

Audience effects in chimpanzee copulation calls

Simon Townsend* and Klaus Zuberbühler

School of Psychology; University of St Andrews; St Andrews, UK; and Budongo Conservation Field Station; Masindi, Uganda

Key words: copulation calls, cognition, female competition, aggression, call production

Audience effects arise when the signaling behavior of animals is affected by the presence of others. Whilst this phenomenon has been documented in numerous animal species, very little research has addressed what effect the listening audience has in the mating context. In this article we discuss our recent findings that the production of chimpanzee copulation calls is effected by the presence of potentially eavesdropping females and males. We relate these results to understanding the function of primate copulation calls in addition to what more they can tell us about the cognitive processes underlying primate call production.

Introduction

In various groups of social animals, mating events are sometimes accompanied by acoustically distinct vocal signals, usually produced by the females.¹ These so called “copulation calls” have intrigued evolutionary biologists and stirred a considerable debate surrounding the proximate mechanisms and ultimate functions of this conspicuous behavior. Copulation calls are defined as acoustically distinct vocalizations produced prior to, during or just after copulations² and explanations for their pervasiveness range from calls just being incidental by-products of the copulatory act to calls synchronizing orgasm between the mating partners.³ To date, no less than 14 different functional hypotheses have been put forward,⁴ with varying degrees of empirical support.

One of the most commonly invoked explanations suggests that these sexually selected traits function to alert males to the receptive condition of the calling female, subsequently inciting competition amongst them.⁵⁻⁹ Competition can occur directly between males or, at a smaller though no less important scale, between sperm, such that the female ends up with the most dominant mating partner and his genes. However, whilst these adaptive explanations address a number of important theoretical points their focus is on how the female's calls affect the nearby adult male audience. The fact that the mating pair is usually part of a complicated social network, consisting of relatives, offspring, allies and social competitors, is not normally considered. In most primate species, females play crucial roles in the social fabric of the group, and it is therefore somewhat surprising that this has

never been properly considered as a selection factor in the evolution of copulation calls. In a recent study of chimpanzee copulation calls, we sought to address this potentially relevant factor, by asking what role the presence of conspecific females plays in the call production of a copulating female.

To Call or Not to Call?

Chimpanzees are interesting for studying copulation calls for a number of reasons, primarily because they produce copulation calls at much lower rates than other primate species⁴ and because of the flexibility of their social system. In our study group at Budongo Forest, Uganda, females only called during a third of all copulations, significantly lower compared to, for instance, Barbary macaques (*Macaca sylvanus*; 86%)¹⁰ or yellow baboons (*Papio cynocephalus cynocephalus*; 98%).⁹ When probing into this difference, we found that calling was mediated by a number of variables, but most surprising was the resounding effect of the nearby female audience. Audience effects can arise when signal production is mediated by the surrounding social environment and not just the product of the original eliciting stimulus.¹¹ Research from numerous social vertebrate species has elucidated the almost ubiquitous nature of the audience on behavior, although the underlying cognitive processes may be very different (e.g., chickens, *Gallus gallus domesticus*;¹² zebra finches, *Taeniopygia guttata*;¹³ brown capuchin monkeys, *Cebus apella*;¹⁴ Siamese fighting fish, *Betta splendens*¹⁵). In this case, we found that when there were high-ranking females near the copulating female, who could potentially hear the copulation calls, low-ranking females were significantly less likely to produce them.¹⁶

Female-Female Competition

Regardless of social organization, free ranging female primates are regularly observed to mate promiscuously, both with males of their own but also with males of neighboring groups.¹⁷⁻¹⁹ One potential consequence is that females may compete with each other over access to high-quality males and their sperm,^{10,20,21} and this is likely to impact on the evolution of their behavioral strategies. In wild chimpanzees, there is now evidence that competition for resources amongst females can be high,²²⁻²⁶ and under certain socio-ecological conditions, females can compete aggressively, even lethally, with each other (reviewed in refs. 24 and 27).

In contrast to most other primate species, chimpanzees are male-bonded with females dispersing around sexual maturity.²⁷ Immigration of new females into a chimpanzee community can alter

*Correspondence to: Simon Townsend; School of Psychology; University of St. Andrews; St Andrews KY16 9JP UK; Email: swt6@st-andrews.ac.uk

the sex ratio quite dramatically and potentially puts increased pressure on resource availability, including access to male partners.^{16,24}

At Budongo, our study group consisted of only five high-ranking adult males compared to almost 30 adult females, suggesting that competition amongst females for accessing males and resources was, at times, high. We found that refraining from calling during copulations with high-ranking males was a common strategy when there were potentially aggressive high-ranking females around, suggesting that low-ranking females tried to dissipate the risks associated with such competition.¹⁶

This female-driven audience effect showed that female primates are not solely concerned about whether potential male mating partners can hear them. Instead they appear to take into account which females are in earshot and modify call production to avoid conflict, allocating a significant role of female-female competition in the evolution of this reproductively important signal.

