrapment.

Given their established relationships with suicidal ideation and behaviour, social problem-solving [37–39], autobiographical memory biases [39–41] and rumination [42,43] are included here as TSMs. Although these factors are likely to affect entrapment as well as defeat and humiliation, we hypothesize that they will have their strongest effect on the defeat–entrapment relationship because they are implicated in problem resolution. As brooding rumination [44] is more strongly associated with suicide risk than reflection [42,43], we hypothesized that brooding would be an important moderator of the defeat–entrapment relationship. Despite limited research into the relationship between coping and suicide risk [45], given the conceptual overlap with social problem-solving, we proposed coping to be a TSM; but depending on how it is operationalized, it is likely to also moderate the entrapment–suicidal ideation relationship [45].

The final part of the motivational phase is the transition from entrapment to suicidal ideation. We posit that the presence of motivational moderators (MMs) will increase or decrease the likelihood that entrapment is translated into suicidal ideation. The MMs include factors that, when present and protective, allow the trapped individual to see alternatives, a more positive future and less pain. Reasons for living [46], attainable positive future thinking [47,48], adaptive goal pursuit [49], belongingness [12] or connectedness [50] are MMs as they are thought to buffer against the emergence of suicidal ideation and intent. Conversely, feeling a burden [51], having little or no social support [52] and depleted resilience [53] will each increase the likelihood that entrapment will be translated into suicidal ideation/intent. Consistent with the TPB, the IMV model also hypothesizes that individuals with less negative attitudes towards suicide/death are also more likely to consider suicide as an option when they are trapped [16,54]. As all human behaviour is influenced by reflective and automatic processes [55], the prediction of suicidal behaviour is no different; therefore, these attitudes are implicit as well as explicit [56,57].

(c) The volitional phase: from suicidal ideation to suicide attempts/suicide

The final phase of the IMV model outlines the factors, entitled volitional moderators (VMs), that govern the transition from suicidal ideation/intent to enaction (the VMs are expanded upon in figure 2). Although factors such as entrapment may be associated with suicide attempts (largely due to entrapment's association with suicidal ideation), a central tenet of the IMV model is that VMs are vital for transition. Drawing from Joiner's IPT, the IMV model proposes that the components of the acquired capability for suicide (fearlessness about death and increased physical pain tolerance [12,51]) are VMs. We believe, however, that the factors that govern the transition from ideation to attempts are broader than capability. We posit that VMs can be environmental, psychological, social or physiological in nature.

Having access to the means of suicide, an environmental VM, is an important risk factor for suicide [3,58]. Exposure to the suicidal behaviour of others (family or friends) is a social VM with an established relationship with suicide risk [59,60]. There are a number of potential mechanisms that explain this relationship. For example, the suicidal behaviour of others may increase the likelihood that an individual models or imitates a loved one's suicidal behaviour. Exposure may also increase the salience and cognitive accessibility of suicide such that an individual is more likely to attempt suicide when they encounter stressors. Similarly, we hypothesize that exposure to inappropriate representations of suicide (e.g. glamorizing suicide) via traditional and new media channels may increase the likelihood that a vulnerable individual engages in a suicidal act (cf. suicidal contagion and suicide clusters, [61]).

Although there is some debate about how best to operationalize impulsivity, and the extent to which impulsivity is associated with the individual versus the act, its relationship with suicidal behaviour is evident [2,62]. The model also predicts that those with detailed (if-then) plans for their suicide or suicide attempt are more likely to attempt suicide/die by suicide than those without plans. There is also growing interest in the role of mental imagery of suicide and suicidal 'flash forwards' where an individual has a mental image of being dead or dying [63]. We hypothesize that mental imagery increases the likelihood of enactment as it acts as a form of cognitive rehearsal for the behaviour.

A past history of self-harm or suicide attempts is a VM. If an individual engages in suicidal behaviour once, they are statistically more likely to do so again [3]. The dotted lines in figures 1 and 2 reflect the dynamic and (for some) cyclical relationship between suicidal ideation and repeat suicide attempts. In addition, when at-risk individuals perceive themselves to have complete control over their suicidal behaviour, which may manifest itself as high capability, suicidal behaviour may be triggered directly, ostensibly bypassing the ideation/intention formation stage of the model. Although the model was developed originally to understand suicidal behaviour *per se*, the basic premises of the model also apply to self-harm, irrespective of motive. For example, volitional-phase moderators have been shown to distinguish between adolescents who have thought about self-harm and those who have self-harmed (for a wide variety of motives) [64].

4. Empirical tests of the model and its components

A growing number of studies have tested the IMV model or its components. As noted above, research has been supportive of the utility of VMs for differentiating between adolescents with self-harm ideation and those who enact the behaviour [64]. In another study of college students, those who reported suicidal ideation did not differ in motivational-phase variables from individuals who had attempted suicide in multivariate analyses, but they did differ on volitional-phase variables, as per the IMV model [65]. A recent study from a population-based birth cohort of 4772 adolescents also found that exposure to the self-harm of others (alongside psychiatric disorder) was the factor that most clearly differentiated those who had attempted suicide from those who had thought about suicide without making an attempt [66].

Prospective research has examined two of the central components from the motivational phase, defeat and entrapment, finding in one study that entrapment and past suicide attempts were the only multivariate predictors of readmission to hospital for self-harm at 4-year follow-up, even when controlling for depressive symptoms and hopelessness [67]. More recently, Owen *et al.* [68] found that defeat predicted suicidal ideation via entrapment at four-month follow-up in a sample of individuals with bipolar disorder. Wetherall *et al.* [69] also found that entrapment was a mediator of the relationship between defeat and suicidal ideation cross-sectionally, supporting the IMV model's prediction. Furthermore, when entrapment was high, resilience also moderated the relationship between defeat and suicidal ideation.

Entrapment is also directly related to suicidal ideation in adolescents, but it also acts as a mediator of the relationship (along with psychosomatic symptoms, resilience and depression) between anger suppression and suicidal ideation [70]. Elevated defeat, entrapment and suicidal behaviour have also been found in individuals with trauma and a diagnosis of post-traumatic stress disorder (PTSD), relative to

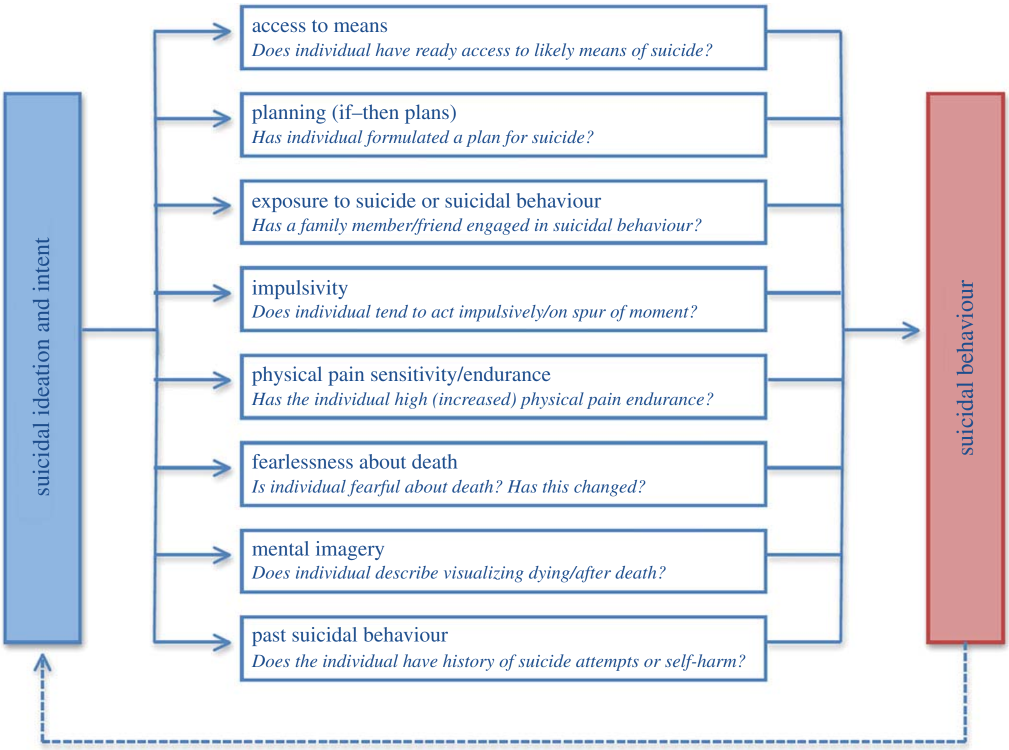

Figure 2. From suicidal ideation to suicidal behaviour within the IMV model: the VMs.

those with trauma but no PTSD diagnosis [71]. Furthermore, defeat and entrapment mediate the relationship between PTSD symptoms and suicidal behaviour [72]. The centrality of entrapment within the suicidal process was also evident in a study of 200 adult psychiatric patients who had been hospitalized following a suicide attempt or suicidal ideation. The authors found that entrapment fully mediated the relationship between ruminative flooding, panic-dissociation and fear of dying with suicidal ideation [73].

Within the IMV model, pre-motivational factors such as socially prescribed perfectionism are posited to lead to the development of feelings of defeat, and in Wetherall *et al.*'s study [69], the relationship between socially prescribed perfectionism and defeat was partially mediated by negative social comparisons. This perception of being of a lower social rank and of making unfavourable comparisons between oneself and others is proposed to be associated with feelings of defeat and entrapment subsequently. The IMV model contends that individuals who are more sensitive to the (perceived) social evaluation of others are more likely to experience feelings of defeat and entrapment, and Wetherall *et al.*'s study provides support for this.

There have, however, been some inconsistencies in the findings between studies of defeat, entrapment and suicidal ideation. Tucker *et al.* [74] found that, in a sample of American college students, defeat was directly associated with suicidal ideation, but not indirectly via entrapment. While this is not consistent with the IMV model, central to this prediction is the temporal context of the transition from defeat/humiliation to entrapment, such that defeat is expected to temporally precede feelings of entrapment. Here defeat and entrapment were measured contemporaneously [74], which may have impacted upon whether the relationship was observed. However, also in Tucker *et al.*'s study [74], as predicted by the IMV model, the relationship between defeat and entrapment was moderated by the presence of brooding rumination, supporting rumination as a threat to self-moderator, affecting the pathway from defeat to entrapment.

Another recent study found that the rumination–suicidal ideation relationship was mediated by entrapment, but the reverse relationship whereby rumination mediated the pathway between entrapment and suicidal ideation was not significant, thus consistent with the sequential relationships outlined within the IMV model [75]. Additionally, a prospective study found baseline defeat, but not entrapment, predicted suicidal ideation at 12-month follow-up [76]. The same finding was also reported in a cross-sectional study of prisoners [77]. These findings may be due to low power, or because defeat and entrapment differ in their longitudinal relationship to suicidal ideation or the assessment of entrapment in prisoners requires closer inspection. For detailed discussion of the role of defeat and entrapment in suicide risk, see O'Connor & Portzky [78] and two recent reviews [79,80].

Novel research using an online community sample also found some support for the IMV model. On the one hand, the authors found that entrapment (alongside burdensomeness) predicted suicidal ideation cross-sectionally [81]. However, they did not find support for the moderating role of thwarted belongingness and burdensomeness in the entrapment–suicidal ideation relationship. This may simply reflect the way in which this relationship was tested and how the variables were operationalized. Drawing from the IPT [12], the IMV model proposes that it is the interaction between thwarted belongingness and burdensomeness that acts as a moderator of the entrapment–suicidal ideation relationship, as opposed to either of these variables independently. Here belongingness and burdensomeness were tested separately as potential moderators [81]. In addition, the measure of suicidal ideation encapsulates a broad spectrum of suicide-related constructs including ideation, planning and impulsivity. How we assess suicidal ideation, in itself, may introduce unwanted variability, rendering it more difficult to investigate *a priori* hypotheses.

In a new approach to understanding the relationship between risk factors, variables from the widely used Beck Scale for Suicide Ideation (SSI; [82]), which span the motivational and volitional phases of the IMV model, have been examined using network analysis in a sample of individuals who presented to hospital following a suicide attempt [83]. Results demonstrated that suicidal behaviour was more directly associated with volitional-phase variables, such as control over action and active planning, whereas factors such as reasons for living and wish to live (motivational phase factors) were more distal predictors. While innovative, this particular analysis was limited by focus on variables from the SSI, which was not designed to assess IMV model components. Future network analyses should assess all of the IMV model factors together.

