

Ecology and taxonomy-driven deviations in the frog call–body size relationship across the diverse Australian frog fauna

C. J. Hoskin^{1,2}, S. James² & G. C. Grigg²

¹ School of Botany & Zoology, The Australian National University, Canberra, ACT, Australia

² School of Integrative Biology, The University of Queensland, St Lucia, Qld, Australia

Keywords

frog call; body size; signal evolution; environmental noise; dominant frequency; stream habitat.

Correspondence

Conrad J. Hoskin, School of Botany & Zoology, The Australian National University, Canberra, ACT 0200, Australia. Email: conrad.hoskin@anu.edu.au

Editor: Tim Halliday

Received 14 September 2008; revised: 15 December 2008; accepted 18 December 2008

doi:10.1111/j.1469-7998.2009.00550.x

Abstract

Relationships between some properties of frog calls and body size are widely recognized. However, generality across call components and diverse faunas, and sources of deviation, remain poorly tested. Using 116 east Australian frog species, we tested the relationship between three call traits and body size, and the effects of taxonomic family and calling habitat. Call dominant frequency (DF) has a highly significant negative relationship with size, whereas call duration and pulse rate do not. Frog families show the same slope of relationship between DF and size, but hylids call at significantly higher frequency relative to size. Within hylids, stream breeders call at significantly lower DF than pool breeders of comparable size – below the DF of stream noise in typical breeding habitat – a shift likely to enhance signal detection against background environmental noise. This contrasts with all previous observations from other regions that frogs call at high (even ultrasonic) frequency to avoid masking by stream noise.

Introduction

Calling is an integral part of anuran biology; the advertisement calls uttered by most male anurans are the primary mechanism for species recognition, female mate choice and male–male competition (Duellman & Trueb, 1994; Gerhardt & Huber, 2002; Wells, 2007). The biological significance of frog calls along with their relative simplicity has made them a classic trait for studies of sexual selection and speciation (e.g. Blair, 1964; Ryan, 1980, 1985; Gerhardt & Huber, 2002; Hoskin *et al.*, 2005). The determinants of, and constraints on, variation in frog calls are therefore of general interest, and of particular interest is the potential for a structural link between components of the call and body size. Resolving such links is important because they may constrain the evolution of call traits within and between species, they may confound interpretations of the role of selection on call or body size, and because deviations from standard relationships offer insights into the mechanism and evolution of call production and perception (Blair, 1964; Nevo & Schneider, 1976; Gerhardt & Huber, 2002; Hoskin *et al.*, 2005).

The frequency of a frog's call is determined largely by the mass of the vocal cords and associated tissues, which in turn are usually tightly correlated with body size (Martin, 1972; Nevo & Schneider, 1976; Gerhardt & Huber, 2002). This derives the expectation that call frequency should be nega-

tively related to body size, with larger frogs having lower frequency calls, which is generally supported by both within and between species comparisons (reviewed in Duellman & Trueb, 1994; Gerhardt & Huber, 2002; Wells, 2007; but see Lardner & Lakim, 2004). In contrast, there are no structural predictions that temporal traits (e.g. call duration and pulse rate) should be related to body size, and such relationships are rarely found (Gerhardt & Huber, 2002; Wells, 2007; but see Blair, 1964; Zweifel, 1968). These generalizations are derived largely from tests within species or between closely related species. The few taxonomically diverse studies that have been conducted (e.g. Menzies & Tyler, 1977; Zimmerman, 1983; Cocroft & Ryan, 1995) have generally only tested a moderate number of species, and have rarely tested temporal call traits or the effect of factors that may impact call–body size relationships (e.g. taxonomic family and calling habitat). Analyses of diverse regional frog fauna have the potential to offer significant insights into call evolution through testing the generality of call trait/body size relationships, and identifying departures from these relationships and the underlying factors causing them. Differences in the mechanisms of sound production and perception have been demonstrated between some anuran families (Duellman & Trueb, 1994; Wells, 2007); however, family-level tests of variation in call–body size relationships in diverse regional fauna have not been conducted.

