Black and White Colobus Monkey (*Colobus guereza*) Roars as a Source of Both Honest and Exaggerated Information About Body Mass

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Abstract

Formant dispersion, the average spacing, in Hz, between the resonant frequencies of a vocalization, has been predicted to provide honest information about signaler body size. Previous descriptions of black and white colobus monkey (*Colobus guereza*, ''guereza'') roars, however, suggest a formant dispersion that is far lower than expected for an animal its size, and could effectively exaggerate its body size. Nonetheless, recent research on red deer shows that even when the formant positions of vocalizations effectively exaggerate body size, they may still provide honest cues within a species. We investigate whether the frequency bands observed in the spectrograms of guereza roars represent formants, and whether roar formant dispersion and/or individual formants provide honest information about body size (specifically, body mass) relative to conspecifics, although perhaps not relative to other species. We document coordinated vertical movements in the frequency bands of guereza roars and show that these bands move independently of fundamental frequency, indicating that they represent formants. We show, for captive adult male guerezas, that signaler body mass significantly predicts roar formant dispersion, even for randomly selected calls. Body mass also predicts formants 2 and 3, but the relationships are not as strong as with formant dispersion. Our roar formant dispersion calculations predict a vocal tract length of approx. 29 cm, but anatomically determined guereza vocal tract length is much smaller: approx. 7–8 cm. Videotaped roars revealed no laryngeal movement during roars, but rather inflation of the subhyoid air sac. We measured the volume of this air sac (approx. 10 cm^3) and speculate that it may function in roars to exaggerate body size, relative to other species.

Introduction

Many studies and reviews (e.g. Morton 1977; Fitch & Hauser 1995, 2002; Fitch 1997, 2000) have discussed the potential for mammalian vocalizations to provide honest signals of body size. Researchers have frequently investigated the link between fundamental frequency, F_0 (i.e. pitch), and body size, but have not always found strong relationships between the two (e.g. Lass & Brown 1978; Masataka 1994; van Dommelen & Moxness 1995; Rendall et al. 2005). Lowest possible F_0 is determined by the length of

the vocal folds (Titze 1994), which are not tightly anatomically constrained by body size. While F_0 may provide a rough cue about body size, with different age classes or species having different F_0 (e.g. Reby & McComb 2003a; Rendall et al. 2005), it is usually not a reliable signal of body size within age classes.

Recent research has instead focused on formants or resonances of the vocal tract that are produced when the vocal tract filters the sound from the larynx (Fant 1960; Titze 1994; Fitch 1997). Formant positions, which show up as frequency bands in a spectrogram, are determined primarily by the length of the vocal tract (Fant 1960; Lieberman & Blumstein 1988); vocal tract shape plays an additional, secondary role. Vocal tract length (VTL), in general, is highly constrained by the bones of the skull and, in species that have been studied, is highly correlated with measures of body size (rhesus macaques: Fitch 1997; humans: Fitch & Giedd 1999; domestic dogs: Riede & Fitch 1999; red deer: Reby & McComb 2003b). Formant dispersion (most simply measured as the average spacing, in Hz, between the formants of a vocalization) is likely to be a source of honest information about body size and is expected to vary inversely with body size in many species (Fitch 1997). It has been shown to predict body size in domestic dogs (Riede & Fitch 1999), rhesus macaques (Fitch 1997), red deer (Reby & McComb 2003a), and human men (Rendall et al. 2005). Recent studies, however, have cast some doubt upon whether formant dispersion is as reliable a body size cue when tested within a given age/sex class, than when tested across age and sex classes (e.g. Rendall et al. 2005).

Adult male black and white colobus monkeys (*Colobus guereza*, hereafter ''guerezas'') produce loud calls, known as roars, during daily, contagious night and morning choruses, and in response to predators (Marler 1972; Oates 1977). They also regularly engage in intergoup aggression where guereza densities are high (Oates 1977; von Hippel 1996; Fashing 2001). Together, these factors provide ample incentive and opportunity for guerezas to assess one another from afar using vocal signals. Adult females are also known to roar, but do not participate in morning choruses (T. R. Harris and P. J. Fashing, pers. obs.).