A few studies have also examined the IMV model in non-Western settings. For example, Hye-Ji & Sung-Woo [84], in a sample of South Korean college students, found that entrapment mediated the relationship between defeat and suicidal ideation, as predicted by the IMV model. In sub-Saharan Africa, Atilola & Ayinde [85] applied the IMV model to examine the suicide of Sàngó, a well-known figure in the culture of the Yorùbá people, discussing how aspects from the narratives of his death map on to the IMV model. These studies provide some early evidence that the IMV model has utility for explaining suicidal behaviour in non-Western cultural settings, but this should be explored further.

A number of studies have also indirectly tested components of the IMV model. For example, innovative work with adolescents using the Card Sort Task for Self-harm (CaTS) by Townsend *et al*. [86], found that individuals outlined a process whereby negative life stressors acted as a backdrop to their distress (pre-motivational phase), leading to negative feelings and ideation about self-harm (motivational phase). Enacting self-harm behaviour was ultimately preceded by feelings of impulsivity and having the access to means for harming oneself (volitional phase). Townsend *et al*.'s work [86] supports the idea of a strong temporal component to the proposed pathways within the IMV model. In addition, work by Littlewood *et al*. [87] also found an indirect relationship between nightmares and suicidal behaviour via defeat and entrapment, supporting the idea that the combination of defeat and entrapment is particularly deleterious and leads to more severe suicidal ideation.

5. Key directions for future research

The shift to ideation-to-action models of suicide represents vital progress in the way we conceptualize, research, and intervene to prevent suicidal behaviour. There is still much we have yet to accomplish, however, and here we discuss a number of key opportunities and challenges for the IMV model and also suicide research more generally. As is the case for the 3ST [13] and IPT models of suicide [12], the IMV model presents a linear picture of the suicidal process, from ideation and intention formation to enactment of suicidal behaviour. Although it is important to note that the potential cyclical nature of the suicidal ideation–attempts–ideation relationship is now acknowledged within the IMV model (see dotted lines in figures 1 and 2). Nonetheless, the linear model structure does not necessarily account for repeat suicidal behaviour; as noted above, if an individual has already made a suicide attempt, it is unlikely that the process of ideation and intention formation for a repeat suicide attempt will begin anew and manifest in the same way as for a first episode of suicidal behaviour. We expect individuals who have engaged in repeated suicidal behaviours to exhibit higher levels of distress than individuals with a single episode of suicidal behaviour, and as such we expect to see higher levels of motivational and volitional-phase variables among individuals repeating suicidal behaviour. Consistent with the differential activation hypothesis [22,88], we would expect that the process between ideation and enactment shortens with repeated engagement in suicidal behaviour, such that over time the transition between intention and behaviour becomes increasingly rapid.

Given the complexity of the pathways to suicide, the model in its current form does not address the issue of whether or not particular combinations of variables from across the three phases of the model result in higher risk trajectories for suicidal behaviour. Identifying such 'risk trajectories' may represent important steps in generating more individually specific profiles or sub-types that may also aid our development of tailored interventions for particular groups.

As is evident from emerging literature on variability in suicidal ideation [89], context and temporal fluctuations are pivotal to our understanding of the specific circumstances under which suicidal ideation and behaviour may occur. To understand the role of context in suicidal behaviour, traditional, retrospective self-report or laboratory measures are insufficient, being highly vulnerable to recall bias and lacking ecological validity [90]. The only way to truly capture such short-term variations in risk factors is to measure these at a momentary level using techniques such as ecological momentary assessment (EMA) methods, allowing data to be collected virtually in real-time, as participants go about their daily lives [91]. Despite its clear potential, however, EMA remains an underused methodology within suicide research [56,92,93] and requires rigorous evaluation.

Since the IMV model was proposed in 2011, much progress has been made in empirically testing the model's predictions but much remains to be done. First, consistent with suicide research more generally, there is a dearth of prospective studies. The issue of temporality returns when considering the proposed temporal pathway from defeat and humiliation to entrapment, then progressing onwards to suicidal ideation. Extant research examining these constructs within the context of the IMV model has consistently investigated these variables contemporaneously [81]. The concepts of defeat and entrapment may also exhibit further nuance, potentially having both state and trait components [94]. Stability of these constructs over time has received little to no attention within the field of suicide research.

As well as new technological developments, the emergence of statistical techniques such as network analysis (e.g. [95]) provides new opportunities for addressing some of the key questions and challenges outlined above. By allowing us to compare the relative importance (centrality) of key variables associated with suicidal ideation and enactment, as well as the strength of these relationships, network analysis gives us new possibilities to investigate variations in risk trajectories in different populations. Other new methods, such as curtailment techniques, allow us to optimize the efficiency of the measures we use to assess suicidal ideation and behaviour, without compromising on their accuracy [96].

Recent advances in machine learning techniques allow the computation of optimized risk algorithms, from hundreds of different individual variable pathways, to suicidal thoughts and behaviours [97,98]. The vast majority of tools to assess the likelihood of repeat engagement in suicidal behaviour rely on self-report. A burgeoning line of research investigates possibilities for detecting cognitive reactivity towards suicide-relevant content that is outside of individuals' conscious awareness, including implicit attitudes via the Death/Life Implicit Attitudes Test [56,57,99]. Other approaches, such as the death evaluation Implicit Relational Assessment Procedure [99], have also found specific cognitive biases towards self-referent versus abstract death-related stimuli in individuals with current suicidal ideation. In short, given that behaviour is governed by reflective and automatic (e.g. implicit) processes [100], more suicide research needs to focus on these automatic (as well as reflective) processes.

6. Implications for intervention and suicide prevention

A corollary of the IMV model is that intervention and suicide prevention activities should be tailored to the phase of the model that the person is presently within. If an individual is distressed and feeling trapped but they are not suicidal, then clearly interventions that reduce the likelihood that suicidal ideation emerges could offer benefit. To this end, targeting factors within the motivational phase of the model should be highlighted. For example, given that entrapment is a potentially modifiable predictor of suicide attempts over time [67], this is an important treatment target. It would also make sense to incorporate the assessment of entrapment into routine clinical care alongside depression and suicidal ideation. The challenge, though, is that there are not yet any evidence-based treatments to reduce entrapment. Nonetheless, there are effective, evidence-based psychological interventions for the management of self-harm that can be drawn from Hawton *et al.* [101]. If an individual is actively suicidal, in addition to trying to alleviate their suicidal distress, it is vital that interventions to reduce the likelihood that they act on their thoughts are prioritized. For example, safety planning [58] is one such promising intervention which targets VMs. Another is a volitional helpsheet (VHS) [102] that encourages an individual to make if-then plans to reduce the likelihood that their suicidal thoughts trigger a suicide attempt. Recent evidence suggests that a VHS may offer promise (as an adjunct to usual care), especially among those with a past history of self-harm [102,103]. More generally though, theoretical models such as the IMV model should be a starting point for the development of interventions, because they specify the potential mechanisms that should be targeted, thereby increasing the likelihood of interventions being effective [104]. Finally, at the macro-level, suicide prevention efforts need to urgently tackle inequality, poverty and disadvantage [18,105], key drivers of suicide (pre-motivational phase).

7. Summary and conclusion

We have presented the IMV model, a contemporary ideation-to-action model of suicidal behaviour. The tri-partite IMV model contends that suicide is a behaviour, preceded by ideation and intention formation and, crucially, it seeks to explain the transition from suicidal ideation to behavioural enactment. Empirical support for the model is growing; however, there remain a number of challenges, as well as opportunities, to be addressed in future research; understanding the roles of temporality and complexity of variable interactions within the model is a priority.

Data accessibility. This article has no additional data.

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The moral standing of the dead

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In choosing to do certain things, we appear to presuppose that we can act in the interests the dead, and that we have a duty to do so. For example, some of us go to great lengths to carry out their final wishes. Given that the dead no longer exist, however, it seems that nothing can be good or bad *for* them: they lack prudential interests. In that case, it is hard to see how we could owe them anything. They seem to lack moral standing altogether. In this essay, I will rebut this line of thought. I will claim that in some cases things that happen after people die are indeed good or bad for them. Their interests can still be advanced or hindered, so the dead have moral standing.

This article is part of the theme issue 'Evolutionary thanatology: impacts of the dead on the living in humans and other animals'.

1. The moral standing of the dead

Must the living act on behalf of the dead? Many of us seem to think so, given things we do after others die. For example, some of us believe that we must carry out the final wishes of friends who have died, and go to great lengths to do so. However, there is a strong case for concluding that the dead lack moral standing altogether, which is to deny that the way we treat them matters from the moral point of view. Roughly stated, the case is this. We would have duties to the dead only if they had prudential interests. Yet they do not: nothing can be good or bad for them. In that way the dead are like bags of sand, armchairs and boulders. So we owe them nothing. In this essay, I will attempt to rebut this argument. My main strategy will be to criticize the assumption that the interests of people are never affected by anything that happens after they die. Elaborating upon previous work [1], I will attempt to clarify why this assumption seems plausible yet is false. If I am successful, it will be clear why and in what sense the dead matter from the moral point of view: they may have interests that are advanced or hindered by those who are still alive, and what affects people's interests is always relevant from the standpoint of morality.

2. Die, dead, death and the dead

I begin with some remarks about the word 'death' and related terms that feature prominently in the discussion.

The term 'death' is ambiguous as between *dying* and *being dead*. In what follows I will disambiguate 'death' when necessary by using the terms 'dying' or 'being dead'. I stipulate that to *die* is to cease to be alive, and I assume that what ceases to be alive ceases to exist. But what is it for you to *be* dead? Is it the state you are placed into by virtue of dying? That suggests that you may be in some state while not existing. Here is a better proposal: to say you are dead is an abbreviated way of stating that you are dead *at some given time*, which, in turn, is simply to say that you died before then. When we omit to mention time of death, we refer implicitly to the present, so that 'you are dead' means you died before *now*. In a similar fashion, we can use 'the dead' as shorthand for 'those who died before now' [2].

Note, finally, that it is one thing to be harmed (or benefitted) by death and another to be harmed (or benefitted) by something occurring after we have

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died. We can call the first sort of insult 'mortal harm' (or benefit) and the second 'posthumous harm' (or benefit).

Now, eventually, we want to look into whether posthumous harm is possible. Because of the relationship between posthumous and mortal harm we will also want to consider whether the latter is possible. But before we can address either question we will need to consider what it is for something to be good or bad for us. Let's do that next.

3. Welfare comparativism

Here is one way in which something may be good for us: it might be intrinsically good for us, which is to say that it is good for us *in itself*, good for its own sake. Pleasure is valuable to us for its own sake, hence it fits the bill. Contrast something like money that is good for us due to things that accompany or are caused by it. The value of money hinges entirely on what it buys. There can also be things, such as pain, that are intrinsically bad for us (I will call these intrinsic evils).

Something can be good for us in a second way: it might be overall good for us, that is, good for us all things considered. As a first pass, we might say that something is overall good for us if and only if it makes our lives go better than they otherwise would have gone. But what is it for a life that goes one way to be better for us than a life that goes another way? Roughly, the answer is that the level of welfare or (what is the same thing) well-being attained by the one is greater than the level attain by the other. To make the idea clearer, then, we will need to say something about the notion of welfare.

How well off we are at a time or over a period of time is determined by the things we accrue during those times that are intrinsically good for us, such as pleasure, and the things we then accrue that are intrinsically bad for us, such as pain. Accruing intrinsic goods without accruing intrinsic evils boosts our welfare, while accruing the latter and not the former lowers it. Thus, other things being equal, someone experiencing a great deal of pleasure and very little pain over the course of an evening has a higher welfare level that evening than she would have had if she had experienced a great deal of pain and very little pleasure during that time. If we wish, we can assign a positive number to a unit of pleasure and a negative number to a unit of pain. Perhaps we can do the same with other intrinsic goods and evils. We could then represent a welfare level as the sum of these numbers, and say that the higher the sum the greater the welfare level.