Calling habitat may also generate deviations in the call–body size relationship. Animal communication relies on detection of the signal against the background environment (Forrest, 1994; Bradbury & Vehrencamp, 1998). For species that communicate with acoustic signals, interference can come from the impact of habitat structure on call transmission (Zimmerman, 1983; Ryan & Wilczynski, 1991; Forrest, 1994), or from masking interference by the calls of co-occurring species (e.g. Amézquita *et al.*, 2006) or other environmental noise (e.g. Slabbekoorn & Peet, 2003; Narins *et al.*, 2004; Brumm & Slabbekoorn, 2005; Brumm & Slater, 2006). The broadband sound of flowing water is the dominant noise in the vicinity of streams (Narins *et al.*, 2004; Brumm & Slater, 2006; Goosem, Hoskin & Dawe, 2007), and is therefore expected to impose selection on the calls of stream-breeding species to avoid masking interference. Stream noise has been suggested as the reason for high-frequency calls in some stream-breeding frog species (e.g. Duellman & Trueb, 1994; Haddad & Giaretta, 1999), including the recent discovery of ultrasonic calls in two species of frog (Narins *et al.*, 2004; Feng *et al.*, 2006; Arch, Grafe & Narins, 2008). However, the broader role of stream noise in driving frog call evolution has not been tested.

Here, we tested the relationship between three call traits (dominant frequency, duration and pulse rate) and male body size across the taxonomically, morphologically and ecologically diverse frog fauna of eastern Australia. We tested (1) the relationship between each call trait and body size across all species and within well-sampled frog families; (2) whether call–body size relationships differ between frog families; (3) whether call–body size relationships differ between pool- and stream-breeding species.

Materials and methods

Call and body size measurements

We obtained male call and body size data from 116 frog species from eastern Australia, representing over half the species diversity and all five frog families present in Australia: Myobatrachidae (50 spp.), Hylidae (48 spp.), Microhylidae (16 spp.), Ranidae (1 spp.) and Bufonidae (1 spp.). Calls for the majority of species came from field recordings on Stewart (1998*a,b*), and data for other species came from recordings and previous call analyses by Hoskin (2004, 2007).

Call traits were measured using Canary version 1.2.1 and Raven version 1.1 sound analysis software. Four replicate advertisement calls were selected randomly from those available for each species to give an average value for each of three call traits: dominant frequency (DF) – frequency at which the maximum energy of the call is emitted, duration (DUR) – from beginning of first pulse of the call to end of last pulse of the call and pulse rate (PULSE) – number of pulses per second averaged across the call. These are standard call traits used in studies of species recognition,

female mate choice, male–male interaction and taxonomy (e.g. Blair, 1964; Ryan, 1980; Gerhardt & Huber, 2002; Hoskin, 2004; Hoskin *et al.*, 2005; Wells, 2007).

No temperature data were available for the recordings on Stewart (1998*a,b*); however, this is unlikely to be problematic for two reasons. First, variation in calls due to temperature is relatively minor compared with variation in calls across species and families. Second, the significant patterns reported herein are for dominant frequency, a trait that has rarely shown to be affected by temperature (Gerhardt & Huber, 2002).

Male body size was approximated using snout–vent length (SVL) and was obtained by taking the median male body size from Barker, Grigg & Tyler (1995), Hoskin (2004) and individual species description papers. Calling habitat for each species was scored as one of four categories: pool (static water bodies), stream (flowing water), subterranean (buried) and terrestrial (on surface, away from water). Habitat scoring was based on Barker *et al.* (1995), Hoskin (2004), species description papers and personal observations. Two families include species that breed (call) in different habitats (representation by family: Myobatrachidae – 33 pool, 11 stream, five subterranean, one terrestrial; Hylidae – 32 pool, 16 stream; Microhylidae – 16 terrestrial; Ranidae – one pool; Bufonidae – one pool).