It is currently unknown whether the pronounced frequency bands of guereza roars (Marler 1972) represent formants (i.e. whether they result from resonances of the vocal tract, and whether the glottal source is functionally independent of the supraglottal filter). If they are, their low frequency (Marler

1972) is intriguing, given recent research on other non-human primates. Fitch (1997) was able to predict rhesus macaque pant threat formant dispersion, D_f, using a simple tube model of the vocal tract. Substituting Marler's (1972) data from guereza roars into this model ($D_f = 600$ Hz) predicts a VTL of 29.2 cm for guerezas. This number is surprising because wild guereza males, at 9.1–11.9 kg ($\bar{x}$ values for different subspecies; Delson et al. 2000), are much smaller than human males; yet the VTL of human males is typically <17 cm (Fitch & Giedd 1999). The low frequency bands in guereza roars, therefore, may exaggerate body size.

It is possible, however, to exaggerate body size relative to other species but convey honest information about body size relative to conspecifics. This can occur, for example, when an evolutionary 'arms race' that favors a lengthening, or apparent lengthening, of the vocal tract reaches an anatomical constraint, blocking any further exaggeration (Fitch & Hauser 2002). If that constraint, itself, is tied to body size, a new, exaggerated, signal that functions honestly within the species will be formed. For example, red deer males can lower their larynges to the sternum (an anatomical constraint) during intense roaring (Fitch & Reby 2001; Reby & McComb 2003a). This extraordinary lengthening of the vocal tract, which lowers the formant frequencies of their roars, highly exaggerates their body size relative to other species. However, larger males still have longer necks, and thus longer vocal tracts, so their roars still provide honest information about body size, relative to conspecifics (Reby & McComb 2003a).

This study tests two hypotheses: (1) the frequency bands of guereza roars are formants; and (2) the roar formant dispersion provides honest information about body size (specifically, body mass) relative to conspecifics, while potentially providing exaggerated body size information relative to other species (as previously documented in red deer).

Methods

Recording and Playback Equipment

We recorded roars using a Sony Professional Walkman (WMD3 for the captive study and at Kibale, Uganda; WMD6C at Kakamega, Kenya) or a Marantz Portable PC Card Recorder (PMD680) (Itasca, IL, USA) and a Sennheiser shotgun microphone (ME66) (Old Lyme, CT, USA). We digitized analog recordings using the Windows program, Sound Recorder, and saved them as WAV files at

16-bit amplitude resolution and 12-kHz sampling rate (roars have little energy over 5 kHz). Where possible, we videotaped guerezas as they roared, focusing on the mouth and laryngeal region, using a Sony (Japan) digital video camera (DCR-TRV230). We transferred the video to computer and viewed it in i-Movie (Apple Computer, Cupertino, NM, USA) software, examining it for laryngeal movement and air sac inflation. We played roars to captive guerezas using two Technomad Vernal 15 speakers, a 12-V amplifier, and a walkman.

Captive Recordings, Weights

We attempted playbacks of wild guereza roars (recorded in 2001 in Kibale National Park, Uganda) at 13 USA zoos (Audubon Zoo, Baltimore Zoo, Brec's Baton Rouge Zoo, Central Park Zoo, Greenville Zoo, Jackson Zoo, Jacksonville Zoo, Memphis Zoo, Monkey Jungle, National Zoo, North Carolina Zoo, Philadelphia Zoo and Stone Zoo) to elicit roars from captive adult guerezas. We recorded roars guerezas produced in response to the playbacks and to other stimuli, for a total of 83 roars at eight zoos, from nine adult males and one adult female (Table 1). We did not use roars from guerezas with deformities that could have altered their vocal tract. Where allowed by zoo staff, we obtained weights of each roaring guereza using a flat digital veterinarian scale (Befour VS-0440T), which we provided. In all other cases, we obtained weights from recent zoo records.

