Forum: Ideas

Paradoxical calls: the opposite signaling role of sound frequency across bird species

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The behavioral literature contains inconsistent results on the function of sound frequency (pitch) across species, offering an unexplored opportunity to investigate evolutionary diversification of communication systems. I review those results for birds, where about half the studied species use lower than average frequency (LAF) as a relevant sexual signal, and the remaining species use higher than average frequency (HAF) for the same functions. This variation appears nonrandom with respect to putative causal factors, suggesting that advertising body size determines which species use LAF as a sexual signal. I evaluate different hypotheses to explain why the remaining species use HAF instead. Integrating tests of alternative hypotheses on focal species will be required to demonstrate the causes for this divergence in communication systems. *Key words:* animal communication, body size, motivational–structural rules, receiver psychology, sound frequency, vocal performance. *[Behav Ecol 23:237–241 (2012)]*

INTRODUCTION

Research on animal vocal communication flourished in the past decades, with the field now addressing quite advanced aspects of communication systems (e.g., signal performance, geographic and ecological differentiation, eavesdropping, etc.; e.g., Slabbekoorn and Smith 2002; Podos et al. 2004). However, work on the function of a very basic aspect of vocal signals, sound frequency or pitch, left a trail of inconsistent results that were not yet systematized or explained.

Focusing on birds, I review these inconsistent results, give an overview of hypotheses to explain them and of their predictions regarding differences across species. I also discuss which hypotheses appear most concordant with the currently available data, in order to guide additional work needed to explain these paradoxical results. Overall, these inconsistencies are an opportunity for empirical research on the evolutionary diversification of vocal communication systems.

The focus on birds is because this is the group where inconsistencies are most apparent: In about half the avian species studied, lower than average sound frequency (LAF) was a preferred or more relevant sexual signal than higher than average frequency (HAF), whereas in the other half of species, the opposite was true (Table 1). In other taxonomic groups, such inconsistencies also exist, but the studies documenting them are more sporadic. For example, in most mammal and reptile species, LAF signals dominance or aggression (Morton 1977), but in some HAF has those functions or is a preferred signal (e.g., Fischer et al. 2004; Galeotti et al. 2005).

OVERVIEW OF HYPOTHESES

The simplest hypothesis for why LAF should be a better signal in aggressive and sexual contexts is that it reflects large body

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Downloaded from permissionse adease coupile in member permissions and a 23/2/237/245835 by guest on 27 July 2018 size and consequently indicates better competitive ability and individual quality. This is because larger vocal organs and vocal tracts produce and radiate lower frequencies more efficiently (Bradbury and Vehrencamp 1998; Fletcher 2004). This relation does not always stand within-species, because size differences among adults can be small or vocalizations may contain frequency modulation, either of which can diminish or override the association between frequency and body size (Patel et al. 2010). This hypothesis (hereafter, the body size hypothesis) predicts that LAF should be a preferred or more relevant vocal signal in species where it reflects body size, but not in the remaining.

An extension of the above hypothesis is known as the motivational-structural rules (Morton 1977). In what respects sound frequency, it proposes that an aggressive function of LAF and an appeasement function of HAF are widespread and stable because 1) of the size-frequency association in adults or across ontogeny (e.g., juveniles are small, and their high frequency vocalizations are nonthreatening for adults) and 2) borrowing from Darwin's principle of antithesis (Darwin 1872), structurally opposed signals are perceived as having opposed meanings or functions. This hypothesis predicts a consistent role of LAF as an aggressive signal (and possibly more generally as a sexual signal because aggressive signals often provide useful indicators for female choice; Berglund et al. 1996; Wong and Candolin 2005) even in the absence of a correlation with body size in adults (Morton 2000).

A third hypothesis is that vocal performance at frequencies closer to the limits of the frequency range provides reliable signals of vocal ability and, thus, individual quality (Podos et al. 2004; Byers et al. 2010). It is expected that motor patterns (such as the ones used to vocalize) closer to physiological limits are more demanding to produce and that these are used in sexual signaling (Byers et al. 2010). This hypothesis (hereafter, the performance hypothesis) predicts that either HAF or LAF become relevant sexual signals, depending on whether the species vocalizations are closer to the upper or the lower limit of its potential frequency range.

