

frogs. International trade regulations and captive breeding efforts exist, but the illegal pet trade still places pressure on natural populations.

What can we learn from poison frogs in the future? The study of these animals is brewing strong amidst a robust foundation of literature and an energetic research community. Exciting new work in poison frogs will incorporate collaborative and interdisciplinary perspectives to elucidate patterns and mechanisms of behavior and evolution. For example, we will likely see research on learning and memory in the context of parental care, the evolution of complex behavior, flexibility and constraints of local speciation and polymorphism, resistance and adaptation to emergent diseases and habitat disturbance, and cellular and physiological mechanisms that regulate poison sequestration, orientation, and communication.

Where can I find out more?

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Is there any evidence for vocal learning in chimpanzee food calls?

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In their study “Vocal Learning in the Functionally Referential Food Grunts of Chimpanzees”, Watson *et al.* [1] claimed that they “provide the first evidence for vocal learning in a referential call in non-humans”. We challenge this conclusion, on two counts. For one, we are not convinced that the authors controlled for arousal (or at least they did not report such data); furthermore, the vocal characteristics of the two groups largely overlapped already at the beginning of the study. Accordingly, we also question the authors’ claim that their finding “sheds new light on the evolutionary history of human referential words”.

Firstly, Watson *et al.* [1] argue that “call structure was not tied to arousal as calls changed while preferences stayed stable”. Given the theoretical and empirical basis for linking vocalization structure (especially aspects related to frequency) to affective states [2], we agree with the authors that controlling for arousal (degree of stimulation) is critical to their conclusion. The authors had investigated the structure of food grunts before and after an integration of individuals from a Safari Park in the Netherlands (BB) into a group of chimpanzees residing at the Edinburgh Zoo (ED). If the BB individuals were simply highly aroused by apples when they moved to Edinburgh compared to ED individuals, and if this arousal declined over time, any changes to BB calls would be best explained by simple habituation to a stimulus (apples).

Watson *et al.*’s [1] conclusion relies on equating arousal and preference, which is fallacious. To demonstrate how different these two are, imagine

a human repeatedly offered his/her favorite food in a series of choice trials (the authors’ measure of preference). Regardless of how stable preference for this food remains, this person is surely going to be more excited to have their favorite food for the first time in months than for the third time in a week. No data are presented on apple feeding rates that BB individuals experienced in the Netherlands vs Edinburgh. It is thus plausible that BB individuals have an established preference for apples that is maintained, while the apple feeding at Edinburgh Zoo nonetheless led to a reduced state of arousal over time. A higher level of arousal of BB individuals at the start of the study could also be related to more excitement or higher levels of stress due to feeding in new environments and social contexts. Either way, it is important to rule out changes in arousal as the simplest explanation for the results, by collecting data on other aspects of behavior, such as submissive or self-directed behaviors [3], and/or physiology.

Secondly, there is an issue with the interpretation of the data. Despite the significant interaction reported for year and group, we observed that only seven calls from three subjects (out of a total of 20 calls from seven subjects) of the BB group recorded at the beginning of the study fell outside two standard deviations of the mean of the ED group (Figure 1). In other words, the majority of calls did not differ in the first place, indicating that irrespective of their provenance, most subjects of both populations had always responded with the general same call type to the presentation of apples. Moreover, the pattern whereby BB group individuals give calls above the range of ED individuals does not convincingly converge when looking at the data (Figure 1) — the seven BB calls above the ED range before group integration (2010) become five calls above the ED range following integration (2013) — weak evidence at best. Obviously two groups of humans from different linguistic backgrounds would most likely have entirely different words for the same things, not vocalizations that largely overlap.