Only adults are known to produce full roars (P. J. Fashing and T. R. Harris, pers. obs.), but we verified the adult status of the individuals we recorded using their ages and by checking for the presence of head humps (present in both sexes as adults, described in Oates 1974). Wild guerezas reach adulthood, including full adult size, at approx. 4 years of age (T. R. Harris, unpubl. data) and captive guerezas would be expected to reach adulthood slightly sooner. The captive guerezas we recorded ranged in age from 3.5 to 18 years (Table 1), with the youngest individual well within the weight range of other adult males.

Wild Recordings

Because the captive roars we recorded were responses to various stimuli, we recorded wild guereza roars to test whether roars produced in response to different stimuli differ in formant dispersion. We recorded roars from four known adult male guerezas at the Ise-cheno field site in Kakamega Forest, Kenya between January 1997 and March 1998. We also recorded the roars of four known adult male guerezas at the Kanyawara field site in Kibale National Park, Uganda between May 2001 and August 2004 (Table 1). In both cases, we recorded both morning chorus roars and daytime predator roars. We considered roars to have been responses to predators if other primates were also alarm-calling, if we observed the predator, and/or if the guerezas were staring down at the ground while roaring (presumably at a predator we could not see).

Table 1: Study subject information

Animal name	Sex	Age (years)	Body mass (kg)	Zoo/field site	No. vocalizations used in analyses
Bisi	M	9	11.6	Baltimore Zoo	14
Kwanza	M	3.5	13.5	Brec's Baton Rouge Zoo	5
Kamante	M	15.5	18.9	Greenville Zoo	5
Tah Dah	M	5	11.1	Greenville Zoo	10
Lincoln	M	Unknown	14.5	Memphis Zoo	2
Springer	M	18	11.6	Philadelphia Zoo	7
Michael Jordan	M	8.5	12.8	Monkey Jungle	19
Amani	M	5	13.4	Audubon Institute	1
Capri	M	9	15.4	Jackson Zoo	17
Jordan	F	9	11.1	Jackson Zoo	3
Mwisi	M	Unknown	Unknown	Kibale, Uganda	2
Mutiini	M	Unknown	Unknown	Kibale, Uganda	12
Kitaito	M	Unknown	Unknown	Kibale, Uganda	2
Araali	M	Unknown	Unknown	Kibale, Uganda	8
Billie Joe	M	Unknown	Unknown	Kakamega, Kenya	2
Oliver	M	Unknown	Unknown	Kakamega, Kenya	10
Anselmo	M	Unknown	Unknown	Kakamega, Kenya	4
Cavalera	M	Unknown	Unknown	Kakamega, Kenya	2

