Cross-population variation in usage of a call combination: evidence of signal usage optionality in wild bonobos

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The relationship between a signal's form and its function is foundational to all systems of communication and profoundly influences a communication system's expressive potential. In language, the relationship between a word's sound and its meaning is said to be 'arbitrary' because the association is a matter of socio-linguistic convention, rather than an obligatory or natural connection. Such arbitrariness is one of the key design features responsible for language's extreme lability and adaptability. Understanding arbitrariness, and its evolution, therefore, is essential in any account of the evolution of language. To shed light on the phylogeny of the phenomenon, it is necessary to take a comparative approach and examine arbitrariness (and related capacities) in the communication of non-human animals.

Non-human communication systems do not appear to exhibit the degree of arbitrariness present in language, but the precise connection between signal and function (or meaning) in animal communication is an open question. Several studies have challenged the notion that arbitrariness is unique to language by documenting changes in call structure across time (Mitani and Gros-Lous 1998; Crockford et al. 1994; Watson et al. 2015), and developmental functional flexibility (Dezecache et al. 2021). The extent to which these examples of 'signal adjustment optionality' (*sensu* Watson et al. 2022), is mirrored by a similar capacity for 'signal usage optionality' (*sensu* Watson et al. 2022) is largely unknown (but see Lameira et al. 2013 for evidence of 'signal usage optionality' in Borean orangutans).

We address this question by comparing the usage of long-distance vocalizations produced in two populations of bonobos (*Pan paniscus*). Previous work has demonstrated that two long-distance signals–high hoots (HHs) and the whistle-high hoot combination (W+HHs) are associated with distinct patterns of behavior and likely have different functions from one another (Schamberg et al. 2016; 2017). Here, we present data on the contexts in which HHs and W+HHs are produced in order to investigate potential shifts in call usage between populations.

Data for this study were collected at two field sites: LuiKotale and Kokolopori. Subjects (n=19 at Luikotale, n=32 at Kokolopori) were followed on foot and vocalizations were recorded with a directional microphone. Observers recorded HH and W+HH, and subsequently assigned each utterance to one of the following contexts: travel, arrival, feeding, or rest.

At both sites, bonobos produced W+HHs in all four contexts, but the predominant context accompanying call production differed between the two populations. At Kokolopori, the majority (22/42) of W+HHs were produced upon arrival at a fruiting tree. At LuiKotale, a plurality (20/52) of W+HHs were produced while resting. Overall, W+HH production contexts differed significantly between the two populations (full-null comparison: df= 3, $\chi^2 = 20.67$, $p < 0.001$).

Subjects produced a majority of HHs during periods of feeding or resting (75/95 at LuiKotale and 37/51 at Kokolopori), and there was no significant difference between HH contexts in the two populations (full-null comparison: df=3, $\chi^2 = 4.311$, p=0.230)

Our results reveal a between-population difference in bonobos' use of the W+HH call combination. Bonobos at the Kokolopori field site were significantly more likely to produce W+HHs upon arrival at a feeding tree, compared to bonobos at the LuiKotale field site. In contrast, we found no difference in the usage of HHs between the two populations. The contrasting findings regarding usage of HHs and W+HHs indicate that the shift in W+HH usage observed between LuiKotale and Kokolopori does not reflect a broader change in activity budgets related to socio-ecological factors; rather, the difference in W+HH usage may represent an example of signal usage optionality–i.e., bonobos in the two populations may use the same signal for subtly different purposes.

Acknowledgements

We would like to thank the LuiKotale Bonobo Project for offering access to the study site, and the people of Lompole village for hosting researchers in their forest. We would also like to thank to thank the Institut Congolais pour la Conservations de la Nature and the Ministry of Scientific Research and Technology in the Democratic Republic of the Congo for their support and permission to work in the Kokolopori Bonobo Reserve and Salonga National Park in Democratic Republic of Congo.

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