The Role of the Male Audience

Copulation calls are likely to function to attract the attention of males other than the mating partner,⁴ but little research has been done to investigate how flexible females are in adjusting their calling behavior in response to the presence or absence of specific males, i.e., to what degree they are capable of taking the potential male audience into account when producing copulation calls.

In a study focusing on the informational content of chimpanzee copulation calls we found that calls have the potential to signal the rank of the mating partner to listening individuals.²⁸ Calls given while mating with high-ranking males consisted of higher-pitched frequency bands than calls given while mating with low-ranking males. Furthermore, although females produced copulation calls with all males, they were much more reluctant to do so when mating with a low-ranking male. Females can receive significant aggression from high-ranking males when mating with other males and our analyses clearly showed that a female's decision to produce copulation calls was mediated by her probability of detection. Specifically, if the female was concealed by dense vegetation and furtive mating was possible she typically refrained from vocalizing, whereas if she was precariously exposed in a tree and potentially visible to surrounding males, the probability of producing a call was significantly higher.²⁸

In chimpanzee societies one advantage of being high-ranking concerns the mating privileges that accompany it.²⁷ As a consequence, high-ranking males tend to aggressively exclude lower ranking males from mating, usually by challenging one or both of the mating partners.^{5,27,29} Anecdotal observations of surreptitious matings with low-ranking males suggest that females understand the potential consequences associated with breaking this "social rule".

By producing an acoustically distinctive copulation call during more risky instances, when males are likely to see them, females are therefore providing honest information regarding the rank of her copulating partner, and we suspect that this "owning-up" potentially decreases male aggression. This is some of the first ecologically valid evidence suggesting that females do not just take into account the mere presence of the male audience, as is generally denoted by the broad "audience" effect, but also potentially what they can see.

Constantly keeping track of ever-changing audience composition, and its social implications, is no simple task. It requires that females monitor their surrounding conspecifics and use this information to

make vocal "decisions". Findings of this sort provide some evidence against the widely held model of primate calls as hardwired response predispositions^{11,30} in favor of explaining call production in terms of complex social cognitive processes. Further experimental evidence will be needed to clarify this issue and identify the specificity of audience sensitivity in primate copulation calling systems.

Conclusions

Over the last thirty years multiple theories for the evolution of copulation calls in primates have been put forward, although it is unlikely that any one is sufficient to explain call evolution in isolation and for all species. In fact, copulation calls may operate at more than one level, with multiple functions.⁹ Whilst this is clear, most hypotheses have only focused on the function of copulation calls as male-orientated signals of receptivity.⁶ No study, as yet, has addressed the potential psychological impact of other group members, male or female. Understanding such "audience effects" is absolutely critical if we are to differentiate between the alternative functional explanations for this widespread behavior.

Recent research on chimpanzees has shown that the surrounding male and, more surprisingly, the surrounding female audience can have a considerable impact on calling behavior in wild chimpanzee females. It is therefore possible that both sexes have played a fundamental role in shaping the evolution of this acoustic signal. In chimpanzees, copulation calls have helped to shed light on the intricacies of social relationships amongst females and the role vocalizations can play as social tools in mediating these relationships. Further research will tell us whether these findings are restricted to chimpanzees or whether similar effects are found more broadly in social primate and indeed other mammal species.

Acknowledgements

We thank the Ugandan Wildlife Authority, the Uganda National Council for Science and Technology, the President's Office, Vernon Reynolds and Fred Babweteera for support and permission to work in the forest. Our sincerest gratitude goes to Monday M Gideon for his invaluable assistance and company in the forest. The Budongo Conservation Field Station receives core funding from the Royal Zoological Society of Scotland.