Roar Analyses

We edited and analyzed all available roars from captive guerezas using the Praat 4.1.13 package (http://www.praat.org.: P. Boersma and D. Weenink, University of Amsterdam, The Netherlands), treating the frequency bands as formants (see below). Before analysis, we edited out of each recording a noisy snort, which immediately precedes most roars (Marler 1972). For each roar, we produced a spectrogram (Fig. 1; window length = 0.05 s, maximum frequency = 3000 Hz, time step = 0.002 s, frequency step = 20 Hz, Hanning window shape) and a list of formant values for each of three formants/roar (burg algorithm, time step = 0.05 s, maximum no. of formants = 3, maximum formant frequencies = 2300–2700 Hz, window length = 0.025 s, preemphasis from 50 Hz). We saved formant frequency values as a text file and transferred them to Microsoft Excel. We corrected by hand some formant values (6.3% of total) that did not visually match with the spectrogram. We then calculated, for each roar, $\bar{x}$ values for each of the three formants. Because the third (highest) formant was not always clear, and
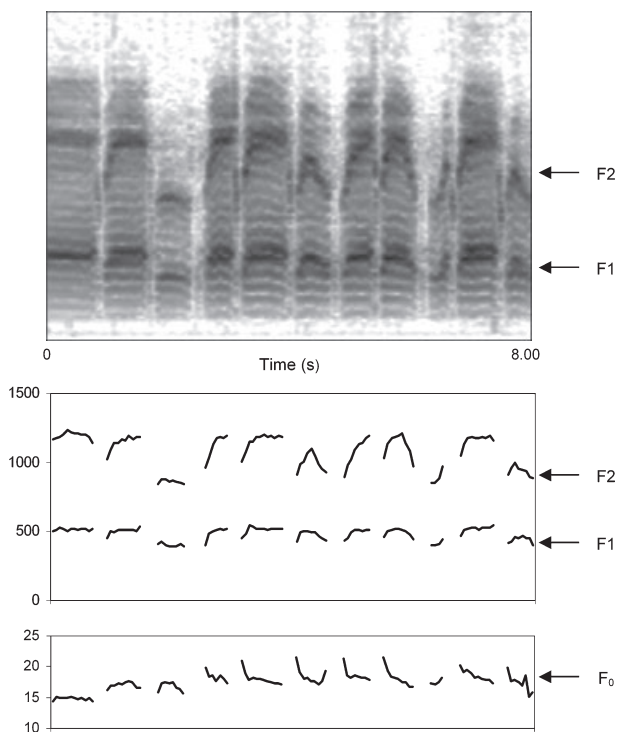

Fig. 1: Spectrogram, formant, and pitch (F_0) analysis results for a morning chorus roar, recorded in Kibale National Park, Uganda. F1 and F2 show coordinated movements, but neither show coordinated movements with F_0

because the calculation for formant dispersion effectively reduces to the highest formant frequency tested minus the lowest formant frequency divided by 2, we calculated formant dispersion both with ($\underline{D_f}$ = ((F2 − F1) + (F3 − F2))/2) and without ($\underline{D_f}$ = F2 − F1) the third formant value for each roar. For one captive guereza (the adult female), F3 was not visible in spectrograms, so we only computed D_f using F1 and F2. To test if formant dispersion significantly predicts, and varies negatively with body size, we regressed both $\bar{x}$ and randomly chosen (one per male) formant dispersion values against body mass using one-tailed linear regression. We ran regressions both with, and without, the one adult female we recorded, as well as with, and without, the heaviest (18.9 kg) male we recorded. We also tested whether $\bar{x}$ formant (F1, F2, and F3) positions for captive adult males predict, and vary negatively with body mass, using one-tailed linear regression.

We edited and analyzed the roars of wild guerezas using the methods described above, except that we calculated formant dispersion using just the lowest two formants, as only these formants had sufficient energy to be above the noise floor in many of the wild guereza roars. Therefore, we made the following changes: (1) spectrogram maximum frequency = 2000 Hz; (2) maximum number of formants = 2; and (3) maximum formant frequencies = 1400–1600 Hz. For each male, we selected and analyzed pairs of morning chorus roars and predator roars, with the same number of phrases (subunits) that the male produced within a month of each other. When possible, we selected pairs of roars that were recorded on the same day. In total, we selected and analyzed 20 pairs of roars from eight males. We tested for differences in formant dispersion between morning chorus and predator roars using a two-tailed paired t-test.

To exclude the possibility that the spectral peaks of roars actually represent harmonics of the fundamental and not formant frequencies, we tested for independent movement of fundamental frequency and frequency bands over the length of a roar. We chose a roar that showed clear vertical frequency band movements for this analysis. The 'pulses' of guereza roars (described by Marler 1972) show very regular periodicity, such that cycles of vocal fold opening and closing, representing the fundamental frequency (F_0) can be viewed from the waveform. Therefore, we measured the period of each cycle of vocal fold opening and closing for the entire roar, excluding the brief pauses between phrases, which most likely correspond to very short inhalations. We

performed a formant analysis on this roar using Praat, as described above, and obtained formant values for F1 and F2 at the midpoint of each cycle of vocal fold opening and closing. We then used two-tailed Spearman correlation analysis to determine if fundamental frequency over time is significantly correlated with frequency, over time, of either F1 or F2.