A fourth hypothesis is that preferences for HAF or LAF can result from learning to recognize signals (Enquist and Arak

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Table 1 Summary of studies reporting a signaling role of lower or higher frequency than average vocalizations in birds

Species	Preferred or most relevant frequency	Vocalization	Summary of results	References ^a
Nonpasserines				
<i>Gallus gallus</i> (Red Junglefowl, domestic)	Higher	Crow	Dominant males have higher frequency crows.	Leonard and Horn (1995)
Perdix perdix (Grey Partridge)	Lower	Rusty-gate call	Females courted more males with lower formant frequencies	Beani and Dessi-Fulgheri (1995)*
Monias benschi (Subdesert Mesite)	Lower	Trill in "song"	More heterozygous males had lower frequency trills. Trend for lower frequency indicating better body condition	Seddon et al. (2004)*
Pygoscelis adeliae (Adélie Penguin)	Lower	Ecstatic display call	Males in better body condition have lower frequency calls.	Marks et al. (2010)
Eudyptula minor (Little Penguin)	Lower	Advertising call	Females responded more to lower frequency calls.	Miyasaki and Waas (2003)
Gavia immer (Great Northern Loon)	Lower	Yodel call	Males in better body condition have lower frequency calls. Receivers responded more to lower frequency song.	Mager et al. (2007)
Centropus grillii (Black Coucal)	Lower	"Song"	Decreased frequency when singing aggressively.	Geberzahn et al. (2009)
Cepphus columba (Pigeon Guillemot)	Higher	Hunch-whistle	Higher frequency predicts subsequent aggression.	Nelson (1984)*
Aethia cristatella (Crested Auklet)	Lower	Trumpet call	Males in better body condition have lower frequency calls.	Klenova et al. (2011)
Passerines ^b			1 7	
Dendroica pensylvanica (Chestnut-sided Warbler)	Higher	Song	Males with higher frequency song gained more extrapair paternity.	Byers (2007)*
Zonotrichia albicollis (White-throated Sparrow)	Higher	Song	Females responded more to higher frequency song.	Ratcliffe and Otter (1996)*
Serinus serinus (Serin)	Higher	Song	Females attended more to higher frequency song.	Cardoso et al. (2007)
Serinus canaria (Canary, domestic)	Lower	Song	Females responded more to lower frequency song.	Pasteau et al. (2007)
Psarocolius montezuma (Montezuma Oropendola)	Lower	Lowest frequency note of song	Lowest note of song decreased in frequency when singing aggressively.	Price et al. (2006)
Turdus merula (Blackbird)	Higher	Song	Females responded more to higher than lower frequency song. Males increased frequency when singing aggressively.	Dabelsteen and Pedersen (1988, 1993), Dabelsteen (1984), and Ripmeester et al. (2007)*
Hirundo rustica (Barn Swallow)	Lower	Rattle in song	Males in better body condition and heavier have lower frequency rattle syllables in song.	Galeotti et al. (1997)
Parus major (Great tit)	Lower	Lowest frequency note of song	Song types with lower lowest-frequency more common during female's fertile period and related to less paternity loss.	Halfwerk et al. (2011)*
<i>Poecile atricapillus</i> (Black-capped Chickadee)	Higher	Song	Only good quality males sing loud higher frequency notes.	Christie et al. (2004)*
Phaenostictus mcleannani (Ocellated Antbird)	Higher	Song	Increased frequency when singing aggressively. More heterozygous males sing higher frequencies.	Araya-Ajoy et al. (2009)

^a References are for the results summarized in the table and in most cases also provide information on frequency for Figure 1. When this was not given (marked with *), dominant frequency was either taken from Hu and Cardoso (2009), for the partridge and guillemot measured with the methods and recording sources described in Hu and Cardoso (2009), or for the mesite taken from Seddon (2002) (average of minimum and maximum frequency of trills).