Human animals are not the only organisms capable of having a welfare level. Any creature will have a welfare level if it is equipped with apparatus that allows it to accrue pleasure or any other intrinsic good or evil. It seems likely, however, that animals will differ in their capacities to accrue goods such as pleasure (if for no other reason than that some tend to live longer than others), in which case it is reasonable to conclude that even in ideal conditions some sorts of animals may fare better than others.

Just as we can assess a subject's welfare level over the course of an hour or two, so we might assess her welfare level over her entire life. Call this—the sum of the intrinsic goods and evils she accrues over the course of her life—her 'lifetime welfare level'.

If we help ourselves to the notion of a lifetime welfare level, we can state more clearly what it is for something to be overall good or bad for us (or for some other sort of organism). Its overall value for us is determined by the way it affects our lifetime welfare level. That is:

> an event is overall good (bad) for us if and only if, and to the extent that, our lifetime welfare level would be higher (lower) if that event occurred than it would be if that event had not occurred.

We might also say that:

> an event is overall good (bad) for us *at some time* if and only if, and to the extent that, our welfare level *at that time* would be higher (lower) if that event occurred than it otherwise would be.

Call this account of something's overall value 'welfare comparativism'. Versions of this account have been defended by several theorists [3–5].

By way of illustration, consider that according to welfare comparativism having a toothache will be overall bad for us assuming that, due to the toothache, our lifetime welfare level will be lower than it otherwise would have been. A toothache might also be overall bad for us *over a period of time*, assuming that during this time our welfare level would otherwise be higher. By contrast, a visit to the dentist is likely to be overall good for us. This is true despite the fact that dentists usually hurt us. The discomfort involved does not make the visit bad for us given the far greater amount of suffering we otherwise would have incurred.

Let me digress briefly to address a question that an evolutionary biologist might raise about the notion of an overall good, namely this: does what is overall good for us coincide with what makes us more likely to survive or reproduce? It does not. To make this clear, we can begin by noting that our survival is not intrinsically good for us. Whether (and the extent to which) it is good for us depends on whether it enables us to accrue things that are otherwise good for us. What is more, survival need not be in our interests. This is shown by the fact that (as discussed below) *dying* at a particular time may be overall *good* for us. Putting aside the implications of retroactive harms and goods (discussed later), dying at a time will be overall good for us if, over the course of the remaining life we otherwise would have had, we would have fared badly. Similarly, something that improves our chances of reproducing may be against our interests; e.g. a medical procedure that reverses sterility might cause uncontrollable depression. We can even imagine a medical treatment that allows us to live well far longer than is normally possible but that leaves us sterile. Note, finally, that while many people (but not all) will enjoy a boost in their welfare as a result of having and rearing a child or two, there is no reason to think that each additional child will make for the same boost in welfare.

4. Harming the dead

Having reached a clearer idea about what it is for something to be good or bad for us, we can better assess the possibility of mortal and posthumous harm. It turns out that the former is definitely possible, while the latter is more controversial.

To illustrate the possibility of mortal harm, let us ask whether it would have been overall bad for Socrates to die young. We can suppose that, on the whole, Socrates lived well until he died at age 70. If he had died at, say, age 10 then his lifetime welfare level would have been far lower than it otherwise would have been—far lower than it actually was. So dying young would have been overall bad for Socrates—bad in direct proportion to how well he lived between age 10 and age 70. It would have been bad for him because of what it would have deprived him of, namely 60 years of good life, and not simply because of the unpleasantness of dying itself. It is also possible for dying at some time to be overall good for a person**.** Setting aside the implications of retroactive harms and goods once again, it is overall good for someone to die at a time if her welfare level over the rest of her life would otherwise be negative, in that she accrues intrinsic evils and no intrinsic goods, or in that the intrinsic evils she accrues outweigh the intrinsic goods she accrues.

Although dying at a particular time, say age 10, would have been overall bad for Socrates, it does not follow that it would have been bad for him *at* any particular time. I would argue that it makes no sense to speak of how well off a person is *while he is non-existent*. (For further discussion, see [5,6]). If that is correct, Socrates could not have had a welfare level at a time after he died, so it makes no sense to say that his welfare level, *while he was dead*, was lower or higher than the welfare level he in fact enjoyed from age 10 to 70. Dying young would indeed have been bad for Socrates, but not at any particular time.

A further implication of welfare comparativism concerns the significance of the deaths of animals: if animals of one kind tend to have lower lifetime welfare levels than animals of another kind, then dying will tend to be less bad for the one than it is for the other. In effect, this is because animals of the first sort have less to lose than those of the second.

So welfare comparativism allows us to make sense of mortal harm. Now let us see if we can use it to make sense of posthumous harm.

We can begin with a concession to the posthumous harm skeptic. Suppose that the only constituents of welfare are pleasure and pain; that is, the only thing that is intrinsically good for us is pleasure, and the only thing that is intrinsically bad for us is pain. We can call this view ‘hedonism’. Together with welfare comparativism, hedonism entails that nothing that happens after we die affects our interests, for no such event causes us pleasure or pain, or precludes our having pleasure or pain that we otherwise would have. We can arrive at a similar result by assuming, as some theorists do (e.g. Mark Bernstein [7] (p. 19) and Walter Glannon [8] (p. 138)), that the only constituents of welfare are things that reduce to our intrinsic, non-relational properties. Pleasure and pain qualify, but so would any other features that depend solely on our intrinsic properties, such as our being partly constituted by carbon atoms. As nothing that occurs after we die modifies our intrinsic properties, it would follow that posthumous events are harmless to us.

Although these concessions are warranted, posthumous harm may still be possible. To see why, note that the welfare comparativist is not committed to hedonism. It is neutral with respect to what things are intrinsically good for us. This is fortunate, as there is good reason to think that the list of things that are intrinsically good for us is not limited to pleasure. Acknowledging the existence of goods other than pleasure may help us to see that posthumous harm is possible.

One standard reason for rejecting hedonism is that it seems imprudent to do various things that nevertheless maximize our pleasure—imprudent for reasons that are incompatible with hedonism. The point can be made vivid using a thought experiment posed by Robert Nozick [9] (p. 42), in the following passage:

> suppose there were an experience machine that would give you any experience you desired. Superduper neuropsychologists could stimulate your brain so that you would think and feel you were writing a great novel, or making a friend, or reading an interesting book. All the time you would be floating in a tank, with electrodes attached to your brain.

If given the option of plugging into this machine for the rest of our lives, most of us would refuse, even if we see that the machine would give us more pleasure than we could get any other way. If we plugged in, our lives, although pleasant, would be impoverished; they would lack some good other than pleasure, perhaps more than one sort of good.

Earlier we noted that posthumous harm skeptics might assume that the only constituents of welfare are things that reduce to our intrinsic properties. This assumption can be rebutted using a thought experiment involving a device that Nozick describes after he mentions his experience machine. The second, more fanciful device lets you change your features, including your intrinsic properties, at will. We would avoid this machine just as we would avoid the first (especially if it will give us the sort of misleading experiences provided by the original machine), which suggests that the constituents of welfare are not limited to our intrinsic properties.

Of course, it is one thing to see clearly that pleasure is not the sole intrinsic good and another to identify all others. In what follows I will attempt to describe one further good, then defend the possibility of posthumous harm.

5. Achievementism

Suppose that achievements count among the things that are intrinsically good for us, and failures among the evils [10]. We can call this view ‘achievementism’. By appealing to achievementism, we can make good sense of posthumous harm. At that point, we will be in a position to conclude that the dead are subject to being wronged. Or so I shall now argue.

Achievementism seems plausible given the value people place on their accomplishments, and it can be further supported on the grounds that it accounts for our reservations concerning the experience machine. One reservation we would have about the machine is that those who plug in accomplish nothing, yet achievements are an important element of a good life.

If succeeding at some of the things that we set out to achieve is intrinsically good for us, then events that occur after we are dead will bear on our welfare when they affect whether we succeed. Suppose, for example, that I set out to do research that will lead to a cure for Alzheimer’s disease, and, although I die before it is complete, my work gives other theorists vital clues, and a cure is discovered that, but for my efforts, would not have existed. So I achieved what I wanted: I did research that leads to a cure. Yet my success depended on events following my death. If my research records had been burned just after I died, I would have failed. That fire would have been bad for me, in that, because of it, I would not have achieved what I did; the additional work of the other researchers benefitted me in that, because of it, I succeeded.

Our formulation of achievementism is rough, so clarification is in order. In effect, the proposal has two elements. One is the idea that some desires may be fulfilled due to posthumous events. The other is the idea that fulfilling a certain sort of desire, namely the desire to achieve some goal that we set for ourselves, is intrinsically good for us. Let us consider each in turn. We can begin by noting some facts about desires.

When we want something, what we desire may be stated in the form of a proposition. This is obvious in the case of my desire *that I have some coffee*, but it is also true in the case of my desire *for fresh air*, which may be restated, without loss of meaning, as the desire *that I have fresh air*. Let us say that, when we want something, *what* we desire is the *object of* our desire. Thus the object of my desire for fresh air is *that I have fresh air*, or *I have fresh air*. For convenience, we can use the capital letter 'P' to stand for a proposition. Thus each desire has some proposition P as its object; to desire is to desire that some proposition P hold.

Let us add that propositions are either true or false, and what *makes* a proposition true is an event or state of affairs that can be labelled its 'truth-maker'. For example, the proposition *I am typing* is made true by my typing right now. In some cases, as when I presently assert *I am typing*, the truth-maker occurs at the same time as the assertion of the proposition. But the two are not always simultaneous. In some cases, as in *I went kayaking last week*, truth-makers antedate asserted propositions. In others, the assertions come before the truth-makers. For example, the sun will rise tomorrow is made true now by the sun's rising tomorrow. If the sun does *not* rise tomorrow, then *the sun will not rise tomorrow* is true now. One proposition or the other concerning the sun's rising is true now even though neither truth-maker has occurred yet. Note that no mysterious sort of reverse causation is involved in a proposition's being made true by states of affairs holding at times before or after the proposition is asserted. Note also that subtle differences in the propositions we assert can affect what makes them true. For example, *the sun is rising* is made true by something occurring now, namely the sun's rising. It is very different from the proposition that *the sun will rise tomorrow*.

With these facts about desires and propositions in place, we can state a plausible view concerning desire fulfillment: the fulfillment of a desire consists in two things coming together at the same time: our having the desire and its object's being true. That is, if the object of a particular desire is the proposition P, one fulfils that desire at time t if and only if, at t, one has the desire for P and P is true.

To be sure, other accounts are possible [1]. One that is likely to come to mind is the view that I fulfil the desire for P at time t if and only if, at t, I have the desire for P and P's truth-maker occurs. (This may be the view of Silverstein [11], who asserts that if I want eventually to be married, my desire is not fulfilled until the marriage takes place.) However, this alternative has implausible consequences. For example, it implies that at no time can we fulfil a desire if its object's truth-maker has already occurred. If, after a lottery is over, you unwittingly give me the winning ticket, and I form the desire to have won, at no time can I fulfil my desire, as its truth-maker has already occurred.

If P's truth-maker occurs only after we desire P, we might say that its fulfillment involves a *retroactive* element. This happens, for example, when a desire is fulfilled by virtue of posthumous events. Suppose that I now want the sun to rise tomorrow. If the sun will indeed rise tomorrow, my desire is fulfilled *now*—I get what I want *now*. (Contrast the case in which I want to be watching the sun rise but it is midnight.) This is true regardless of whether I live to see it rise. Most of us do have desires about what will happen after we are dead; if these cannot be fulfilled, retroactively, by virtue of posthumous events, then they cannot be fulfilled at all, which makes it puzzling why we would ever form them.

Recall the second element of our proposal concerning achievements: the idea that the fulfillment of the desire to achieve a goal is intrinsically good for us. Let us see if we can sharpen this view. Let us use the term 'achievement desire' to refer to a desire to achieve something—that is, a desire whose object is a proposition setting forth an accomplishment. In the previous example, I wanted to do research that would have a certain result; the object of my desire was that *I will do research that leads to a cure for Alzheimer's*. We can refine achievementism by saying that it is intrinsically good for us when two things come together: we have an achievement desire, and its object is true. That is, according to achievementism:

> it is intrinsically good for us at time t that, at t, we have an achievement desire and the object of that desire, P, is true; it is intrinsically bad for us at t that, at t, we have an achievement desire and its object, P, is false.

