Brevity is not always a virtue in primate communication

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Semple et al. (Semple et al. in press, Biol. Lett. (doi:10.1098/rsbl.2009.1062)) argued that the ‘law of brevity’ (an inverse relationship between word length and frequency of use) applies not only to human language but also to vocal signalling in non-human primates, because coding efficiency is paramount in both situations. We analysed the frequency of use of signals of different duration in the vocal repertoires of two Neotropical primate species studied in the wild—the common marmoset (Callithrix jacchus) and the golden-backed uakari (Cacajao melanocephalus). The key prediction of the law of brevity was not supported in either species: although the most frequently emitted calls were relatively brief, they were not the shortest signals in the repertoire. The costs and benefits associated with signals of different duration must be appreciated (and understood properly) to predict their frequency of use. Although relatively brief vocal signals may be favoured by natural selection in order to minimize energetic costs, the very briefest signals may be ambiguous, contain reduced information or be difficult to detect or locate, and may therefore be selected against. Analogies between human language and vocal communication in animals can be misleading as a basis for understanding frequency of use, because coding efficiency is not the only factor of importance in animal communication, and the costs and benefits associated with different signal durations will vary in a species-specific manner.

Keywords: law of brevity; Neotropical primates; vocal repertoire; signalling

1. INTRODUCTION

I strive to be brief, and I become obscure.
(Horace)

Are animal signals that are produced most frequently the briefest in duration? Such a prediction was made by Semple et al. (in press) who argued that an inverse relationship between signal length and frequency of use is expected, given that long signals can be costly to produce, and because the frequent use of brief signals (as in human language) maximizes coding efficiency according to the ‘law of brevity’ (Zipf 1936).

We hypothesize that coding efficiency alone is insufficient to explain the relationship between frequency of use and signal duration in animal communication, and so tested whether the law of brevity is upheld in two species of Neotropical primates studied in the wild: the common marmoset (Callithrix jacchus) and the golden-backed uakari (Cacajao melanocephalus). Common marmosets are small and diurnal, live in groups of up to 15 individuals and usually have well-defined home ranges in the Atlantic rainforest of Brazil (Hershkovitz 1977). They have 13 different signals in their vocal repertoire, increasing to 17 if the different types of phoe calls are considered as different signals (Bezerra & Souto 2008). Golden-backed uakaris are medium sized and diurnal, live in groups of up to 200 individuals, have a complex fission–fusion social organization and typically live in habitats with dense vegetation, such as the igapó and terra firme forests in the Brazilian and Colombian Amazon (Defler 2003; Bezerra et al. in press a). They have nine call types in their vocal repertoire (Bezerra et al. in press b).

2. MATERIAL AND METHODS

For the vocal repertoire of common marmosets (Bezerra & Souto 2008) and golden-backed uakaris (Bezerra et al. in press b), we related call duration to frequency of use, and describe call contexts in electronic supplementary material, tables S1 and S2. Animals from three social groups contributed to the final sample size in both species. Data for call use in common marmosets came from 493 focal observations (5 min duration each) distributed unevenly across 17 adults during 338 h of fieldwork between December 2004 and April 2005. Vocalizations are readily distinguishable (see spectrograms in electronic supplementary material, figure S1) and were categorized by BMB on a Panasonic RN-305 dictaphone. Data for golden-backed uakaris came from spectrogram analysis of 850 min of sound recordings made during ad libitum observation of the animals in 575 h of fieldwork in January–June 2008.

Our analyses only included data from adults; therefore, we used 12 out of 17 call types for common marmosets (predator-specific alarm calls were not included owing to their very infrequent use; only heard four times), and seven out of nine vocalizations in the repertoire of golden-backed uakaris (the ‘ahh’ call (Bezerra et al. in press b) was only heard regularly from a captive individual). To investigate the relationship between ‘signal duration’ and ‘frequency of signal use’ we first performed Spearman’s rank correlations (r_{s}) as the data were not normally distributed and we wanted to make our analyses comparable with that of Semple et al. (in press). Tests were two-tailed and conducted in SPSS for Windows v. 15 (SPSS Inc., Chicago, IL, USA).

For marmosets, we also controlled for repeated measures from the same individual by conducting a mixed model, which allows the inclusion of both random and fixed terms (see the electronic supplementary material for details); calls could not be assigned to individuals for the uakaris, so a similar analysis was not possible. To assess whether call duration influences frequency of use, we used a linear mixed model (LMM) based on a total of 1046 calls of 12 different types from 10 individuals (each were observed in more than 20 focal observation sessions; total of 417 sessions). Call types were ranked according to the mean duration (figure 1) and frequency of use was calculated as the proportion of all calls given by a particular individual. To control for variation in the number of calls recorded from different individuals, we included the total number of calls as a term in the model. The LMM was conducted in GENSTAT (10th edn, Lawes Agricultural Trust, Rothamsted, Harpenden, UK).