Anatomy

We obtained magnetic resonance images (MRI) of an adult female guereza from Dr Takeshi Nishimura (Primate Research Institute, Kyoto University). The images were taken with a General Electric Signa Profile MRI scanner with a spatial resolution of 0.585931 mm/pixel and a slice thickness of 3.00 mm. We measured VTL using Scion Image software by drawing and measuring a curvilinear line equidistant from the medial and external walls of the oral vocal tract, from the middle of the glottis to the opening of the lips.

We used the VTL measurement from the adult female to calculate expected formant dispersion and expected formant values based on a simple tube model of the vocal tract, with one end of the tube closed and the other open, using the following equations:

$$\underline{D}_{f\ pred} = \frac{c}{2L},\qquad(1)$$

$$F_n = \frac{(2n-1)c}{4L},\qquad(2)$$

where n is the formant number, c is the speed of sound (350 m/s in warm, moist air), and L is the length of the tube in cm. We also recalculated the expected formant dispersion and formant values using an estimate of adult male VTL. Based on published weights for *Colobus guereza occidentalis* (Delson et al. 2000), adult male body mass is approx. 1.22 times that of adult females. Given that length scales as the cube root of mass, we estimated adult male VTL as 1.07 times that of adult females.

We also examined and dissected the larynx of an adult female guereza at Smithsonian's US National Museum of Natural History. To measure the maximum volume of air the air sac held, we inserted tubing into the female's subhyoid air sac, using a metal clamp to hold the tubing firmly in place so that no air escaped, and inflated the sac by pumping air into it using a graduated syringe.

Results

Are Roar Frequency Bands Formants?

The spectrograms of wild roars revealed coordinated vertical movements in the putative formant frequency bands of some males' roars (Fig. 1). Analysis of simultaneous video and audio recordings of wild guereza roars reveals that these movements are probably tightly correlated with lip rounding/protrusion, which effectively elongates the vocal tract, lowering each formant as well as formant dispersion (Lieberman 1968; Lieberman & Blumstein 1988); that all roar frequency bands move together, in synchrony with lip movements, suggests that they result from resonant frequencies of the vocal tract and are, thus, formants (Lieberman 1968; Ohala 1983, 1984; Fitch & Hauser 1995).

Guerezas' roars have extremely low fundamental frequencies, in the 10- to 25-Hz range, for several roars we examined: quite remarkable for an animal their size, and presumably tied to their very large larynx (Hill & Booth 1957). This low fundamental generates a second set of frequency bands, at a much lower spacing than formants, which are also visible in the spectrogram of Fig. 1. It is obvious on inspection that the fundamental and harmonics change together, and independently of the formant bands. We ran a pitch and formant analysis on the roar shown in Fig. 1 and found that fundamental frequency is not significantly correlated with frequency, over time, of either F1 (Spearman correlation: $\rho = -0.038$, $N_{points\ sampled} = 108$, $p = 0.711$) or F2 (Spearman correlation: $\rho = -0.161$, $N_{points\ sampled} = 108$, $p = 0.114$). These data provide additional confirmation that the spectral peaks of roars do not represent harmonics of the fundamental but, rather, formants.

Does Roar Formant Dispersion Potentially Convey Honest Information About Body Mass?

