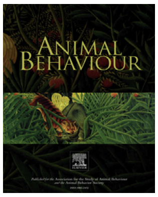
SPECIAL ISSUE: WHISPERED COMMUNICATION

Animal Behaviour 105 (2015) 281–288

Contents lists available at ScienceDirect

Animal Behaviour

journal homepage: www.elsevier.com/locate/anbehav



Special Issue: Whispered Communication

A survey of the context and structure of high- and low-amplitude calls in mammals

Morgan L. Gustison [a, *], Simon W. Townsend [b]

[a] Department of Psychology, University of Michigan, Ann Arbor, MI, U.S.A.
[b] Institute of Evolutionary Biology and Environmental Studies, University of Zurich, Switzerland

ARTICLE INFO

Article history:
Received 29 December 2014
Initial acceptance 12 February 2015
Final acceptance 15 April 2015
Available online 11 May 2015
MS. number: SI-14-01054R

Keywords:
amplitude variation
comparative approach
high-amplitude call
loud call
low-amplitude call
mammalian vocal communication
soft call
vocal repertoire

Quantifying how animal vocalizations vary is central to understanding their function and evolution. One commonly documented feature of mammalian calls is the systematic variation in amplitude across call types. Despite a large body of existing data, there has been little attempt to assess how common calls of varying amplitude are in mammals, how broadly they are distributed at the taxonomic level, and whether similarities in context and structure across species can inform our understanding of the selective pressures promoting the evolution of amplitude variation. Here, we perform a comparative survey of amplitude variation in adult vocal repertoires from 47 species belonging to nine mammalian orders. Our data set demonstrates that low-, medium- and high-amplitude calls are not restricted to certain mammalian groups but occur widely across taxa. Furthermore, contextual analyses indicate that there are consistent differences in the contexts that accompany low-, medium- and high-amplitude calls. Specifically, we found that high-amplitude calls are reported to occur more often in agonistic and alarm-related contexts and less often in affiliative social contexts compared to low- and medium-amplitude calls. In addition, acoustic comparisons indicate that calls of varying amplitude are divergent in terms of underlying call structure. Our findings suggest that low-amplitude calls are shorter in duration and lower in frequency than medium- and high-amplitude calls. We compare and contrast our findings with similar recent approaches investigating amplitude variation in birds and discuss the implications our findings have for unpacking the adaptive significance of amplitude variation in animals more generally.

Vocal communication is a common feature of animal social life and plays a critical role in coordinating behavioural interactions between conspecifics (Bradbury & Vehrencamp, 1998; Hauser, 1997). A substantial body of data demonstrates that significant variation underlies the acoustic structure of vocalizations. Furthermore, our understanding of the physical mechanisms generating vocalizations has helped elucidate how and why these differences arise and their potential adaptive function in survival and reproduction (Fitch, 2000, 2002; Taylor & Reby, 2010). Many studies emphasize the acoustic variation generated by the source (larynx) and filter (vocal tract) in mammals, which are components of vocal production anatomy largely constrained by other physical features such as body size (Charlton et al., 2011; for extensive reviews see Taylor & Reby, 2010; Taylor, Charlton, & Reby, in press). It is also clear, however, that these are not the only physical mechanisms generating structural differences. One additional dimension of acoustic variability is the relative amplitude of calls, defined as the maximum departure of an alternating sound wave from its average value, which is caused by changes in subglottal pressure generated by the lungs (Fitch, Neubauer, & Herzel, 2002; Taylor & Reby, 2010).

To date, a wealth of research studies have focused on the function, context and acoustic structure of mammalian vocalizations ranging on the high end of the amplitude spectrum. Researchers often discuss these obvious and easy to hear ‘loud calls’ in light of contexts related to multirecipient long-distance communication and competitive situations relevant to intra- and intersexual selection. Common examples include the alarm calls of rodents (e.g. Pollard & Blumstein, 2012) and primates (e.g. Fischer, Hammerschmidt, Cheney, & Seyfarth, 2002; Zuberbühler, Noë, & Seyfarth, 1997), the rutting roars of male deer (e.g. Clutton-Brock & Albon, 1979; McComb, 1987), and the display calls of male primates (reviewed by Delgado, 2006). In primates, there is evidence to suggest that higher-amplitude vocalizations also can have distinctive acoustic properties, such as being longer in duration and

---

* Correspondence: M. L. Gustison, University of Michigan, Department of Psychology, 530 Church Street, Ann Arbor, MI 48109-1043, U.S.A.
E-mail address: gustison@umich.edu (M. L. Gustison).

http://dx.doi.org/10.1016/j.anbehav.2015.04.021

lower in fundamental frequency, features that are proposed to play an important role in effective signal transmission across long distances and noisy environments (Brumm, 2004; Egnor & Hauser, 2006; Mitani & Stuht, 1998). Altogether, there is a general consensus that high-amplitude calls have an advertising function in mammals, particularly in males, widely transmitting information about competitive ability or potential threats to surrounding conspecifics.