^b Passerines on this list are Oscines (songbirds, suborder Passeri) with the exception of the antbird, which is a suboscine (suborder Tyranni).

1993; Guilford and Dawkins 1993). Greater sensitivity to more extreme stimuli is predicted as an error minimizing strategy both when learning to discriminate stimuli (peak shift; Guilford and Dawkins 1993) or as a "hard-wired" recognition rule (Enquist and Arak 1993). Thus, for example, if a species has higher frequency vocalizations than most of the sympatric species, then a preference for HAF could result. This hypothesis (hereafter, the recognition hypothesis) predicts that either HAF or LAF become relevant sexual signals, depending on whether the vocalization is higher or lower frequency than the relevant stimuli being discriminated against (be those heterospecific vocalizations or those of a different age class or sex).

A final hypothesis, in this nonmutually exclusive list, is runaway sexual selection (Lande 1981, Kirkpatrick 1982). Taken alone, the process is arbitrary and predicts an arbitrary distribution across species of using HAF or LAF as sexual signals. This can be viewed as a null prediction, supported if the alternative nonarbitrary hypotheses fail to explain the trait distribution across species (Prum 2010). Runaway selection can also be initiated by any of the above hypotheses, and if it is initiated primarily by one of them, then it merely reinforces its predictions regarding trait distribution across species.

OVERVIEW OF EMPIRICAL STUDIES

This overview considers whether empirical results fit the predictions of the body size, motivation–structural rules, or performance hypotheses. Predictions of the recognition hypothesis cannot be evaluated at this stage. I then integrate across all hypotheses in a general discussion. As we will see, most predictions regarding species differences are taxonomically confounded, and the currently available data set of species is still limited. This prevents formal comparative approaches at this stage. Instead, I simply review the empirical literature and discuss which hypotheses are broadly concordant with the existing results, in order to guide additional empirical work that is needed for further progress.

I searched the literature for studies documenting functional roles of LAF or HAF and back- and forward-tracked citations of the most relevant articles using ISI Web of Knowledge, consulting over 700 articles. I used studies on vocal signals (not on nonvocal sounds; e.g., Madsen et al. 2007) and did not consider comparisons between structurally different signals (e.g., long- vs. short-range songs of some passerines [e.g., Anderson et al. 2007] or flight-whistles vs. perched songs of cowbirds [O'Loghlen and Rothstein 2002]). Reported functional roles for frequency included female preferences, agonistic function, and quality signaling, which I used collectively as indications of whether LAF or HAF is a more relevant sexual signal, because those several functions are interrelated. For example, often the same trait used to attract mates is also used in male-male competition, and aggressive signals used in malemale competition can provide cues on male quality or dominance for female choice (reviewed in Berglund et al. 1996; Wong and Candolin 2005). The results are summarized in Table 1.

The major pattern emerging is that LAF is a more relevant signal in most nonpasserines (7 of 9 species), but this is less frequent in passerines (instead, HAF is a more relevant signal in 6 of 10 passerine species). Furthermore, all passerine work used song, which, unlike other avian vocalizations, generally does not reflect body size (reviewed in Patel et al. 2010), likely because it comprises extensive frequency modulation and variation across individuals. This pattern broadly agrees with the prediction of the body size hypothesis, that LAF should be a more relevant agonistic or sexual signal in vocalizations that indicate body size, but not in others (birdsong). The trend

Downloaded from https://academic.oup.com/beheco/article-abstract/23/2/237/245835 by guest on 27 July 2018 becomes more convincing if noting that all 4 passerine studies reporting a prominent role of LAF in song need qualification: The barn swallow study used a single song syllable (the "rattle," a series of clicks) whose frequency does indicate body size (Galeotti et al. 1997); the oropendola and great tit studies used the lowest frequency note of song rather than overall song frequency (Price et al. 2006; Halfwerk et al. 2011), and although it is not known whether the lowest note indicates body size, interspecific evidence across oropendolas suggest it might (Price et al. 2006); lastly, the canary study (Pasteau et al. 2007) used domestic birds, which underwent artificial selection for lower song frequency (even varieties not bred for song; Güttinger 1985), and it would be interesting to know whether its result relates to domestication.