Statistical analyses

Statistical analyses were performed in SPSS version 15 and SAS version 8. Each trait for each analysis group was tested for normality and homoscedasticity. Log transformation of SVL, DUR and PULSE, and a square-root transformation of DF, was required to achieve normality. Linear regressions were performed to test for an overall relationship between call traits and body size. Analyses of covariance (ANCOVA) were performed to test for differences in the relationship between analysis groups. Owing to multiple testing, significance values were compared with sequential Bonferroni values (Holm, 1979). Outliers to call trait/body size relationships were defined as those species outside the 95% confidence interval for the regression of the data for each group in each analysis. Correlation between the frog call traits was tested at the level of all frogs. There was no significant correlation (Pearson's) between sqrtDF and either lnDUR ($C_p = 0.068$, $P = 0.471$, $n = 116$) or lnPULSE ($C_p = -0.048$, $P = 0.666$, $n = 83$). However, there was a highly significant correlation between lnDUR and lnPULSE ($C_p = -0.733$, $P < 0.001$, $n = 83$).

The analyses were carried out in a hierarchical framework. First, we asked the question *Are call traits dependent on body size?* Linear regressions of each call trait against body size were performed, for all species and then within each of the three well-sampled families (Hylidae, Myobatrachidae and Microhylidae). Because only dominant frequency showed a relationship with size in these analyses, duration and pulse rate were not used in further analyses.

Second, we asked *Does the relationship between dominant frequency and body size differ between families?*

An ANCOVA of dominant frequency and body size was performed, with univariate contrasts specified to test whether this relationship differed between hylids, myobatrachids and microhylids.

Finally, we asked *Does the relationship between dominant frequency and body size differ between pool- and stream-breeding species?* An ANCOVA of dominant frequency and body size was performed to test whether the relationship between dominant frequency and body size differed between pool- and stream-breeding species. Hylids and, to a lesser extent, myobatrachids had sufficient data to test for differences between pool- and stream-breeding species. Hylids and myobatrachids were analysed separately due to differences in the dominant frequency versus body size relationship between these families revealed in the previous analysis.

Results

Are call traits dependent on body size?

There was a highly significant negative relationship between sqrtDF and lnSVL across all species from the five families, and within each of the three well-sampled families (hylids, myobatrachids and microhylids) (Table 1, Fig. 1). *Philoria loveridgei*, *Philoria kundagungan*, *Philoria pughi* and *Philoria richmondensis* were outliers to the myobatrachid relationship, and the fifth species of *Philoria*, *P. sphagnicolus*, was a marginal outlier (Fig. 1). *Cyclorana cryptotis* was an outlier to the hylid relationship (Fig. 1). All outliers had dominant frequencies below the range expected for their body size. In contrast to the relationship between sqrtDF and lnSVL, there was no significant relationship between lnSVL and either of the temporal traits (lnDUR, lnPULSE), either across all species or when analysed within the three well-sampled families (Table 1).

Does the relationship between dominant frequency and body size differ between families?

The four outliers to the myobatrachid relationship and the one outlier to the hylid relationship were removed. The slope of the relationship between sqrtDF and lnSVL did not

differ between the three families (ANCOVA common slopes model: $\ln\text{SVL} \times \text{family } F_{2,103} = 0.58, P = 0.563$). Removing the interaction revealed a significant common relationship between sqrtDF and lnSVL ($\beta = -24.16, F_{1,105} = 237.80, P < 0.001$), but different adjusted means among the families (ANCOVA common intercept model: $F_{2,105} = 17.64, P < 0.001$, y -intercepts: hylid = 135.57, myobatrachid = 127.62 and microhylid = 129.21). Univariate contrasts revealed this is because hylids have a higher frequency call for their body size than myobatrachids ($F_{1,105} = 34.53, P < 0.001$) or microhylids ($F_{1,105} = 8.68, P = 0.004$) (Fig. 1). The adjusted means did not differ between myobatrachids and microhylids ($F_{1,105} = 0.58, P = 0.449$).