Comparatively little is known, however, about mammalian vocalizations ranging on the lower end of the amplitude spectrum. While a number of species belonging to a range of taxonomic groups, from primates to rodents, are reported to produce soft, low-amplitude vocalizations (e.g. pika, *Ochotona princeps*: Conner, 1985; tree shrew, *Tupaia belangeri*: Binz & Zimmermann, 1989; ringtailed lemur, *Lemur catta*: Macedonia, 1993; European ground squirrels (*Spermophilus* spp.): Matrosova, Schneiderová, Volodin, & Volodina, 2012; Iberian red deer, *Cervus elaphus hispanicus*: Passilongo, Reby, Carranza, & Apollonio, 2013; Asian house shrew, *Suncus murinus*: Schneiderová, 2014; giant otter, *Pteronura brasiliensis*: Leuchtenberger, Sousa-Lima, Duplaix, Magnusson, & Mourão, 2014), few mammalian studies directly address the potential function and subsequent adaptive benefit of low-amplitude calls. In comparison, a growing body of research on low-amplitude vocalizations in birds reveals that low-amplitude calling plays an important role in warning conspecifics of predator threats (Dabelsteen, McGregor, Lampe, Langmore, & Holland, 1998) and in mediating a multitude of social contexts, such as competitive interactions (Akçay, Tom, Holmes, Campbell, & Beecher, 2011; Searcy & Nowicki, 2006), courtship (Dabelsteen et al., 1998; Reichard, Rice, Vanderbilt, & Ketterson, 2011; Reichard, Rice, Schultz, & Schrock, 2013) and pair bond maintenance (Elie et al., 2010).

Recently, Reichard and Welklin (2014) performed an extensive meta-analysis of soft songs and calls of North American birds as a way to better understand not only the distribution of this class of vocalizations on a broad taxonomic scale, but also to determine the extent of convergence in function across species. Such a comparative approach helps disentangle competing hypotheses regarding the selective factors driving low-amplitude signalling. Analysis of data from 749 species belonging to 22 avian taxonomic orders confirmed courtship as a particularly common context in which low-amplitude vocalizations are produced (Reichard & Welklin, 2014), suggesting a general reproductive function of low-amplitude calling. More detailed sex-based analyses provided further insight into how such calls may function. Specifically, Reichard and Welkin showed that males were more likely to produce low-amplitude songs than females, potentially to further stimulate and attract females during courtship and deter male competitors during territorial encounters. Lastly, due to the inherent influence of changes in subsyringeal pressure on acoustic structure (e.g. fundamental frequency; Zollinger, Podos, Nemeth, Goller, & Brumm, 2012), low-amplitude songs differed structurally from higher-amplitude songs produced by the same bird species. The authors argued that this suggests that low-amplitude vocalizations are not simply less intense variants of high-amplitude vocalizations but structurally and functionally distinct types (Reichard & Welklin, 2014).

In contrast to the song-biased vocal systems of birds, mammalian vocal repertoires primarily consist of relatively discrete sounds that are, in turn, often produced in distinct contexts (Hauser, 1997). Therefore, they are amenable to investigating the occurrence, distribution and functional significance of amplitude variation in animal vocal systems. Such data are also useful in further clarifying the extent to which there exists convergence in the vocal systems of birds and mammals in both acoustic form and function, which is central to understanding signal evolution more generally (Hauser, 1997). In line with the approach of Reichard and Welklin (2014), we therefore synthesized existing published literature on high-, medium- and low-amplitude vocalizations in mammals. Comparative analyses previously have been used to probe call repertoire variation in mammals (Blumstein & Armitage, 1997; McComb & Semple, 2005; Wilkinson, 2003); however, to our knowledge, no study has employed similar approaches to unpack amplitude-related variation across a disparate array of mammalian taxonomic groups. In particular, we quantified the presence of calls of varying amplitude within adult mammalian vocal repertoires and, as a way to better understand the underlying functional significance of amplitude variation, we explored how such variation maps onto accompanying contextual, structural and more subtle sex-based differences.

Given the previously highlighted advertising function of loud and soft calling in sexual selection, we predicted that vocalizations on the extreme ends of the amplitude spectrum (i.e. high- and low-amplitude calls) would be male biased. We also predicted an increased occurrence of high-amplitude calls in competitive and warning contexts, as a way to communicate threat as widely as possible, in addition to potentially signalling to a predator that it has been detected (e.g. mobbing calls: Macedonia, 1993; Zimmermann, 1985). On the other hand, we predicted that low-amplitude calls would occur less often in contexts in which widely transmitting information is beneficial and more often in contexts where receivers are within close proximity, such as during social interactions involving mating and other affiliative behaviours. Lastly, as a result of anatomical constraints associated with sound production (Taylor et al., in press), we expected to find acoustic differences between calls of varying amplitude. Specifically, we predicted that increased subglottal pressure during high-amplitude calling would lead to longer temporal parameters than during lower-amplitude calling. Because of the resultant increased vibration rate of the vocal folds during high-amplitude calling, we predicted spectral frequency-based parameters to be higher in higher-amplitude calls compared to lower-amplitude calls. However, it also has been suggested that producing calls at relatively low frequencies can aid transmission over large distances or when environmental noise is high (Mitani & Stuht, 1998). Therefore, an alternative prediction would be that high-amplitude vocalizations will be characterized by low-frequency measures.

METHODS

We surveyed published accounts of mammalian vocal repertoires for evidence of low-, medium- and high-amplitude calls. Articles were found from a Web of Science search that included the following Title search terms: ‘acoustic repertoire’, ‘vocal repertoire’ and ‘call repertoire’. From this list of sources, 42 articles (47 species) were chosen because they directly assessed the adult vocal repertoire (not a specific call type) of airborne calls in one or more mammalian species, and the calls were not elicited by an invasive technique such as drug administration. Of the 42 articles, 17 articles reported on acoustic recordings made from animals living in wild conditions, 4 articles on animals living in free-ranging conditions (e.g. a tourist park), 16 articles on animals in captive conditions (e.g. zoo or laboratory), and 5 articles reported on acoustic recordings made from animals living in both wild and captive conditions. Also, species were divided into taxonomic orders based on the most recent classification (Wilson & Reeder, 2005).

Calls were defined as the smallest discrete units for which there was contextual and/or acoustic information. If a species produced combinations of multiple call types, these additional combined calls were excluded from our data set if the smaller components were already represented. Any calls produced exclusively by infants or juveniles also were excluded from the data set. First, we