A more direct test of the body size hypothesis would relate the signaling role of frequency with whether frequency indicates body size in individual species. We only know whether frequency indicates size for 8 of the species in Table 1. For those species, there is a good match with the predictions (6 of 8 correct match): In 5 of the 6 species where the frequency of vocalizations is known to reflect body size or mass (the 2 penguins, coucal, loon, guillemot, and swallow; Nelson 1984; Galeotti et al. 1997; Miyasaki and Waas 2003; Mager et al. 2007; Geberzahn et al. 2009; Marks et al. 2010), LAF was either preferred or contained more relevant information (Table 1, the exception was the guillemot); for the 2 cases where frequency is known not to reflect size, serin song and auklet calls (Cardoso et al. 2008, Klenova et al. 2011), as predicted HAF was a preferred signal in the former, but LAF was still a good indicator of condition in the latter (Table 1).

The hypothesis of motivational–structural rules predicts that LAF but not HAF should be employed in agonistic communication or be a preferred signal. Therefore, the large proportion of passerine species using HAF as an aggressive or sexual signal is contrary to this hypothesis.

The performance hypothesis predicts that in species with vocalization frequency closer to the upper limit of its potential frequency range, HAF makes for better signals of quality



Figure 1

Plot of vocalization frequency against body mass for the species in Table 1, and predicted dominant frequency based on Wallschläger's (1980) equation (solid curve). Passerines are represented by circles, nonpasserines by squares, and whether higher or lower frequency than average was a more relevant signal is represented by open and closed symbols, respectively. Male body masses from Dunning (2008) and dominant or center frequency of vocalizations from the references in Table 1.

and is more used as an agonistic or sexual signal and the opposite (LAF) for species with frequency closer to the lower limit. As an approximation to where vocal frequency falls relative to potential range, Figure 1 plots the dominant or center frequency of the vocalizations analyzed in Table 1 and compares it to the predicted frequency for each species' body size. To do this, I used the equation of Wallschläger (1980) relating dominant frequency to body mass and calculated residual frequency for each species. This empirical equation is the most comprehensive in the literature, and although it only used passerine data, it fits well the nonpasserines in Figure 1. Although there are suggestive cases (e.g., the guillemot, highest point in Figure 1, whose frequency is extremely high for its size and where HAF is a more relevant signal), overall residual frequency was not larger for species where HAF is a more relevant signal (open symbols in Figure 1, average residual frequency = $1.16 \text{ kHz} \pm 0.64 \text{ standard error}$) than for species where LAF is a more relevant signal (filled symbols in Figure 1, 0.19 kHz \pm 0.37; $t_{17} = 1.38$, P = 0.18). Controlling for phylogenetic effects could make this comparison more conservative.

DISCUSSION

About half the avian species studied use LAF as a more relevant sexual signal, and the remaining use HAF. The distribution across species of this trait appears nonrandom, both with regards to phylogeny and putative causal factors. With regards to phylogeny, for the currently available data set most variation coincides with the passerines vs. nonpasserines contrast, which makes formal phylogenetic comparisons unviable, and therefore, causal associations are suggestive rather than proof.

With regards to causal associations, results most closely match the predictions of the body size hypothesis, with most species where frequency is known to indicate body size using LAF as a more relevant sexual signal. In contrast, HAF was more often a relevant signal in birdsong than in other vocalizations. This broadly agrees with the predictions of the body size hypothesis and suggests that it may explain why LAF is a relevant signal in most nonpasserines but not in most passerines. Passerines, particularly oscines (songbirds), have a more complex and muscled syrinx (Ames 1971), and the latter also learn their songs (Catchpole and Slater 2008), resulting in generally complex and variable vocalizations. This can erode the frequency cues of body size and, accordingly, the frequency of birdsong is rarely related to body size (Patel et al. 2010). Nonpasserines, on the contrary, have simpler and stereotyped vocalizations that more easily reflect differences in size among individuals, causing LAF to be a signal of large size and, thus, quality.