Drawing on this account, we can explain the sense in which events that occur after we are dead might harm or benefit us: such events can make the objects of achievement desires true while we have those desires, which is intrinsically good for us, or false, which is bad for us [12]. Because the fulfillment of these desires involves future events, we might say that we are harmed or benefitted *retroactively*. However, the account does not imply that posthumous events 'change' our welfare level after we are dead. Nor does it imply that we incur harm or benefit while dead. If, by virtue of a posthumous event, we have a fulfilled desire that contributes to our welfare, then we accrued that boost before the posthumous event occurred. We accrue it while we are getting what we want. According to Joyce Jenkins [13], my account of posthumous harm, defended elsewhere [14], seems committed to the claims that posthumous events may 'change' our welfare level for the worse, and that we incur the reversal posthumously. However, my view is actually inconsistent with these claims.

We can also explain why it might be in our interests for others to do certain things after we have died, and why others might want to do such things on our behalf: their actions can benefit us retroactively. If I set out to have a novel published, and do everything necessary to achieve my goal except send in the manuscript, my untimely death need not prevent me from achieving the task I have set myself, for you could send in the manuscript for me. Recall, however, that what counts as a desire's object's truth-maker hinges on the precise formulation of that desire's object. My desire to have a novel published can be fulfilled, in part, due to the actions others take after I die. My desire to *be a published novelist now* cannot be.

Fulfilling their desires will not always benefit the dead, for often our intervention will not help them achieve goals they once set for themselves. For example, suppose you desire that, upon your death, I will have your body cremated. Your cremation is no achievement of yours, hence my intervention would not benefit you. Nor would I harm you if, instead of cremating it, I buried your body or donated it to science. (Those who reject this view presumably think that it is intrinsically good for us to fulfil not just achievement desires but other desires as well.)

Earlier I noted that what makes us more likely to survive or reproduce need not coincide with what is overall good for us. We can add that no posthumous events that benefit us will make our survival or reproduction more likely. However, in some cases the *belief* that posthumous events may harm or benefit us can have survival value whether that belief is true or not. It will have such value when it prompts us to leave behind a certain sort of legacy and to secure our legacy, as best we can, from any threats it might face after we die. The salient sort of legacy is one that would probably help our offspring to survive and to have children of their own. We can be prompted to leave such a legacy if we believe that it is in our interests to do so. (Of course, the desire to leave this sort of legacy might also be prompted by other things, such as our love for our children, or the belief that helping others is morally required.)

Let us review. The case for the possibility of posthumous harm rests on two main claims: (a) some desires may be fulfilled retroactively, and (b) fulfilling (thwarting) some desires retroactively is intrinsically good (bad) for us. The two claims are related in this way: if we accept (b) we must accept (a), but while it is possible to accept (a) and reject (b), I suspect the main source of suspicion concerning the possibility of posthumous harm is the denial of (a). If that suspicion is correct, then accepting (a) clears the way to accepting (b), together with the conclusion that what happens after we die may affect our interests.

With this reasoning in place, we can reach a verdict about the moral standing of the dead. People may be wronged by things we do after they have died because such actions may harm them, and, other things being equal, it is wrong to harm someone.

6. Harmlessly wronging the dead

I have defended the claim that the dead have moral standing on the grounds that they have prudential interests. However, nothing said so far implies that the dead have moral standing *only* if they have prudential interests. Hence readers who remain skeptical about the interests of the dead might be tempted to argue that the dead have standing *even though* they are beyond harm. That the dead are subject to improper treatment might even explain why they seem vulnerable to harm: perhaps cases in which the dead appear to be harmed are really cases in which they are wronged. In what follows I will briefly discuss this line of thought.

Now, wronging an individual might involve damage to her person (for example, it might involve the ending of her existence or, less drastically, the destruction of one of her capacities, such as her capacity to make moral judgments). It might involve coercing or manipulating her. It might involve a setback to her interests. And it might involve a combination of these. However, damaging, coercing or manipulating the dead is impossible, as they no longer exist. In fact, it seems that if it is possible to wrong the dead at all, it must consist in some kind of setback to their interests.

But if wronging the dead must implicate their interests, and we deny that the dead have interests, it is reasonable to conclude straightaway that they cannot be wronged. The argument seems straightforward. We begin with the concession we are considering:

1. The dead lack prudential interests.

We can then assume that only if they had interests would the dead have moral standing:

2. To have moral standing, the dead must have interests—it must be the case that things that happen after people die may be good or bad for them.

From these premises it follows that the dead are owed nothing:

3. The dead lack moral standing.

If we accept 1 we must either accept 3 or give up 2. Yet the second option will be tough sledding, as things to which the concept of well-being is clearly inapplicable, such as chairs and stones, clearly lack standing; in cases where it is *unclear* if the concept of well-being applies, such as trees or *species* of animals (as opposed to animals themselves), it is not clear whether it is appropriate to speak of standing; and subjects to whom the concept of well-being *no longer* applies seem to have lost standing.

Suppose we press ahead anyway, and attempt to defend the idea that the dead are subject to being wronged but not to being harmed. Having denied that wronging the dead amounts to some sort of setback or threat to their interests, presumably we will need to supply an alternative account. But in what else might wronging the dead consist?

We might consider the idea that we are obligated to fulfil some desires that dead persons once had, despite the fact that the dead are no longer subject to harm or benefit, and that wronging them simply consists in failing to fulfil these desires. They have standing, we might add, in virtue of the fact that (unlike stones) they *were* once able to want things.

However, a further difficulty now arises. We saw earlier that one of the main reasons for doubting the possibility of posthumous harm is the contention that events occurring after a subject's death cannot help fulfil that subject's desires. If that claim is true then we are powerless to fulfil any desires of the dead, and cannot possibly be duty-bound to do so.

Is there anything we might do for the dead? Only one other option has any promise: it may be possible to *bring about states of affairs* that they desired. For example, even if, after I die, you are powerless to *fulfil my desire* to do research that will lead to a cure for Alzheimer's disease, you can still help *make it the case* that I did research that will lead to a cure. So maybe we are doing something for the dead when we bring about things that they wanted to happen. Perhaps we are obligated to do some such things, and wrong the dead when we fail.

Of course, we might bring about a state of affairs that someone wanted without doing it for her, as we might have had independent reasons for doing what we did. We might even be obligated to do something that coincides with what another wanted, yet not because she wanted it.

For example, it might fall to us to look after a child whose parents died—not because they once cared about their child but rather because we ought to care for helpless children. The proposal on offer is that we are doing something for dead people when we make something happen *because* they once wanted it to happen, and that, in at least some cases, we have an obligation to make something happen *because* they once wanted it to happen.

Thus clarified, however, the proposal is implausible indeed. If we lack independent grounds for bringing about some state of affairs, and assume that so acting neither fulfils anyone's desires nor benefits anyone, we would not be moved to act by the discovery that someone once wanted that state of affairs to occur, let alone be bound to do so.

Given that the dead lack prudential interests, then, there seems to be nothing in which wronging them might plausibly consist. But before we conclude that they cannot be wronged let us consider a final reservation.

7. Promises

When we make someone a promise we seem to bind ourselves in a way that is not contingent on her interests or even on her continued existence (unless she releases us from our burden before she dies). Now, admittedly we rarely promise people that we will do things after they die. (Even the wills people leave behind at death express wishes, not anyone's promise to honour those wishes.) But occasionally we do. Aren't the dead wronged when we break our promises?

Many questions about promises arise. (Can we make bona fide, binding promises to creatures or things that are incapable of grasping our meaning, such as people in the final stages of dementia, or our pets, or the land on which we dwell? Can we make promises to someone who has yet to come into existence, or to someone *after* she is dead?). It is not obvious that we must keep a promise to someone after she has died. However, for the sake of argument, let us take it for granted that it is indeed wrong to renege on promises to the dead. Nevertheless, given the assumptions that the dead are beyond harm and their desires cannot be fulfilled, it seems best to deny that *the dead* are wronged when we renege. At worst, reneging on our promise is a *victimless* misdeed. The situation is very different if we now drop these assumptions. Only if we drop the second is it plausible to say that we can do *for* people what we promise them we will do for them after they are dead. Only if we drop both assumptions can we plausibly say that reneging on our promises wrongs the dead. It wrongs them, other things being equal, when it constitutes a setback to their interests that would have been avoided had we done what we promised.

8. Summing Up

If it is good for us to fulfil some sorts of desires (and bad not to) and, as suggested here, the fulfillment of our desires can be brought about by posthumous events, then others may benefit (or harm) us after we are dead by fulfilling (or thwarting) these desires. On this view, it also makes good sense to say that we may wrong the dead, given the principle that, other things being equal, it is wrong to harm anyone. If, on the other hand, posthumous events cannot affect their prudential interests, it is best to conclude that wronging them is out of the question. If beyond being harmed, they are beyond being wronged.

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Review

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Complicated grief: recent developments in diagnostic criteria and treatment

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Although grief is a natural response to loss among human beings, some people have a severe and prolonged course of grief. In the 1990s, unusual grief persisting with a high level of acute symptoms became known as 'complicated grief (CG)'. Many studies have shown that people who suffer from CG are at risk of long-term mental and physical health impairments and suicidal behaviours; it is considered a pathological state, which requires clinical intervention and treatment. DSM-5 (2013 *Diagnostic and statistical manual of mental disorders*, 5th edn) proposed 'persistent complex bereavement disorder' as a psychiatric disorder; it is similar to CG in that it is a trauma- and stress-related disorder. In recent years, there has been considerable research on the treatment of CG. Randomized controlled trials have suggested the efficacy of cognitive behavioural therapy including an exposure component that is targeted for CG. However, experts disagree about the terminology and diagnostic criteria for CG. The ICD-11 (*International classification of diseases*, 11th revision) beta draft proposed prolonged grief disorder as a condition that differs from persistent complex bereavement disorder with respect to terminology and the duration of symptoms. This divergence has arisen from insufficient evidence for a set of core symptoms and the biological basis of CG. Future studies including biological studies are needed to reach consensus about the diagnostic criteria for CG.

This article is part of the theme issue 'Evolutionary thanatology: impacts of the dead on the living in humans and other animals'.

1. Introduction

Most people will experience the death of a loved one due to disease, disaster, accident, war, homicide or suicide. Although bereavement is inevitable, it leads to severe psychological suffering, and it sometimes profoundly changes one's way of living. Bowlby [1] stated: 'Loss of a loved one is one of the most intensely painful experiences any human being can suffer. And not only is it painful to experience but it is also painful to witness, if only because we are so impotent to help. To the bereaved nothing but the return of the lost person can bring true comfort; should what we provide fall short of that it is felt almost as an insult'.

Given that death is an irreversible process, people have to withstand the feeling of sadness and continue living with it. However, in most cases, the bereaved do not require help from professional therapists; they gradually recover to normal life on their own. Freud [2] described the reaction to the loss of a significant other as 'mourning (Trauer)'. He stated that mourning is a normal response, and that over time mourners relinquish the bond with the deceased by accepting their absence and transferring libido to others. The concept of mourning is similar to grief, which is a normal reaction to the death of a loved one and which has both psychological and physiological manifestations [3]. Freud [2] also indicated that mourning leads to a sequence of psychological processes that include reality testing. From the psychodynamic viewpoint, he explained that this process was susceptible to interference from external and internal conditions. External conditions include critical situations such as a severe disease of a family member or violent death. Internal conditions refer

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to a hostile or excessive relationship with the deceased and various psychological defence mechanisms including suppression of emotions and disbelief in the death to avoid distress. Mechanisms for an impeded grief process as suggested by Freud [2] have been examined in recent studies. Simon [4] proposed that the nature of the relationship with the deceased and the nature of death itself, such as sudden and violent death, were risk factors for the development of pathological grief. For Lobb *et al*. [5], cognitive behavioural conceptualizations including a negative view of the self and the world, and avoidance of emotional problems, predicted pathological grief. Lindemann [6] found that the Cocoanut Grove fire in 1942 led to delayed grief and distorted perceptions among some acquaintances of the victims; this pathological type of grief can be transformed to normal grief by appropriate intervention. More recently, grief researchers have sought to conceptualize unusual/pathological grief such as complicated grief (CG) [7,8], traumatic grief [9] and prolonged grief disorder (PGD) [10].