More generally, even if Watson *et al.* [1] can provide new data that rule

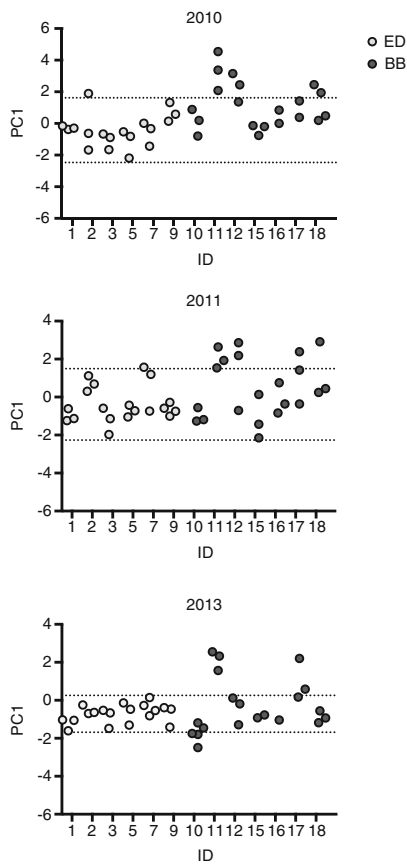


Figure 1. Individual values for the principal component for each individual and year. Light grey: Edinburgh subjects; Dark grey: BB subjects. Dotted lines indicate the 2SD plus/minus of the mean of the Edinburgh subjects. Details on the statistical analysis (calculation of the principal component) can be found in the Supplemental Information.

out the possibility that the observed changes result from habituation to the stimulus or the novel social context, there are still underlying conceptual issues that call into question the authors' suggested implications of their findings. Specifically, we disagree that their study "challenges long-held assumptions that [...] functionally referential primate calls cannot be decoupled from the arousal state experienced by the signaler and are completely fixed in their acoustic structure". There are two main problems with this statement. First, it is not clear how one plausibly explains the observation that, at the beginning of the study, most individuals from the two groups already produced the same call type in response to

the same stimulus as anything other than a reaction to the stimulus that is mediated by the affective state that the stimulus elicits. Second, Watson *et al.* [1] create a straw man for themselves to knock down in stating that it is assumed that functionally referential calls are "completely fixed" structurally. The core of the argument against functionally referential calls being a precursor to linguistic reference is that functionally referential calls do not differ fundamentally from other call types [4], and the authors acknowledge the well-documented variation in non-functionally referential call types based on variation in the social environment. Indeed, such modification of fine aspects of otherwise species-specific vocalizations has been shown in a number of anthropoid primates [5], as well as goats (*Capra hircus*) [6]. Further, this phenomenon is not limited to social influence, but has been documented in response to changes in the physical environment [7]. The most generous conclusion to draw from the Watson *et al.* [1] study is that it provides additional evidence of an already well-documented phenomenon: some terrestrial mammals (including chimpanzees [5]), which appear unable to learn unique call types in the way that vocal learners such as songbirds, cetaceans, and humans can [8], have the ability to modify their species-specific call types within a limited range. Watson *et al.* [1] offer no new evidence to link this modest modifiability (of what appears to be largely emotionally-driven call types) to the open, highly flexible system underpinning language.

In sum, there is no conclusive evidence that chimpanzees alter their vocalizations in response to auditory experience. Further, the purported evidence for limited vocal modification is like that already seen in other call-types and in other taxa, leaving no new evidence that the so-called "functionally referential signals" of chimpanzees or other taxa warrant special consideration for understanding language evolution. If any such limited modification should be considered vocal learning, we would ultimately need a new term to distinguish this from the matching of vocal output to a template, seen in

true vocal learners such as songbirds, dolphins, and humans. For future studies, we recommend critical inspection of the data to ensure biologically-meaningful conclusions rather than relying solely on statistical significance [9], a more careful consideration of plausible simpler explanations, and a greater effort to distinguish the effects of affect from auditory experience.

SUPPLEMENTAL INFORMATION

Supplemental Information includes details on the statistical analysis and can be found with this article online at <http://dx.doi.org/10.1016/j.cub.2015.09.010>.

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