The body size hypothesis, however, does not explain the role of HAF in species where vocalization frequency does not indicate body size; it does not predict that they would use LAF but does not explain why they use HAF either. Both the performance and recognition hypotheses could explain this.

The performance hypothesis did not predict which species use HAF or LAF for sexual signaling and therefore does not seem to explain the distribution of these traits across species. This test used frequency relative to body size as a proxy for whether it falls closer to the upper or lower limit of the potential frequency range (in which cases, HAF or LAF, respectively, was predicted to be preferentially used). Better tests could use experimentally derived physiological information on actual potential range; knowledge that for the most part is not yet available. Nevertheless, this hypothesis remains interesting as a potential general explanation for why species where the body size hypothesis does not apply use HAF as a sexual signal because available evidence for birds suggests that higher frequencies may generally be more demanding (Lambrechts 1996; Christie et al. 2004; Araya-Ajoy et al. 2009; Cardoso 2010; but see also Nelson 2000). This asymmetry toward HAF being more demanding rests on indirect evidence (comparisons of aspects of performance across the frequency range), and more work on this would be useful.

The recognition hypothesis cannot be tested at this stage because we do not know which recognition task is more important in influencing perceptual biases for frequency. If discrimination against juveniles is the most important, this should give rise to preferences for LAF and therefore not explain the role of HAF in passerines. If discrimination against heterospecifics is the most important, then this could give rise to preferences for HAF but probably only in some of the highest frequency species. It would not, therefore, be as general a potential explanation as the performance hypothesis.

The motivational-structural rules and runaway hypotheses predicted, respectively, consistent use of LAF as agonistic or sexual signals or an arbitrary distribution of using LAF and HAF across species, both of which are contrary to the observed. This does not mean that these mechanisms are not acting (e.g., runaway selection may act in conjunction with other mechanisms, intensifying their effects) but that they do not offer an explanation for the heterogeneity of results across species.

Based on this overview, the tentative conclusion is that the heterogeneity of results is best explained by the body size hypothesis, with an additional mechanism needed to explain the use of HAF in species where the body size hypothesis does not apply. The performance hypothesis is the most promising, but yet untested, general explanation for the use of HAF in those species. This overview also showed that comparative approaches with the currently available data have limitations (strong dependence on the passerine vs. nonpasserine contrast), which call for further empirical data, especially if capable to discriminate among alternative hypotheses.

The available empirical studies, my own included, discuss hypotheses consistent with using LAF or HAF, depending on their result, without assessing whether the prerequisites for alternative hypotheses apply in the study species. This prevents much insight into the reasons for the diversity of results. Some studies showed that frequency indicates aspects of individual quality (e.g., body condition, heterozygosity; see Table 1), which suggests that this is the cause for frequency to be a relevant communication trait. But on a mechanistic level correlations with individual quality can be accounted for by different hypotheses (e.g., the body size or performance hypotheses, if better quality individuals grow larger or perform more demanding vocalizations, respectively). Therefore, further progress requires empirical work that disentangles among the different hypotheses. In this respect, the tentative conclusions in the preceding paragraph are useful guidelines to prioritize questions for coordinated empirical tests: does frequency indicate body size; are some frequencies more physiologically demanding; and does the task of recognizing vocalizations make some frequencies perceptually salient?

In conclusion, the opposed use of sound frequency as a communication signal has been an overlooked paradox in animal communication. The variation across avian species appears nonrandom in relation to putative causal factors, suggesting causal explanations. These require proof by empirical work that integrates tests of alternative hypotheses. Overall, the apparently inconsistent signaling role of frequency across species offers a valuable but little explored opportunity to investigate causes of diversification in vocal communication systems.

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