In the 2000s, based on empirical studies, the opinion that unusual/pathological grief represented by CG should be defined as a psychiatric disorder increased among grief researchers [8,10]. Accordingly, the American Psychiatric Association introduced ‘persistent complex bereavement disorder’ (PCBD) in the 2013 *Diagnostic and statistical manual of mental disorders*, 5th edn (DSM-5) [11]. At the same time, effective interventions for CG have been required following major man-made and natural disasters that have occurred in various parts of the world, such as the 9/11 incident, synchronized terrorist attacks and the Great East Japan Earthquake.

This review is based on empirical studies and systematic reviews from PubMed and Psycho INFO related to CG, PGD and PCBD mainly in the last two decades. It outlines the concept of normal grief based on attachment theory, development and arguments concerning diagnostic criteria for pathological grief, and recent advances in CG treatment.

2. What is ‘grief’?

Grief is primarily an emotional reaction to the loss of a loved one through death. A ‘loved one’ refers to a person with whom an individual shares a particularly strong emotional bond, including attachment figures and carers. Bowlby [1] drew parallels between the reaction following the death of the partner among adults and separation distress in infants who manifest protest, despair and detachment. He suggested that grief is essentially a reaction to the loss of an attachment figure. This ‘attachment theory’ view of grief has influenced many studies [12], supported by attachment mechanisms in various species and animals including cats, dogs, goats, non-human primates and elephants, which manifest grief-like reactions for a dead peer or family member [13]. In her book *How animals grieve*, King [13] describes examples such as a cat looking for its lost sister with plaintive cries and a group of elephants encircling the bones of a dead group leader, as if commemorating the deceased individual. It appears common for some animals as well as humans to experience grief due to the loss of an attachment figure.

The presence of grief among animals raises the question of the pertinence of grief for survival. In the case of an infant temporarily detached from the mother, it is beneficial for the infant to experience separation distress and to protest by crying in order to restore proximity or contact with her. However, when the separation is permanent, as in the case of a loved one’s death, grief reactions such as longing and yearning are in vain; they do not reinstate the deceased individual and may interfere with forming new attachments [1]. In addition, if bereaved animals stay by the dead body when grieving, there may be increased risks of infection or predation. King [13] stated that manifestations of grief in animals indicate the possibility of a strong positive emotion—‘love’—for another individual, which means that grief itself may not be beneficial for survival, but an inevitable consequence of the rupture of a bond with a loved one or attachment figure [1]. According to Archer [14], grief is the cost of the overall adaptive separation reaction, and Parkes [15] described grief as a price to be paid for having a loving bond with another.

By contrast, also within an evolutionary framework, Nesse [16] proposed that grief has an adaptive function. He stated that grief is useful for coping with bereavement ‘by signaling others, by changing goals, by preventing future losses, by reassessing priorities and plans and other relationships’ [16]. The view that grief promotes the reconstruction of life after bereavement is common in ‘relearning the world’; Attig [17] proposed that people who lose a loved one relearn and experience continuity and meaning in their life in a narrative manner.

This perspective on grief, wherein a person overcomes the painful emotions caused by bereavement and reconstructs their life to adapt to the world without the deceased, appears similar to post-traumatic growth [18] and resilience [19], and acknowledges that humans have the strength to recover and grow following a traumatic event.

3. Normal grief and the mourning process

In 1961, Engel [20] described grief as a deviation from a healthy or normal condition and argued that people recover from this pathological state to normal in a manner similar to the recovery process from a burn. In recent years, however, fewer grief researchers appear to share Engel’s views. This is because attachment theory-driven views see grieving reactions, such as intense sorrow, longing, yearning and depression, as a typical manifestation of separation distress rather than a pathological reaction.

Many researchers including Parkes [15], Stroebe *et al.* [3] and Worden [21] interpret grief as a normal reaction, and for most people intense separation distress becomes manageable, and they gradually adapt to their new life without the deceased. For these researchers, the most important point that distinguishes normal grief from pathological grief is the mourning process. Therefore, it is important to understand what a normal mourning process entails.

Grief researchers have proposed various theories about the mourning process, including stage theory [1,15], task theory [21] and dual process theory [22] (see table 1 for a summary). The stage theory proposed by Bowlby [1] and Parkes [15] considered the adjustment to bereavement over a period of several weeks to a few months. This theory describes four stages: shock–numbness, yearning–searching, disorganization–despair and reorganization. This theory has been widely accepted by clinicians and the general population, in part owing to the stage theory of acceptance of

Table 1. Summary of the mourning process models.

model	authors	components of mourning process	summary
stage theory	Bowlby (1982) [1]	1. shock–numbness 2. yearning–searching 3. disorganization–despair 4. reorganization	this model focused on the natural emotional shift the findings of two recent studies [23,24] were inconsistent with this theory; however, the studies validated that the peak of emotions of grief is shifted over time
task theory	Worden (2008) [21]	1. to accept the reality of death 2. to process the pain of grief 3. to adjust to a world without the deceased 4. to find an enduring connection with the deceased in the midst of embarking on a new life	this model focused on the mourner's task of facing the situation and actively coping with it the overall validity of this model has not been examined by empirical studies the importance of maintaining a connection with the deceased in order to adapt to the loss was supported by another study [25]
dual process model	Strobe & Schut (1999) [22]	1. loss-oriented coping 2. restoration-oriented coping	this model focused on the two coping strategies for stressors related to grief the mourners recover from grief by oscillating between the two coping strategies in daily life some studies have attempted to validate this model. Chen *et al*. [26] supported the importance of this model in their study on disaster survivors

death by Kübler-Ross [27]. However, it has also been criticized. Weiss [28] suggested that issues with this theory include lack of empirical testing, and that each stage implies intercorrelations within grief manifestations. For Neimeyer [25], the stage theory is prone to be misunderstood as implying that all people should go through all of the stages.

In response to such criticisms, Stroebe *et al*. [3] pointed out that Bowlby did not imply these stages as a concrete model, and that his theory might be misunderstood. Maciejewski *et al*. [23] examined the relative magnitudes and patterns of post-loss changes over time on five grief indicators, including disbelief, yearning, anger, depression and acceptance, to assess consistency with Bowlby's stage theory. Their findings indicated that disbelief was the initial, dominant grief indicator. Acceptance was the most-frequently selected item, which increased throughout the study observation period. Yearning was the dominant negative grief indicator from 1 to 24 months after bereavement. The normal stages of grief following a natural death showed that negative grief indicators peaked within approximately six months post loss. This finding was inconsistent with the stage theory; however, it partly supported the peak of negative emotions according to Bowlby's stage theory. Holland & Neimeyer [24] also failed to fully corroborate the stage theory, although their finding was partly consistent with it in the short time period after the loss. These studies indicate that grieving emotions, such as yearning, anger and depression, did not shift stepwise, but their peaks transferred over time.

Worden [21] partly agreed with the phase or stage theory proposed by Bowlby [1] and Parkes [15] but suggested using the term 'task' in the mourning process, because whereas 'phase' implies a passive process, 'task' requires the bereaved to engage actively. He emphasized that most people faced and overcame the four basic tasks, namely acceptance of death, processing the pain, adjustment to the world without the deceased and acknowledging the continuing bond with the deceased over time [21]. The idea of the continuing bond contrasts with Freud's [2] view that people should transfer their 'libido' from the deceased to someone else through the mourning process. However, in recent years, there has been an increasing acceptance of the necessity of the continuing bond with the deceased for adapting to the loss [29].

Stroebe & Schut [22] proposed another theory to explain how people accept the death of a loved one and recover from distress in day-to-day life. They called these modes the dual process model of coping with bereavement. This model identifies two types of stressors, loss- and restoration-oriented, and a dynamic, regulatory coping process of oscillation, whereby the grieving individual at times confronts or avoids the different tasks of grieving. In daily life, the bereaved experiences both aspects; in other words, people repeat confrontation and avoidance with the distress related to death. This pattern is critical in accepting the death and starting a new life without the deceased. This model is characterized by recognizing the importance of avoidance of grief work. The role of avoidance in the recovery process from acute grief seems to be different from that in post-traumatic stress disorder (PTSD). The emotional processing theory of PTSD proposed by Foa & Kozak [30] regards harmless stimuli as a non-functional factor interfering with the natural recovery process. This means that memories related to the patient's traumatic event are seen as in the past, and at present it is not necessary to avoid them. By contrast, the bereaved individual is forced to confront the reality of the loss of the loved one; death cannot be treated as a past event because it is permanent. Parkes [15] stated that the reality of death is too catastrophic to be quickly accepted by the bereaved. Therefore, the bereaved lower their distress levels through adaptive avoidance, similar to protective exclusion and reappraisal of the meaning of death, while oscillating between avoidance and confrontation. Validity of the dual model process in different contexts with various types of bereavement has been addressed in several studies [26,31,32]. Chen *et al*. [26] reported that six mothers who lost their children in the 2008 China earthquake primarily coped with loss-oriented stressors and shifted their focus to restoration-oriented stressors to deal with the situation over time.

4. Is CG a mental disorder?

Usually, grief follows a natural course, and people make a compromise with their loss and move onto their new life. However, for some, painful yearning and longing persist. Freud [2] considered any mourning that deviated from the usual process as not pathological, and he viewed melancholia as a distinct disorder from mourning.

At present, the concept of pathological grief is widely accepted among researchers [3,7–11]. Grief that deviates from the normal process is variously referred to as delayed grief [6], distorted grief [6], CG [7,8], traumatic grief [9], PGD [10] and PCBD [11]. One of these attracted considerable attention among researchers in the 1990s. Stroebe *et al*. [3] identified some of its common features and summarized CG as follows: 'a clinically significant deviation from the (cultural) norm in either (a) the time course or intensity of specific or general syndromes of grief and/or (b) the level of performance in social, occupational, or other important areas of functioning'.

The development of a validated scale for CG has stimulated empirical studies. Prigerson *et al*. [33] developed the inventory of CG (ICG), which is a self-administered scale with 19 items. As a result of the availability of a validated CG scale, epidemiological studies have revealed the clinical status of CG, including prevalence, risk factors and prognosis. Additionally, various scales such as ICG-R [33] and the brief grief questionnaire [34] were developed and used to measure the prevalence of CG. In a recent meta-analytic study [35], the estimated prevalence of CG among mourners was 9.8% (95% CI: 6.8–14.0%).

The issue of whether or not CG is a psychiatric disorder has been discussed in the past two decades. According to Prigerson *et al*. [10] and Shear *et al*. [8], CG—which Prigerson *et al*. [10] termed 'PGD' —is a mental disorder which requires providing treatment to the patient for the following reasons.

(a) The symptoms of CG are outside the scope of usual grief

The characteristic symptoms of CG include intense yearning, longing or emotional pain, frequent preoccupying thoughts and memories of the deceased person, a feeling of disbelief or inability to accept the loss and difficulty imagining a meaningful future without the deceased person. Many of these symptoms are similar to the acute phase of normal grief. Acute grief reactions such as yearning, longing and pangs of sadness usually diminish with time. Maciejewski *et al*. [23] reported that in the normal stages of grief following a natural death, the grief indicators peaked including yearning, anger and depression within approximately six months post loss. However, the symptoms of CG continue for a prolonged period of time. Among bereaved adults of the 11 September attack in New York, 43% met the criteria for CG 2.5–3.5 years after the event [36]. Some symptoms of CG such as excessive avoidance of reminders of the loss, constant preoccupation with the deceased and excessive survivor's guilt lead to dysfunctional thoughts, maladaptive behaviours and emotion dysregulation [8]. Furthermore, CG is associated with a variety of symptoms of poor physical health, mental problems and social dysfunction, such as high blood pressure, heart disease, cancer, headache, flu, suicidal ideation [37,38], low subjective health [39], various psychiatric symptoms [39,40], poor quality of life [39,41] and reduced vitality [40].