In the spectrograms of most roars obtained from captive adult males (92.5%), three formants were visible, with the highest formant (F3) typically of considerably lower amplitude than the other two. Overall $\bar{x} \pm SE$ for each formant (using each of the nine males' $\bar{x}$ values as raw data) were: F1 = 551.8 ± 7.1 Hz, F2 = 1145.9 ± 17.8 Hz and F3 = 1711.9 ± 18.4 Hz. There was far more among-individual than within-individual variation in formant dispersion. Body mass significantly predicted $\bar{x}$ formant dispersion for adult males (Fig. 2), regardless of
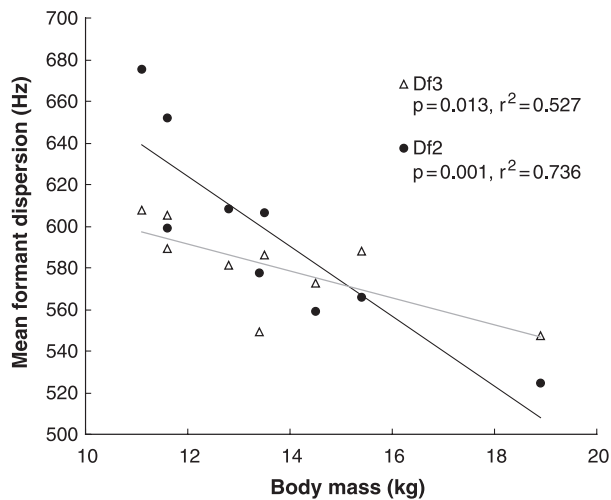
Fig. 2: Mean formant dispersion vs. body weight for adult guereza roars. D_{f2} and D_{f3} are formant dispersion calculations made using the lowest two, and all three formants, respectively

whether we used two (linear regression: n = 9, F-ratio = 22.18, p = 0.001, r^2 = 0.736) or three formants (linear regression: n = 9, F-ratio = 7.79, p = 0.013, r^2 = 0.527) to calculate D_f. The results remain the same if the adult female, whose roars only contained F1 and F2, is added to the sample (linear regression: n = 10, F-ratio = 28.52, p < 0.001, r^2 = 0.781). When we removed the heaviest male (18.9 kg) from the adult male sample, body mass still significantly predicted formant dispersion when we used F1 and F2 to calculate D_f (linear regression: n = 8, F-ratio = 19.48, p = 0.002, r^2 = 0.736) but not when we used all three formants (linear regression: n = 8, F-ratio = 2.55, p = 0.090, r^2 = 0.277). Body mass also significantly predicted formant dispersion for randomly selected adult male roars (linear regression, two formants: n = 9, F-ratio = 15.10, p = 0.003, r^2 = 0.683; linear regression, three formants: n = 9, F-ratio = 12.742, p = 0.005, r^2 = 0.645). There was far more variation in formant dispersion when only the two lowest, most prominent formants were used to calculate it, and the slopes of the regression lines from all tests described above were steeper when D_f was calculated using only these formants. Body mass also significantly predicted, and varied negatively with individual formants – F2 and F3, but the relationships were not as strong (linear regression, F2: n = 9, F-ratio = 8.809, p = 0.010, r^2 = 0.557; linear regression, F3: n = 9, F-ratio = 4.556, p = 0.035, r^2 = 0.394) as the relationship between body mass and formant dispersion. Body mass did not predict F1 – the formant

with the least amount of among-individual variation (linear regression: n = 9, F-ratio = 0.495, p = 0.252, r^2 = 0.066).

Does Roar Formant Dispersion Potentially Convey Exaggerated Information About Body Size?

Mean formant dispersion for captive adult male guerezas (using each of the nine males' $\bar{x}$ values as raw data) was 596.4 ± 15.6 Hz and 580.7 ± 7.1 Hz, when calculated with the lowest two or all three formants, respectively. Substituting these values into equation 1 ($D_f = c/2L$), predicts VTL of 29.1 and 30.1 cm, respectively. Actual VTL, as measured from an MRI image for an adult female, was much smaller: 7.0 cm. With this VTL, $D_{f\,pred}$ = 2500 Hz and the predicted formant values (equation 2) are: 1250, 3750, and 6250 Hz. With an estimated adult male VTL of 7.49 cm (7.0 × 1.07), $D_{f\,pred}$ = 2336 Hz and the predicted formant values are: 1168, 3505, and 5841 Hz. Thus, measured formant frequencies are considerably lower than predicted for an animal of this size (see Discussion).

Do Roars Produced in Response to Different Stimuli Differ in Formant Dispersion?