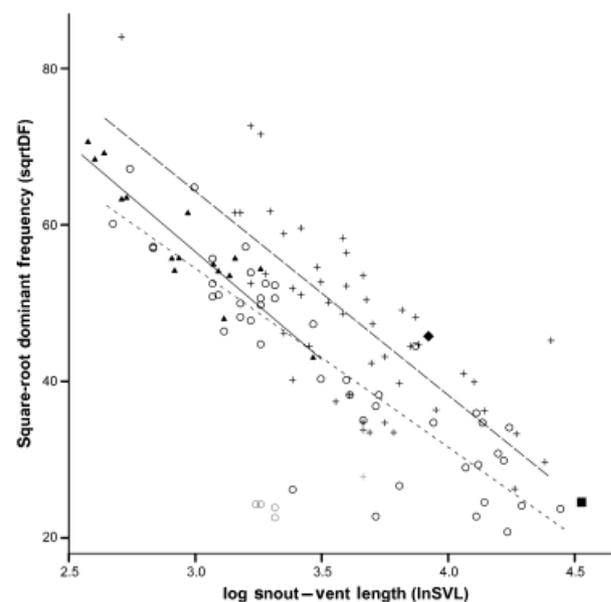


Figure 1 Relationship between dominant frequency and body size across 116 Australian frog species. The symbols for each family are: Hylidae (data points – cross, regression – long dash line), Myobatrachidae (data points – open circle, regression – short dash line), Microhylidae (data points – closed triangle, regression – solid line), Ranidae (data points – closed diamond) and Bufonidae (data points – closed square). Lines represent the mean regression line for that family. Symbols in grey are outliers to the relationship in that family.

Table 1 Relationship between three call traits and male body size across all species and within each of the well-sampled families

Group	sqrtDF					lnDUR			lnPULSE		
	<i>F</i>	d d.f.	<i>P</i>	β	α	<i>F</i>	d d.f.	<i>P</i>	<i>F</i>	d d.f.	<i>P</i>
All frogs	295.96	104	<0.001	-21.86	122.84	0.08	114	0.779	0.76	81	0.387
Myobatrachidae	164.82	44	<0.001	-22.86	123.03	<0.01	48	0.969	0.25	37	0.620
Hylidae	61.63	45	<0.001	-26.06	142.48	1.54	46	0.221	0.05	25	0.818
Microhylidae	73.69	14	<0.001	-27.54	139.19	1.94	14	0.185	2.35	14	0.148

ANCOVA parameters: *F*, *F*-ratio; d d.f., denominator degrees of freedom; *P*, *P*-value; β , slope; α , y -intercept; sqrtDF, square-root of dominant frequency; lnDUR, natural log of call duration; lnPULSE, natural log of pulse rate; lnSVL, natural log of snout–vent length.

Does the relationship between dominant frequency and body size differ between pool- and stream-breeding species?

Hylids

One outlier to the pool-breeding data was removed from the analysis (*C. cryptotis*). The slope of the relationship between $\sqrt{\text{DF}}$ and $\ln\text{SVL}$ did not differ between the two habitats (ANCOVA common slopes model: $\ln\text{SVL} \times \text{habitat } F_{1,43} = 0.02, P = 0.876$). Removing the interaction revealed a significant common relationship between $\sqrt{\text{DF}}$ and $\ln\text{SVL}$ ($\beta = -27.17, F_{1,44} = 136.63, P < 0.001$), but different adjusted means between the two habitats (ANCOVA common intercept model: $F_{1,44} = 48.20, P < 0.001, y\text{-intercepts } (\alpha)$: stream = 138.82, pool = 150.49). Therefore, stream-breeding hylids have a lower frequency call for their body size than pool-breeding hylids (Fig. 2).