(b) CG differs from responses to a common stressor and other mental disorders

The prevalence of CG among the general population worldwide ranges from 2.4% in Japan [42] to 6.7% in Germany [43]. This means that only a small proportion of the bereaved population develops CG. Studies have reported that the prevalence of CG rises following traumatic events such as homicide (22% [44]) and terrorist attacks (43% [36]). CG often exists with other psychological co-morbidities including major depressive disorder (MDD) and PTSD [34,44,45]. The lifetime prevalence of a co-morbid disorder among the patients with CG is 84.5%, with the most prevalent being depression (71.8%) [45]. In recent years, however, it has generally been thought that CG is distinguishable from MDD and PTSD. The bereaved with CG suffers from intrusive memories of the loved one's death and avoids memories and reminders related to the loss. These symptoms of intrusion and avoidance are also seen in those with PTSD, particularly in the case of a traumatic death. However, patients with PTSD do not feel sadness but are fearful of trauma reminders, and they never seek proximity to the event-related situations or memories [8,46]. MDD has some features in common with CG, including feelings of sadness, guilt, suicidal ideations, decline in interest in daily and social life, and social isolation. Although symptoms of MDD are widespread across many aspects of life, CG symptoms are restricted to the deceased [8,46]. Furthermore, the finding that antidepressants are not effective for CG [47,48] underlines the difference between depression and CG. The diagnostic overlap between CG, MDD and PTSD has been reported to be modest [34,44].

(c) CG is universal across nations and cultures

There has been considerable research on CG among various cultures and nations, including both Western [43,45,49] and Eastern countries [26,42].

(d) CG has diagnostic validation in biological studies and responds to therapy

O'Connor *et al*. [50], in an fMRI study, suggested that the brain region related to CG was a reward system including the nucleus accumbens, which differed in reactivity to grief-related stimuli between CG and non-CG patients. Treatment studies have demonstrated that cognitive behavioural therapies designed for CG are more effective than other, non-specific therapies including interpersonal therapy [46,47] and supportive counselling [51].

(e) A diagnosis of CG might have more advantages than disadvantages

One of the reasons for opposing the view of CG as a mental disorder is the risk of regarding normal grief as pathological and stigmatizing the bereaved [3,52]. However, based on their experience and the results of the study by Johnston *et al*. [53], Shear *et al*. [8] suggested that many people were relieved to know that their symptoms had a name and were treatable. A field study by Prigerson *et al*. [10] found that a CG diagnosis could relieve the anxiety in bereaved individuals who feared a total mental and emotional breakdown.

In terms of cost, considering CG as a mental disorder might be advantageous. In Japan, unless diagnosed as a psychiatric disorder, a mental problem is not recognized for medical insurance. If CG were included as one of the psychiatric disorders, like PTSD, the burden of treatment costs to the patient with CG would be reduced.

5. Complications regarding diagnostic criteria for CG

Based on multiple studies on CG, in 2013, the American Psychiatric Association considered 'CG' as a psychiatric disorder and named it 'PCBD' in the DSM-5 [11]. PCBD is seen in other specific trauma- and stress-related disorders, and its diagnostic criteria were described in the chapter on conditions for future study [11]. It was also mentioned that grief researchers had not reached consensus regarding diagnostic criteria.

Prior to the revision of DSM-IV TR to DSM-5, two sets of diagnostic criteria were published. Prigerson *et al*. [54] used the diagnostic name PGD rather than CG. Shear *et al*. [8] continued using the term 'CG', arguing that the notion of 'complication' implied the nuance of interference with the natural process of recovery; CG was thus a commonly used term in the literature.

The diagnostic criteria for CG, PGD and PCBD share core symptoms of separation distress, including persistent yearning/longing, emotional pain and preoccupation with the deceased (table 2). However, the most important difference among them is the duration of the symptoms. The diagnostic criteria for PCBD require persistent symptoms for at least 12 months [11], compared with six months in PGD [54] and CG [8]. In ICD-11, which is scheduled to be revised in 2018, PGD will be defined as a condition that persists for six months (ICD-11 beta draft, December 2017).

Other aspects of the diagnostic criteria for PCBD have been debated. Boelen & Prigerson [59] criticized the criteria of PCBD based on the inclusion of some new items such as 'difficulty in positive reminiscing', which were not included in the sets proposed for PGD [54] and CG [8], and that there was no evidence that the 12-month post-loss criterion was effective for distinguishing CG from normal grief. Many authors have considered the appropriateness of the diagnostic criteria for ICD-11 and revising the DSM-5 [55–58,60]. In a study of clinical and community samples, Cozza *et al*. [57] found that CG criteria showed higher accuracy than PGD and PCBD, which excluded non-clinical cases and identified more than 90% of clinical cases. Maciejewski *et al*. [58] compared the four proposed criteria for distorted grief, including PGD, PCBD, CG and PGD of the ICD-11 beta draft, among community samples. They reported PGD, PGD of ICD-11 and PCBD having a high consistency of diagnosis (0.80–0.84) and similar sensitivity (0.83–0.93) and specificity (0.95–0.98) [58]. They suggested that CG criteria differed from the others because CG had a moderate pairwise agreement with the other criteria (0.48–0.55) and had a high sensitivity (1.0) and moderate specificity (0.79) [58]. Maciejewski *et al*. [58] expressed concern that CG might identify a high rate of false-positive cases and pathologize normal grief. However, Reynolds *et al*. [56] argued that the sample used in Maciejewski *et al*.'s study [58] was biased towards non-clinical and elderly female subjects, and that CG criteria were superior to PGD for detecting clinical samples. Underlying the controversy about diagnostic criteria is a lack of consensus regarding the core concept and biological evidence of the pathology of grief.

6. Recent trends in CG treatment

Despite the lack of consensus regarding diagnostic criteria for CG, studies on treatment have made progress over the past decade. In pharmacotherapy, the focus is on the effectiveness of antidepressants. One study [48] reported that a tricyclic antidepressant (nortriptyline) was effective for depressive symptoms, but not for grief symptoms. Studies using other types of antidepressant, namely serotonin-selective reuptake inhibitors including escitalopram [61,62] and paroxetine [63], showed a significant reduction in ICG scores in a before-and-after procedure without a control group. However, a randomized clinical trial to examine the efficacy of citalopram [47] found that it significantly improved depressive symptoms such as suicidal ideation, but was not effective for CG symptoms. At present, there is no evidence that antidepressants are effective for treating CG.

Stroebe *et al*. [64] conducted a systematic review of the effectiveness of psychosocial and psychological counselling at three stages including primary, secondary and tertiary preventive interventions. Primary interventions were effective for all bereaved individuals including those with higher levels of mental health problems before intervention. Secondary interventions for high-risk bereaved individuals were effective when associated with stringent risk criteria, showing the need for further differentiation within groups and tailoring intervention for subgroups. In the tertiary intervention for bereaved individuals with mental disorders, the specific individual treatments for CG were effective.

Wittouck *et al*. [65] reported a meta-analysis of the prevention and treatment of CG. They were unable to establish the effectiveness of a preventive intervention for CG; however, treatment interventions, especially cognitive behavioural therapy (CBT) [46,51,66] focused on CG, could effectively reduce CG symptoms. In addition, it was reported that some randomized

Table 2. Comparison of the characteristics of PCBD, CG and PGD. PCBD, persistent complex bereavement disorder; CG, complicated grief; PGD, prolonged grief disorder. Criterion B and C are the diagnostic criteria for PCBD. The grey colour shows common items across these criteria.

	PCBD (DSM-5) [11]	**CG (Shear *et al.* [8])**	**PGD (Prigerson *et al.* [54])**	**PGD (ICD-11)**
definition of pathological grief	a state in which severe grief reactions persist	a state in which complications impede healing after a loss and lead to a period of prolonged and intensified acute grief	persistent and pervasive grief reactions	persistent and pervasive grief reactions
needed duration of symptom persistence for diagnosis	twelve months	at least one month (the person experienced the death of a loved one, for at least six months)	six months	six months
symptoms				
criterion B: separation distress				
yearning/longing	B	B	B	B
sorrow/emotional pain	B	B	B	B
preoccupation with the deceased	B	B	B	B
preoccupation with circumstances of the death	B	C		
criterion C: reactive distress to the death				
difficulty accepting the death	C	C	C	C
emotional numbness/being stunned	C	C	C	C
difficulty in positively reminiscing	C			C
bitterness/anger	C	C	C	C
self-blame and the other maladaptive cognitive appraisal	C	C		C
avoidance of reminders	C	C	C	
social/identity disruption				
desire to die (suicidal ideation)	C	B		
difficulty trusting others	C	C	C	
loneliness	C	B		
considering life as empty, meaningless and unfulfilling	C	B	C	
confusion regarding self-identity/part of yourself died	C		C	C
difficulty moving on	C		C	C

(*Continued.*)

Table 2. (*Continued.*)

	PCBD (DSM-5) [11]	**CG (Shear *et al.* [8])**	**PGD (Prigerson *et al.* [54])**	**PGD (ICD-11)**
CG symptoms				
difficulty caring for others		C		
envious of others who have not faced a loss		C		
experiencing symptoms of the deceased		C		
hearing or seeing the deceased		C		
excessive proximity seeking		C		
intense emotional/physiological reactivity to memories/ reminders		C		
disturbing emotional/physiological reactivity to reminders		C		
valuable aspects		CG has a high sensitivity and accuracy to identify clinical cases in both community and clinical samples [55–57]	PGD has a high sensitivity and specificity among the general population [58]	
criticized issues	lack of evidence that 12 months are required for diagnosis some symptom items are inconsistent with those of the previous studies [59]	CG has shown a lower sensitivity and higher rate of false positive among general samples. It might pathologize normal grief [58]	the examination of the performance of the PGD was insufficient because the study sample was a non-clinical sample and limited to elderly, white and female participants [56]	

controlled trials of CBT focused on CG including the exposure components to death situations [47,67] were effective, with a large effect size. Shear [68] stated that imaginal revisiting—the name of the exposure strategy in their treatment—was intended to facilitate the ability to both think about death and set it aside. Boelen *et al*. [51] reported that the effect size of the exposure component in CBT for CG (0.94) was greater than the cognitive restriction component (0.44), and exposure appeared effective in terms of avoidant thoughts and behaviours. Bryant *et al*. [67] reported that CBT with exposure therapy was more effective for CG than CBT alone, and that the exposure component might promote emotional processing of memories of the death. Although the method of exposure component varies across treatment studies, it is commonly used to reduce avoidance of reminders and memories of the deceased, and to promote the acceptance of death and restriction of negative thoughts. The results of these treatment studies are considered to provide insights into the pathology of CG.

7. Conclusion

This article briefly reviewed progress in our understanding of pathological grief as typified by CG, the debate regarding new diagnostic criteria and recent trends in CG treatment. The loss of a loved one is inevitable, and the psychology of grief, especially pathological grief, has been increasingly intensively studied in recent years. In the 1990s, a type of pathological grief was studied; it was similar to CG, characterized by an extended period of acute grief and impaired physical, psychological and social functioning, and treatment measures were developed. Naming this condition as PCBD and including it as a psychiatric disorder in DSM-5 marked a milestone in CG research. The prevalence rate of CG is 2.4% [42] to 6.7% [43] among the general population; this means that many people in the world suffer from this condition for a long time, especially in disaster- and conflict-affected regions. Given the importance of developing effective and convenient treatment methods for these people, we need to reach a consensus on diagnostic criteria and continue to develop standardized assessment tools.

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Research

Social bonds with the dead: how funerals transformed in the twentieth and twenty-first centuries

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Evolutionary thanatology includes the study of necrophoresis—the removal of dead individuals by the living among social insects. In human societies, 'necrophoresis' is performed via the funeral ceremony. In pre-modern societies, relatives and local community members helped to conduct funerals. In this way, holding a funeral was a form of mutual help, a social exchange of duty and responsibility essential to individuals. These societies developed systems to ensure the survival of humans as social animals based on mutual trust built over long periods of time within the same community. Contemporary societies are undermining these systems. Compared to funerals in pre-modern societies, holding a funeral in a modern society is a complicated process that requires professionals with specialized knowledge and skills. If people feel they can face mortality without support from relatives or the local community, and that they cannot necessarily expect a future return on the effort invested in community-based social relationships, they may begin to disengage from such relationships. In the context of modernization, the clearest changes in collective funerary behaviours include decreased funeral attendance and the above-mentioned outsourcing of funerary services. As such, it can be said that bonds with the dead changed completely under modernization, especially in the twentieth and twenty-first centuries. To establish a sociology of death with a clearer focus on how funeral ceremonies have been affected by modernization, there is a need for research concerned with human behavioural changes regarding the treatment of corpses—that is, a 'funeralogy'. Accordingly, this study aimed to investigate how modernization has complexified the handling of deceased bodies as death-related services have become commoditized and outsourced while, at the same time, local communities are becoming disengaged from their traditional roles in funeral ceremonies. To this end, fieldwork was conducted in several countries. Moreover, data from surveys conducted by the Social Well-Being Research Consortium in Asia in five East and Southeast Asian countries were quantitatively analysed. The findings highlight the modernization of funerals with the outsourcing of funeral services from the perspective of socio-economic development.