3. RESULTS

Call duration and frequency of use were not significantly correlated with each other in either common marmosets (Spearman’s rank correlation: r_{s} = 0.056, n = 12, p = 0.863) or golden-backed uakaris (r_{s} = -0.357, n = 7, p = 0.432; figure 1). Rather, the distribution of frequency of use was skewed strongly...
the shortest calls were associated with vigilance behav-
common marmoset individuals also demonstrated no
the different call types came from focal observations of 17
the very briefest signals. Indeed, in the marmosets,
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that the briefest signals are not the most frequently
used is perhaps not surprising, given the different costs
and benefits associated with signals of different durations. Very short calls may contain limited informa-
tion, such as cues that identify the signaller. Although
The data shown by Semple et al. (in press) and in
in figure 1 are potentially influenced by pseudoreplica-
tion—if, for example, one aberrant individual
controlled most calls to the dataset, spurious con-
clusions may be reached. However, a mixed model
trolling for repeated measures from the same
vocalises bridging a range of short calls to advertise
the macaques used the two briefest signals less
and frequency of use is still virtually flat ($r_c = 0.091,
n = 11, p = 0.790$).
In the marmosets, the longest duration calls were again
associated with long-distance communication, while
the shortest calls were emitted during play (electronic
the use in vocal repertoires (i.e. there is stabilizing
information, such as cues that identify the signaller.
4. DISCUSSION
Our results indicate that the vocal repertoires of adult
common marmosets and golden-backed uakaris do not
follow the pattern predicted by the law of brevity (Zipf
1936), unlike the situation in Formosan macaques
(Macaca cyclopis) (Semple et al. in press). For the
latter, an inverse relationship existed between signal
duration and frequency of use (Semple et al. in press). However, even in Semple et al.'s analysis, the
macaques used the two briefest signals less
frequently than the third briefest signal.

The briefest signals are not the most frequently
used is perhaps not surprising, given the different costs
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tion, such as cues that identify the signaller. Although
long calls may be costly to produce, they
may nonetheless be honest signals of quality and
hence will be favoured by sexual selection in some
cases (Maynard Smith & Harper 2003). Signal
duration will also depend on factors such as home-
range size: for example, animals that defend large
territories tend to use long duration calls to advertise
presence and location of signalers (Bradbury &
Vehrencamp 1998).

In marmosets, the shortest signals are associated
with vigilance (e.g. at territorial boundaries, when
crossing between forest patches, when encountering
novel observers), where rapid and clear signalling of
potential danger is paramount. Vigilance behaviour is
relatively uncommon, however, and so these signals
are produced less frequently than other signals used
in close-range contact communication among mem-
ers of a social group. In the latter case, there is
perhaps a greater need for encoding details about
signaller identity and context, so there is selection for
longer signals. In both species, the longest signals
were produced for long-range communication, perhaps
to maximize the likelihood of the signaler being
detected.

Frequency of use will also depend on other factors
that affect the costs of calling. For example, call
amplitude—if brief, high-amplitude calls are more
energetically expensive to produce, they may be
selected against in comparison with longer duration
signals of lower amplitude. Moreover, costs associated
with increased conspicuousness to predators or prey
(Semple et al. in press) are only applicable in certain
species. In both our study species (and indeed in the
Formosan macaques; Semple et al. in press), relatively
brief signals were the most frequently used, perhaps
suggesting that brevity is favoured to a certain extent,
but that costs associated with very brief signals limit
their use in vocal repertoires (i.e. there is stabilizing
selection acting on signal duration).

Analogies between frequency of use in human
language and animal communication may be mislead-
ing. Language involves extensive use of syntax whereby

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a large vocabulary can be arranged into sentences that convey a vast number of meanings to convey complex messages. Although Campbell’s monkeys (Cercopithecus campbelli) use ‘proto-syntax’ by producing combinatorial signal sequences associated with specific meanings (Ouattara et al. 2009), the extent to which syntax is used is very limited in non-human animals. Language can convey complex messages of a virtually unlimited variety often about abstract situations via combinations of words, and the use of brief components in a vocabulary can be an efficient means of transmitting information in syntax-rich language.

Although human vocabularies can be very large, speech is broken up into a relatively small number of brief phonemes (Chomsky & Halle 1968; Hauser et al. 2002) that facilitate the learning of a vocabulary, and here brevity may be important. Brevity is likely to be vital in memorizing the components of a large vocabulary, especially given the important role of vocal imitation in human language (Hauser et al. 2002). Brevity brings benefits to both signallers and receivers in language (Ferrer i Cancho & Solé 2003). Conversely, vocalizations of non-human animals must be subject to a wider range of constraints, and single signals might need to convey accurate information about situation-specific contexts regarding, for example, risk, urgency, referential specificity and signaller identity (Seyfarth & Cheney 2003). Such information is not necessarily best encoded in brief signals, and coding efficiency alone is insufficient to explain frequency of use in animal vocal communication. Semple et al. (in press) encouraged a wider range of studies to test the generality of the law of brevity. Our study of two additional species does not support the hypothesis that the law of brevity is widely applicable in animal communication—we argue that relationships between signal duration and frequency of use are best considered on a species-specific basis, and must take account of the costs and benefits of different signal durations in a wide range of contexts.

The studies were non-invasive and complied with Brazilian law.

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