Myobatrachids

Seven species were removed from the analysis: five subterranean breeders (all *Phyllorhina*), one terrestrial breeder (*Assa darlingtoni*) and one outlier to the pool-breeding data (*Notaden melanoscapus*). The slope of the relationship between $\sqrt{\text{DF}}$ and $\ln\text{SVL}$ did not differ between the two habitats (ANCOVA common slopes model: $\ln\text{SVL} \times \text{habitat } F_{1,39} = 0.37, P = 0.548$). Removing the interaction revealed a significant common relationship between $\sqrt{\text{DF}}$ and $\ln\text{SVL}$ ($\beta = -24.01, F_{1,40} = 235.02, P < 0.001$), but no significant difference in adjusted means between the habitats [ANCOVA common intercept model: $F_{1,40} = 2.00,$

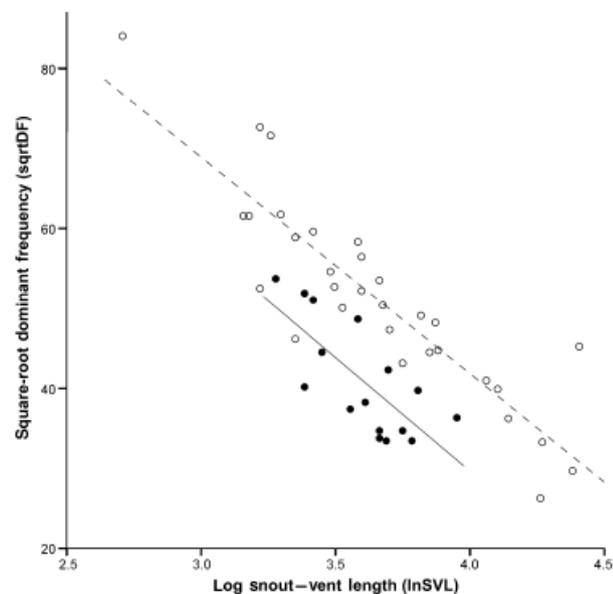


Figure 2 Relationship between dominant frequency and body size in pool-breeding (data points – open circles, regression – dashed line) and stream-breeding (data points – closed circle, regression – solid line) hylids.

$P = 0.165$, common y -intercepts (α) = 129.78]. Therefore, stream- and pool-breeding myobatrachid species do not have different call frequencies relative to their body size.

Discussion

This analysis shows a strong and universal relationship between call frequency and male body size. Body size constraints on call frequency have been widely reported in anuran studies (reviewed in Duellman & Trueb, 1994; Gerhardt & Huber, 2002; Wells, 2007; but see Lardner & Lakim, 2004), as well as in insects (Bennet-Clark, 1998) and birds (Ryan & Brenowitz, 1985; Seddon, 2005). This structural link has the potential to both constrain evolution, and/or generate a correlated evolutionary response on one trait when there is selection on the other, thereby confounding interpretations of the role of selection on each (Blair, 1964; Ryan, 1988; Gerhardt & Huber, 2002). Call duration and pulse rate showed no relationship to body size and therefore these call traits are more likely to be direct indicators of selection for call differentiation. Our data also supports the generalization that temporal call traits are rarely coupled with body size (Gerhardt & Huber, 2002, but see intra- (Zweifel, 1968) and interspecific (Blair, 1964) variation in *Bufo*); however, it is surprising how rarely this has been tested, particularly across species.

Given the strength of the call frequency–body size relationship across such a taxonomically, morphologically and ecologically diverse frog fauna, any deviations from this relationship may offer significant evolutionary insights. Here, we reveal two sources of such deviations: frog taxonomic family and calling habitat. The relationship between call frequency and body size of hylids, myobatrachids and microhylids differ in that hylids generally have calls of higher frequency relative to their body size. Differences in the mechanism of sound production between these families are not known, but differences in vocal apparatus have been found between other frog families (Duellman & Trueb, 1994; Wells, 2007).