This article is part of the theme issue 'Evolutionary thanatology: impacts of the dead on the living in humans and other animals'.

1. Introduction

In the world of living things, only humans hold funeral ceremonies. In this paper, a funeral refers to the ritualized acts performed to physically sever the bonds of the living with the deceased and place them in social memory. These include how and to where the body is moved once a person has been confirmed to have died and the form of disposal used for the body, such as ground

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burial or cremation. What significance do these acts hold for humans as social animals? The purpose of this article is to contribute to the field of evolutionary thanatology through a discussion of the effect that the modernization of societies has had on funerals.

In Anderson's [1] discussion of responses to and understanding of death in non-human animals, he described the phenomenon of necrophoresis in social insects—that is, the systematic removal of dead colony members from the communal nest. He also intimated that some primates grieve following the death of individuals, usually those to which they are related. However, only human adults appear to understand all of the following four components of death: inevitability, irreversibility, non-functionality and causality. In other words, while some other animal species show necrophoric behaviours, in order to fully perceive and mourn the loss of another individual, a higher level of cognitive functioning is necessary, allowing the survivor to feel an emotional bond with that absent other, i.e. a bond with the dead [2]. This is why only humans perform funeral rites.

Funeral rites represent an important part of collective behaviour in human societies. However, with some exceptions, such as the historical analysis by Ariès [3] and Mitford's [4] critique of the commercialization of the funeral, sociologists have not viewed funerals as an important topic for research. This suggests a need to establish a field within the study of human societies that focuses on their funerals, i.e. a 'funeralogy', which would include research from the perspectives of sociology, archaeology, history, ethnology and cultural anthropology. If the purpose of evolutionary thanatology is the exploration of how, through evolutionary processes, animals developed species-specific ways of responding to the deaths of other individuals, funeralogy would be distinctive by focusing on changes in funeral rites in human societies. Within that field, one area of enquiry for sociologists would be exploring how modernization has transformed funeral ceremonies.

The author of the present study has used participant observations and quantitative surveys to examine how, under modernization, the process by which bonds with the deceased are severed and reconstructed has shifted from communities to funerary service specialists. These changes reflect communities' increasing disengagement from funerals.

2. Increasing complexity in the treatment of the dead

When did humans first begin holding funerals? According to Pettitt [5], *Homo sapiens* conducted the earliest unequivocal burials (i.e. bodies deposited in deliberately excavated graves), deriving from caves in Israel (Skhul and Qafzeh) dating to 90 000–110 000 BP.

Among social insects, necrophoresis consists of two major components: carrying the corpse away from the colony (separating the dead from the living) and disposing of the remains (abandoning or transforming them) [1]. While these functional aspects are essentially the same in non-human and human societies, in the latter case there has been a progression from relatively unchanged, primitive funerals to transformed, modern versions. Moreover, unlike social insects, which tend to simply remove the corpse from the nest and dispose of it, human processes involve a singular change involving both the social and psychological bonds of the living with the deceased.

Archaeological studies have traced how the handling of corpses by earlier hominids was comparatively simple. From a sociological perspective, the question concerns how funerals change as societies become more complex. In Mongolia, for example, a small number of nomadic tribes used to live scattered over a vast area. Habenstein and Laners [6, pp. 89–90] described Mongolian funerals in the following way: 'Three methods are available to the Mongolians: earth burial, cremation, or abandonment to scavengers.... Among Mongolians, exposure or abandonment of the dead is the simplest and commonest method of disposal.' The Mongolian ethnologists Nyambuu and Aryasuren [7] also mentioned that in the traditional funeral the bodies of the dead were abandoned to the elements. They explained that the nomadic tribes disliked disturbing the grassland environment by digging graves. Additionally, in a land where wood for fuel was scarce, cremation was impractical. Exposure of the dead to the elements was contrastingly simple. The body was wrapped in a sanctified piece of cloth for transport and, after a funeral ceremony, it was laid naked on the ground and abandoned in the grassland according to customary practice. After praying for the deceased's remains to be safely eaten by beasts or birds of prey, the attendees then simply returned to their tents.

With the Mongolian Revolution and the concentration of the population in cities in the 1920s, ground burials spread, and government-managed cemeteries were established on the outskirts of Ulaanbaatar. Now, the body would be laid in a coffin in the home before being buried in a cemetery. With this change, it became necessary to buy coffins and gravestones. Mongolian funerals changed again in 2004 when the government established a funerary complex 25 km from Ulaanbaatar, consisting of a modern crematorium, funeral hall and Tibetan Buddhist temple. As a result of rapid population concentration in the capital, people were now living in areas formerly on the city's outskirts. Most were poor people who drew water from underground rivers that flowed beneath the cemeteries. Concerned about the potential health risks, the government decided to build a modern crematorium. The present study was conducted soon after it opened. At that time, cremations were still infrequent, but, according to people familiar with the situation, the percentage of cremations has increased since then.

In short, in the last 100 years, the disposal of human remains in Mongolian society shifted from abandonment to burial to cremation. Underlying those changes were factors related to urbanization and developments in political, economic and cultural conditions. Each new funerary method brought increased complexity to the process. When a body was abandoned to the elements, the naked remains were simply left on the ground in the grassland. For ground burials, the remains had to be put in a coffin and transported to a graveyard; this required new businesses to manufacture coffins and gravestones. Finally, to institute cremation—where the body is laid in a coffin, transported to a crematorium, and burned—significant modernization was required, given that experts were needed to use the equipment, and fuel was needed to operate the furnaces.

Figure 1. Funerals in Uganda (2015) and in Japan (2007). (Online version in colour.)

3. Provision of funerary services by the local community

As in Mongolia, funeral practices in Uganda have undergone significant changes. Habenstein and Laners [6, p. 263] described the transformation in Baganda funerals in Uganda: 'Owing to missionary influence and the acceptance of Christianity by natives, there have been rather drastic modifications in folkways.... However, in many ways, the present practises of burial represent an admixture or conglomerate of Christian and primitive practises'.

The present author had the opportunity to attend a funeral on the outskirts of the Ugandan capital, Kampala, in 2015. Because the family was Christian, after a religious ceremony in the family home, the coffin, borne by young men, was transported to the neighbourhood church for the formal funeral. Afterwards, the body was buried in a forest near the family home. These places were all within walking distance, and all transport took place on foot (figure 1).

Concerning the provision of services needed for the funeral, based on interviews with the family, it was estimated that around 500 people attended the funeral. However, the author was unable to confirm the existence of any businesses that specialized in carrying out large-scale funerals. The only things the family purchased from others were the coffin, the gravestone and ingredients for a meal for the attendees. Reflecting their tribal society, they were assisted by family and acquaintances with everything that needed to be done, including the meals for the attendees and transport of the body. As explained by the family, 'His friends from his high school brought a car to go to the burial place at the village. When the body was taken to the village, family members had organized how the burial was supposed to be (e.g. the organization of food and the church mass). A mass was conducted in the church, which was followed by the burial, after which food was served to the attendees. Family members and friends contributed a lot during this burial.' In this context, 'family members' meant 'members of the tribe with whom they felt a strong kinship' rather than 'nuclear family', as in Japan and the West. In other words, the community took responsibility for providing all the services needed for the funeral.

In 2011, the author observed a funeral in a Vietnamese village in which the role of the local community was also important [8]. However, in urban areas in Vietnam, funerals are also undergoing major changes [9].

4. Transformation of the Japanese funeral

The author has previously written about the cultural evolution of the funeral in Japanese urban society [10]. That study argued that, in the Japan of 100 years ago, funerals could not be conducted without the assistance of the local community and kin, that they were conducted according to strong social norms, that burial was more frequent than cremation and that the funeral consisted of three parts, in which the funeral procession was the most ceremonially important.

By contrast, in contemporary Japan, it is the role of the nuclear family to host the funeral, and because in urban areas local community involvement can no longer be expected, funerals are becoming smaller. Given the longer distances that bodies need to be transported due to the increase in the number of people dying in hospitals and the increasing trend of having funerals in dedicated funeral halls, holding a funeral has become impossible without hiring outside specialists to supply necessary services such as arranging a hall, transporting the remains, conducting the ceremony and providing meals for guests. Moreover, the way funerals are held continues to change as a consequence of the unprecedented ageing of Japanese society and the country's declining birth rate. The result of this is that the funeral must be supported by a small number of children and relatives who are also aged (figure 1).

Clearly, Japanese funerals have also changed significantly during the last 100 years. For example, looking at changes in rates of interment and cremation, in the 1920s, the rate of interment (56.8%) exceeded that of cremation. In the 1930s, the interment and cremation rates became transposed; then, during the period of rapid economic growth in the 1960s, there was a drastic increase in the rate of cremations. In the 1970s, the cremation rate reached more than 90% and since 2000 has exceeded 99% [11] (figure 2). This change emerged as a solution to the problem of how to safely dispose of bodies in a country with limited available space.

Similarly, regarding the place of death, until the 1950s, around 80% of Japanese people died at home, far surpassing the 10% who died in a hospital. However, a rapid increase in the number of hospital deaths meant that, by around 1975, the relative rates of home versus hospital deaths had reversed. In 2010, 77.9% of deaths occurred in hospitals, whereas only 12.6% occurred at home [12]. Compared to dying at home, after someone dies in a hospital, the body usually has to be transported a longer distance. In addition,

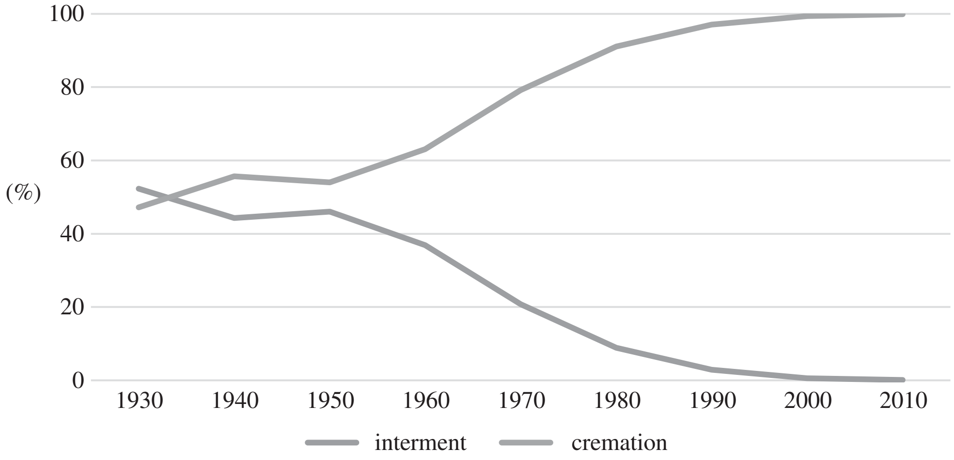

Figure 2. Rates of interment and cremation in Japan. (Online version in colour.)

as more families started to use places such as funeral halls and temples, the percentage of funerals held in the home decreased to 6.3% [13]. This change also means that the journeys travelled by bereaved family members and attendees have become longer and more complicated.

These statistics suggest that by around the end of the twentieth century, the modernization of the funeral in the urban areas of Japan was almost complete; that is, the provision of funerary services was no longer in the hands of local communities but was instead outsourced to professionals.