References

1. Hauser MD. The evolution of communication. Cambridge, Mass.: MIT Press 1996.
2. Semple S. The function of Barbary macaque copulation calls. *Proc R Soc Lond B* 1998b; 265:287-91.
3. Hamilton WJI, Arrowood PC. Copulatory vocalizations of chacma baboons (*Papio ursinus*), gibbons (*Hylobates hoolock*), and humans. *Science* 1978; 200:1405-9.
4. Pradhan G, Engelhard A, van Schaik CP, Maestripieri D. The evolution of female copulation calls in primates: a review and a new model. *Behav Ecol Sociobiol* 2006; 59:333-43.
5. Hauser MD. Do Chimpanzee copulatory calls incite male-male competition? *Anim Behav* 1990; 39:596-7.
6. O'Connell SM, Cowlshaw G. Infanticide avoidance, sperm competition and mate choice: the function of copulation calls in female baboons. *Anim Behav* 1994; 48:687-94.
7. Henzi SP. Copulation calls and paternity in chacma baboons. *Anim Behav* 1996; 51:233-4.
8. Semple S. Individuality and male discrimination of female copulation calls in the yellow baboon. *Anim Behav* 2001; 61:1023-8.
9. Semple S, McComb K, Alberts S, Altmann J. Informational content of female copulation calls in yellow baboons. *Am J Primatol* 2002; 56:43-56.
10. Pfefferle D, Brauch K, Heistermann M, Hodges JK, Fischer J. Female Barbary macaque (*Macaca sylvanus*) copulation calls do not reveal the fertile phase but influence mating outcome. *Proc R Soc Lond B* 2008; 275:571-8.
11. Zuberbuhler K. Audience effects. *Curr Biol* 2007; 18:189-90.
12. Marler PM, Dufty A, Pickert R. Vocal communication in the domestic chicken: II. Is a sender sensitive to the presence and nature of a receiver? *Anim Behav* 1986; 34:194-8.

13. Vignal C, Mathevon N, Mottin S. Audience drives male songbird response to partner's voice, *Nature* 2004; 430:448-51.
14. Pollick AS, Gouzoules H, de Waal FBM. Audience effects on food calls in captive brown capuchin monkeys (*Cebus apella*), *Anim Behav* 2004; 70:1273-81.
15. Doutrelant C, McGregor PK. Eavesdropping and mate choice in female fighting fish. *Behaviour* 2000; 137:1655-69.
16. Townsend SW, Deschner T, Zuberbühler K. Female chimpanzees use copulation calls flexibly to prevent social competition. *PLoS One* 2008; 3:2431.
17. Gagneux P, Woodruff DS, Boesch C. Furtive mating in female chimpanzees. *Nature* 1997; 387:358-9.
18. Vigilant L, Hofreiter M, Siedel H, Boesch C. Paternity and relatedness in wild chimpanzee communities. *Proc Natl Acad Sci USA* 2001; 98:12890-5.
19. Reichard U. Extra-pair copulations in a monogamous gibbon (*Hyllobates lar*). *Ethology* 1995; 100:99-112.
20. Brauch K, Pfefferle D, Hodges K, Mohle U, Fischer J, Heistermann M. Female sexual behavior and sexual swelling size as potential cues for males to discern the female fertile phase in free-ranging Barbary macaques (*Macaca sylvanus*) of Gibraltar. *Horm and Behav* 2007; 52:375-83.
21. Heistermann M, Brauch K, Möhle U, Pfefferle D, Dittami J, Hodges JK. Female ovarian cycle phase affects the timing of male sexual activity in free-ranging Barbary macaques (*Macaca sylvanus*) of Gibraltar. *Am J Primatology* 2007; 69:1-15.
22. Pusey AE, Williams J, Goodall J. The influence of dominance rank on the reproductive success of female chimpanzees. *Science* 1997; 277:828-31.
23. Pusey AE, Murray CM, Wallauer W, Wilson ML, Wroblewski E, et al. Severe aggression among female chimpanzees at Gombe National Park, Tanzania. *Int J Primatol* 2008; In press.
24. Townsend SW, Slocombe KE, Emery-Thompson M, Zuberbühler K. Female-led infanticide in wild chimpanzees. *Curr Biol* 2007; 17:355-6.
25. Kahlenberg SM, Emery Thompson M, Wrangham RW. Female competition over core areas among Kanyawara chimpanzees, Kibale National Park, Uganda. *Int J Primatol* 2008; in press.
26. Kahlenberg SM, Emery Thompson M, Muller MN, Wrangham RW. Immigration costs for female chimpanzees and male protection as an immigrant counterstrategy to intrasexual aggression. *Animal behaviour* 2008; in press.
27. Goodall J. *The chimpanzees of Gombe: patterns of behaviour*. Cambridge: Harvard University Press 1996.
28. Townsend SW, Deschner T, Zuberbühler K. Chimpanzee copulation calls convey social information.
29. Boesch C, Boesch-Achermann H. *The chimpanzees of the Tai forest. Behavioral ecology and evolution*. Oxford: Oxford University Press 2000.
30. Tomasello M. *Origins of Human Communication*. Boston: MIT Press 2008.