Masking interference from background noise is expected to impose selection for increased signal contrast against the environment (Slabbekoorn & Peet, 2003; Brumm & Slabbekoorn, 2005; Amézquita *et al.*, 2006). In this case, we tested the hypothesis that the calls of stream-breeding species should show a spectral shift away from stream noise. We found that stream-breeding hylid species have lower frequency calls for their body size than their pool-breeding counterparts and we attribute this to a shift towards lower call frequencies in stream-breeding hylids to avoid masking by the sound of flowing water. Stream noise is the dominant environmental sound at typical breeding habitats for these species. Measurements at stream sites in north-east Australia show stream noise to be a broadband noise with a dominant frequency averaging 2.5 kHz across sites (Goosem *et al.*, 2007). The calls of the stream-breeding hylids in this study centre on an average dominant frequency (1.7 kHz) that falls below that of typical stream noise (2.5 kHz). The calls of the pool-breeding hylids of equivalent size range

centre on an average dominant frequency (2.7 kHz) that would be masked by stream noise. More detailed information is required on the properties of stream noise to better assess call masking, including variation in spectrum and amplitude across stream habitats, sites and breeding seasons.

To our knowledge, ours is the first broad-scale test of the effect of stream noise on frog calls and the first demonstration that stream-breeding species utilize the sound window below dominant stream noise. This contrasts with all previous observations, which are from other regions and are generally species specific. Previous observations are that stream breeders avoid call masking through high-frequency calls (e.g. Duellman & Trueb, 1994; Haddad & Giaretta, 1999), including the recent discovery of ultrasonic calls in two species (Narins *et al.*, 2004; Feng *et al.*, 2006; Arch *et al.*, 2008). Shifts to high-frequency (including ultrasonic) calls have also been found in birds calling near noisy streams (Narins *et al.*, 2004; Brumm & Slabbekoorn, 2005; Brumm & Slater, 2006). Our results suggest that the calls of stream-breeding frogs of different groups/regions have shifted in opposing directions (i.e. below and above stream noise) to attain signal contrast against the background environment. Similar analyses are required in other regions to test the generality of this pattern and to address the fascinating question of why spectral shifts occur in opposing directions in different regions or frog groups. Phylogenetic data were not available to correct for relatedness among the hylids within this analysis; however, it is clear that the stream-breeding species are not all closely related. Myobatrachid frogs showed no difference between stream and pool breeders but, because there were too few stream-breeding species, we may not have had the power to rigorously test this.

The analysis of outliers to the DF–body size relationship across all species and within myobatrachids revealed that *Phyllorhina* emit calls of markedly lower frequency than expected for their body size. However, in this study we do not have enough data points to statistically test this observation, particularly given the close phylogenetic relationship between these species. *Phyllorhina* call from buried positions and were the only subterranean calling species in the analysis. We hypothesize that these species have evolved low-frequency calls for more effective call transmission through soil, a suggestion made previously for fossorial Papuan microhylids (Menzies & Tyler, 1977).

Call frequency has been shown to play a role in mate choice in frog species (e.g. Ryan, 1980), and females generally display stabilizing or weakly directional preference for call frequency (Gerhardt & Huber, 2002). Selection on call frequency may be constrained by body size or could drive change in male body size if associated costs were limited, thus moving the species along the call frequency–body size slope. Such shifts would be hard to detect. Alternatively, species could shift off the slope through mechanisms that enable call frequency to change independent of body size, for example increased relative mass of the vocal cords or associated structures, or active modification of vocal cord tension (Martin, 1972; Gerhardt & Huber, 2002). It is intriguing how rare such shifts are, suggesting that these

mechanisms entail costs such as those associated with energetics, acoustics or the environment (Ryan, 1988; Gerhardt & Huber, 2002). The mechanisms underlying the deviations seen here, between frog families, stream- and pool-breeding hylids, and in *Phyllorhina*, remain unresolved, and will offer significant insights to the evolution of frog calls and body size.

Acknowledgements

We thank David Stewart for quality call recordings, Megan Higgie for statistical advice and other assistance, and Megan Higgie, Scott Keogh, Andrew Taylor and Carl Gerhardt for comments that improved the paper.

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