5. Community disengagement from funerals

As Japanese society modernized, an important factor in funerals becoming more elaborate and growing in scale was the commoditization of funerary services and the ability to collect large amounts of condolence money to pay for those services. Instead of using labour provided by the local community, families collected large sums of condolence money from their workplace communities, which made it possible to outsource the funerary services. However, when the Japanese economic bubble collapsed in the 1990s and the economy entered a slump, the trend towards increasingly extravagant funerals began to be replaced by a trend towards more modest events.

One consequence of the change in economic circumstances was a trend towards families holding smaller, more private family funerals, with only the nuclear family, close relatives, friends and acquaintances in attendance. In earlier, traditional funerals, the family was obligated to inform a large number of people about the death, including close relatives, members of the wider community and acquaintances. At the same time, people who were personally acquainted with the deceased or the family were obligated to adjust their personal and work schedules to attend the funeral. However, in contemporary Japan, deaths in the family are no longer so widely announced, and in some cases they are intentionally kept secret. The first to become disengaged from the funeral in this transition were people from the local community, next were work colleagues and then more distant relatives.

Although no accurate statistical data are available, based on statements from undertakers, cases have been increasing in urban society where even family (parents, children and siblings living far away) have no involvement in arranging the funeral; everything is left to the undertakers to organize. The same phenomenon has been documented in France [14].

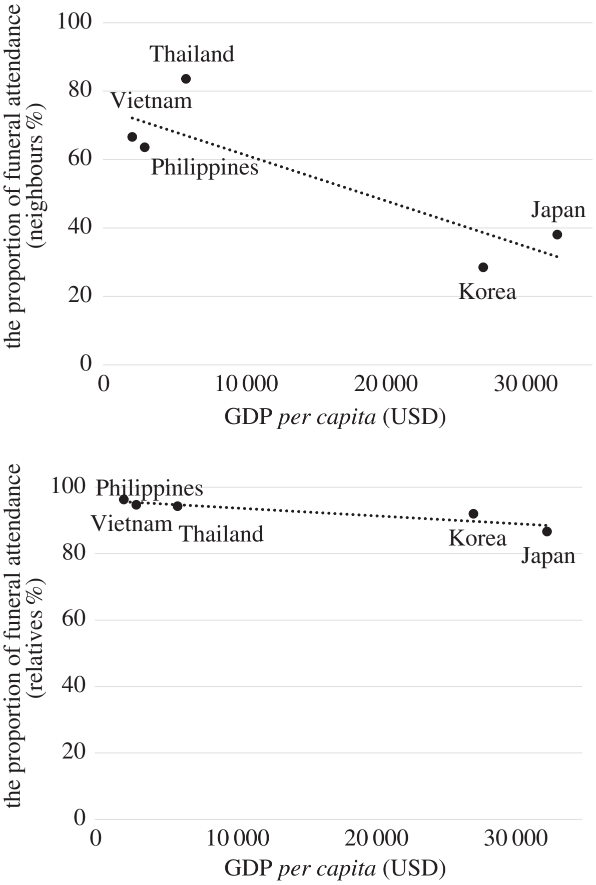

Figure 3. GDP × proportion of funeral attendance (above: neighbours, below: relatives).

It has become very common in Japan for elderly people to hire funeral professionals themselves because they cannot expect their children to take care of their funeral arrangements—so common, in fact, that the government has considered the issue at the policy level [15].

6. Economic development and changes in funerals in Asian societies

To support what has been argued so far regarding the modernization of societies and changes in funeral customs, some statistical research is presented here, based on opinion polls conducted by the Center for Social Well-Being Studies of

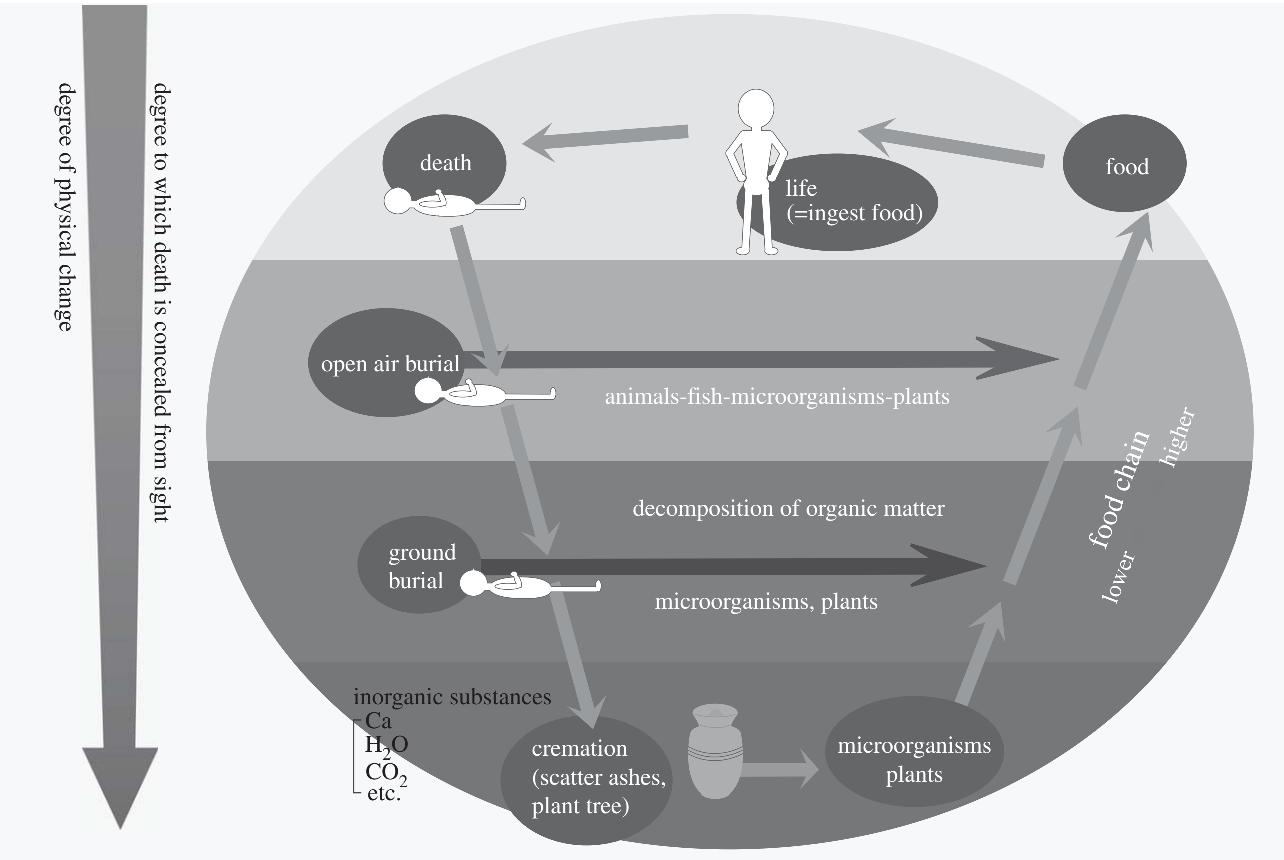

Figure 4. Burial practices and the cycle of nature. (Online version in colour.)

Senshu University and the Social Well-Being Research Consortium in Asia. The data came from five East and Southeast Asian countries nationwide. The names of the institutes conducting the surveys, the methods of the polls (Web or face-to-face interview (FF)) and sample size are as follows: Japan (Senshu University, Web, 11 804), South Korea (Seoul National University, Web, 2000), Vietnam (Vietnam Academy of Social Science, FF, 1202), Thailand (Chulalongkorn University, FF, 1126) and the Philippines (Ateneo de Manila University, FF, 1200). The surveys were conducted in 2015 and 2016 [16–20].

One of the questions asked in the survey was, ‘Do you feel that you have to attend the funerals of the following people?’ followed by a list that included ‘close family’, ‘relatives’, ‘friends and acquaintances’ and ‘neighbours’. Note that the researchers did not precisely define the nature of these relationships; rather, respondents answered using their subjective judgement of the meanings of the words as translated into each country’s language. The most notable finding was related to ‘proportion of funeral attendance’ (PFA)—that is, the percentage of respondents saying they attended the funerals of people in each relationship category. In the PFAs for ‘neighbours’ by GDP for each country, a negative association can be seen between the level of economic development and the percentage of respondents who attended the funerals of neighbours. Similarly, there is an association between PFAs for ‘relatives’ and GDP. Although not to the same extent as for funerals of neighbours, attendance rates again decreased with higher economic development. These data suggest that economic development may liberate individuals from the funeral-related responsibilities they might have had as members of a more traditional local community or extended family (figure 3).

7. Burial practices and the food chain

Burial, in the sense of disposing of the remains of the dead in a way that separates them from the community of the living, is ultimately a process by which the body’s organic matter is returned to nature. Whether that takes the form of abandonment to the elements, ground burial, cremation or other methods, the flesh returns to the earth in the natural cycle of life and death (figure 4).

When the body’s organic matter is abandoned to the elements, it returns to nature as food for animals and birds—living organisms that are relatively high in the food chain—as well as for microorganisms and plants. In ground burial, insects and microorganisms decompose the body into substances that may eventually be absorbed by plants and animals. Cremation may result in the most extreme regression, as the carbon dioxide and other elements resulting from gasification return to the atmosphere and the leftover bones and ash are eventually returned to the soil. However, burning the body was originally done with the same fundamental idea in mind: returning the deceased to nature by scattering their ashes in the sea or in a forest. In any case, the degree of human intervention involved in returning the body to nature became progressively larger as burial practices evolved from abandonment to the elements, to burial in the ground, to cremation.

In tandem with the increasing importance of human intervention in disposing of remains is an increase in the extent to which the method of disposal conceals the fact of death itself. As argued by Yoro *et al*. [21] an increasingly decomposed corpse is seen as the most virulent evidence that humans are a part of nature, even though they are cloaked by culture. As a result, societies have increasingly adopted disposal practices that distance the living from the dead. For example, the practice of abandonment, which allows people to witness the tearing up and devouring of a body by birds or animals and the process of decay, reinforces the fact that humans are merely part of nature. However, if the body is buried underground, the process by which it is returned to nature is concealed from sight. Further, cremation might be considered as artificially camouflaging the process entirely by instantly returning the body to inorganic substances. In other words, more modern human interventions in the process of returning the body to nature increasingly shield us from 'the smell of death' [22]. The more culture develops, the more people conceal the reality of death.

8. Conclusion

In pre-modern societies, funerals were held with the assistance of people in the local community and relatives who helped transport and bury, cremate or otherwise dispose of the body, in a process that converted the physical relationship with the deceased into a psychological one. Holding a funeral was a form of mutual help—a social exchange of duty and responsibility essential to individuals and families left behind—performed to promote survival within the group. These societies developed systems to ensure the survival of humans as social animals based on mutual trust built over long periods of time within the same community.

However, compared to funerals in pre-modern societies, holding a funeral in a modern society is a very complicated process that requires the intervention of professionals with specialist knowledge and skills. As it is no longer possible to simply use uncompensated labour from the community, funerary services must be purchased. While local, religious and workplace communities have continued to play a role, systems have also appeared to help with the purchase of services. With the development of social security, if people feel they can face mortality without the support of their local communities or relatives, they may begin to disengage from local community-based social relationships, given the many constraints and obligations from which they cannot necessarily expect a future return. The clearest changes in collective behaviour resulting from modernization include a decrease in funeral attendance and the outsourcing of services related to the treatment of the body.

Thus, in the relatively short period of modernization, the ways humans dispose of dead bodies have changed from simply abandoning the body outside of the group, to disposal via ritualized practices, to the current complex processes involved in cremation. To this trend can be added the development of cryogenics and the recent appearance of space burials involving the launching of ashes into space. To borrow Dawkins' evolutionary concept of the 'meme' [23], it seems reasonable to suggest that one or more 'funeral memes' have evolved among humans. While it may be difficult to say what burial method will prove to be the best survival strategy for humans, what began as necrophoresis—the disposal of deceased members of the same animal colony—is undergoing rapid modernization in human societies. As part of that evolution, social bonds with the dead are also undergoing significant change.

Ethics. All study participants provided informed consent, and the study design was approved by the appropriate ethics review board.

Data accessibility. The micro-dataset of the surveys will be published in KOSSDA (Korea Social Science Data Archive) after April 2019.

Competing interests. I declare I have no competing interests.

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