Morning chorus roars produced by wild male guerezas did not differ significantly in formant dispersion (using two formants) from predator roars of the same number of phrases (paired t-test: n = 20 pairs, t = 0.731, p = 0.474).

Potential Mechanisms for Producing Low Formant Dispersion

Careful analysis of digital video recordings of roaring guerezas revealed no signs of larynx-lowering, visible in roaring red or fallow deer (Fitch & Reby 2001; Reby & McComb 2003a) and in large cats, such as lions (W. T. Fitch, pers. obs.). However, the subhyoid air sac, as described by Hill & Booth (1957), was often inflated at the beginning of roars (Fig. 3). The maximum volume of air held by the subhyoid air sac, measured from an adult female guereza at Smithsonian Natural History Museum, was 10.0 cm^3.

Discussion

Our results strongly suggest that the frequency bands of guereza roars are formants, and show that roar formant dispersion, as well as formants 2 and 3,

Fig. 3: Tracings of consecutive video frames (30 frames/s) of an adult male's left profile, showing subhyoid air sac inflation at the beginning of a roar

Pre-vocalization resting state   Subhyoid air sac inflation   Lip-opening and vocalization
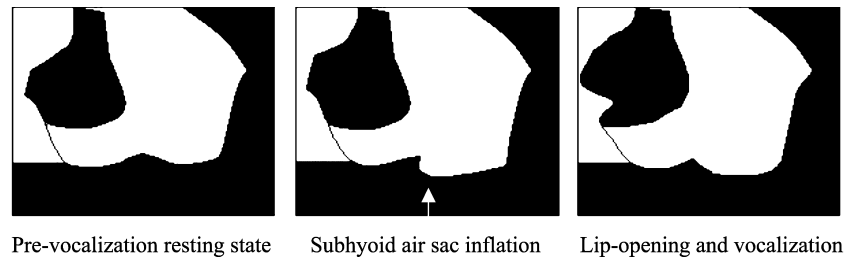
conveys honest information about body mass, relative to conspecifics. However, relative to other species, guerezas have exaggerated, low formants and formant dispersion. We found no difference in formant dispersion of roars produced in response to different stimuli (morning chorus vs. predator roars). Digital video observations indicate that inflation of the subhyoid air sac, but not larynx-lowering, occurs during roaring. Air sac inflation may, therefore, be involved in lowering the formant dispersion values of guereza roars, thus exaggerating body size relative to other species, and relative to predictions based on a simple physical model.

Our preliminary analyses suggest that guerezas may sometimes lengthen their vocal tracts using lip rounding/protrusion. Despite this, we found that body mass significantly predicts roar formant dispersion, even within a single age/sex class – in this case, adult males. This finding was robust in that body mass explained most of the variation in $\bar{x}$ formant dispersion (i.e. high r^2) and because the relationship was still significant even when a single, randomly chosen roar/individual was regressed against body mass. Our results indicate that formant dispersion, calculated using the two lowest, most prominent formants, is the best predictor of body mass.

Studies have shown that many vertebrates are capable of discriminating formant differences (Japanese macaques: Sommers et al. 1992; whooping cranes: Fitch & Kelley 2000; baboons: Hienz et al. 2004; red deer: Reby et al. 2005), suggesting that roar formant dispersion is a potential source of honest information that guerezas could use to gauge one another's relative size. Adult males, which roar during contagious morning choruses (Marler 1972) and frequently engage in intergroup aggression (Oates 1977; von Hippel 1996; Fashing 2001), may be able to make decisions about which individuals to avoid or approach, not only based on individual recognition and past experience, but also based on formant dispersion cues that provide an a priori indication of body size (Harris 2005). This could be especially useful when making decisions about whether to approach unfamiliar males or groups that are less well known.

The strong relationship between body mass and formant dispersion also means that researchers may use formant dispersion as a proxy for body mass in guerezas. This finding may prove useful because it is very difficult to non-invasively obtain weights from wild guerezas and many other arboreal mammals. The relationships we and others (e.g. Fitch 1997; Riede & Fitch 1999; Reby & McComb 2003a,b; Rendall et al. 2005) have found between body mass and formant positions also have implications for the use of formant frequencies in taxonomic and phylogenetic studies. Such studies, which are relatively common for primates (e.g. colobus monkeys: Oates & Trocco 1983; Oates et al. 2000; lion tamarins: Snowdon et al. 1986; bushbabies: Zimmermann et al. 1988), use frequency band/formant frequencies (sometimes mistakenly referring to F1 as fundamental frequency) to separate out clusters of species with similar, and, according to the assumption, homologous vocalizations. If formant frequencies are influenced by body size, however, it is possible that the species are being separated out by their body sizes, and body size is not likely to be a good character for such analyses.

Even though formant dispersion is an honest signal of body mass relative to conspecifics, our results suggest that it may not be honest relative to other species. The critical question raised by this study stems from our finding that the relatively low formant dispersions of guereza roars predict a VTL that is more than three times longer than the actual guereza VTL. The most plausible physiological explanation of these low formant frequencies currently available is that they are made possible by the air sac. Inflation of the subhyoid air sac during roars could violate the uniform tube assumption of the equations (1 and 2) normally used to predict formant dispersion and frequencies (Lieberman & Blumstein 1988; Titze 1994). Given the elasticity of air sacs, however, it is unclear whether there is any specific anatomical constraint that would tie air sac size to body size. As of yet, therefore, we cannot explain

why formant dispersion provides an honest signal of body size relative to conspecifics – we can only show that it reliably does.

A simple model of a vocal tract terminated by an air sac attached at the glottis results in a pattern very similar to that observed in guereza roars: the lowest three formants are lowered by about half, and the upper formants greatly reduced in amplitude (W.T. Fitch, unpubl. data). However, other possibilities exist (e.g. some covert movements of the rest of the vocal tract articulators are responsible, as suggested for Diana monkeys by Riede et al. 2005), and more research will be necessary to resolve this issue. Low formant frequencies are characteristic not only of guerezas, but also of other closely related *Colobus* species (Oates et al. 2000), so they most likely evolved in a common *Colobus* ancestor (they are not characteristic of *Procolobus*).

There are several possible non-mutually exclusive functions of, and selective pressures that may have led to the low formant frequencies and low formant dispersion of guereza roars. The characteristic acoustic structure of roars may have initially evolved to intimidate predators by giving false information about body size. The relatively low frequencies of roars may also facilitate travel of the signal through forested areas which tend to have low levels of low-frequency ambient noise, particularly in early morning hours (Waser & Waser 1977; Waser & Brown 1986), thus improving intergroup communication. Female choice for males with low formant dispersion and/or male–male competition through body size exaggeration may have also been selective pressures leading to lowered formant dispersion throughout the species/genus, but these possibilities seem less likely, given that both sexes produce roars with low formant dispersion. Some of these factors may currently be important for *Colobus* species, but predator intimidation seems the most plausible as the original selective force, given that all *Colobus* species generally roar in response to predators (Marler 1972; Oates 1977; Walek 1978; Oates et al. 2000), but not all regularly use roars for intergroup communication (Oates et al. 2000).

In summary, our results show that roar formant dispersion is a reliable source of information about body mass, relative to adult male conspecifics. Further research is necessary to determine whether guerezas actually utilize these formant cues in the wild to assess one another. Given that so many primate species have loud calls that function in intergroup spacing, and that all animal species that have been tested thus far appear to be able to discriminate formant frequencies, the use of formant cues to assess body size may be widespread in primates. The present research, as well as that on rhesus macaques, shows that formant dispersion in primates may function as an honest signal of body size relative to conspecifics, despite the prevalence of laryngeal air sacs in primates (Hewitt et al. 2002). Further research on the function of air sacs, however, is needed to determine how they affect formant frequencies and whether they can effectively elongate the vocal tract, thus exaggerating body size cues relative to other species.

Acknowledgements

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