

RESEARCH ARTICLE

Striking Differences in the Loud Calls of Howler Monkey Sister Species
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Comparing vocalizations across species is useful for understanding acoustic variation at mechanistic and evolutionary levels. Here, we take advantage of the divergent vocalizations of two closely related howler monkey species (*Alouatta pigra* and *A. palliata*) to better understand vocal evolution. In addition to comparing multiple acoustic and temporal features of roars and the calling bouts in which they are produced, we tested several predictions. First, *A. pigra* should have roars with lower fundamental frequency and lower formant dispersion because they are larger than *A. palliata* and have a larger hyoid apparatus. Second, *A. pigra* should have faster calling rates, longer roars, longer bouts, and exaggerated call features linked to vocal effort (e.g., nonlinear phenomena and emphasized frequencies) because they are the more aggressive species during intergroup encounters. We found significant interspecific differences supporting our predictions in every tested parameter of roars and bouts, except for roar duration and barking rate. Stepwise discriminant function analyses identified the best features for differentiating roars (acoustic features: formant dispersion followed by highest frequency; temporal features: longest syllable duration followed by number of syllables). Although resembling each other more than they resemble South American howler monkeys, our comparison revealed striking differences in the vocalizations of the two Mesoamerican species. While we cannot completely rule out the influence of body size or the environmental conditions in which the two species evolved, vocal differences were likely influenced by sexual selection. The exaggerated roars and intense calling patterns in *A. pigra* seem more suitable for intergroup competition, whereas *A. palliata* calls may be better suited for mate attraction and competition within groups. With interspecific acoustic differences quantified, we will now be able to examine how vocalizations contribute to the evolutionary dynamics of the *A. palliata* × *A. pigra* hybrid zone in southern Mexico. *Am. J. Primatol.* 78:755–766, 2016. © 2016 Wiley Periodicals, Inc.

Key words: acoustic analysis; chaos; formant dispersion; howling bouts; roaring rate

INTRODUCTION

Comparing the sounds produced by closely related species is the best way to understand how and why vocalizations evolve. Mechanistically, comparing across species can lead to a fuller understanding of morphological–acoustic relationships within species. For example, comparing vocalizations across finch species has shown how beak morphology and song structure co-evolve [e.g., Huber and Podos, 2006]. Similarly, in some mammalian species, animals attend to formant dispersion [Ghazanfar et al., 2007; Reby et al., 2005], which reliably tracks body size [Charlton et al., 2009; Ey et al., 2007; Fitch, 1997; Reby and McComb, 2003; Riede and Fitch, 1999]. If a similar relationship between morphology

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and vocalizations is found between related species of different sizes, this would suggest that the relationship emerges from a physiological constraint that is resilient across species [Dunn et al., 2015; but see Stachowicz et al., 2014]. Functionally, vocalizations are often used in species recognition. Documenting vocal variation across species can reveal causes of reproductive isolation and speciation (e.g., primates: [Braune et al., 2008]). Finally, mapping acoustic variation onto phylogenetic relationships can reveal patterns of vocal evolution (e.g., birds: [de Kort and ten Cate, 2004; Price and Lanyon, 2002]; frogs: [Irisarri et al., 2011]; whales: [May-Collado et al., 2007]; primates: [McComb and Semple, 2005]).

A great deal of research in primate vocal comparative studies has been devoted to the function and distribution of loud calls [e.g., Wich and Nunn, 2002]. Some of these studies have used vocalizations to better understand taxonomy [e.g., Thinh et al., 2011; Whittaker et al., 2007], while others have tried to understand the selective pressures involved in the evolution of the vocalizations themselves [e.g., Dunn et al., 2015; Fichtel, 2014; Masters, 1991; Mitani and Stult, 1998; Wich and Nunn, 2002]. Here, we investigate the extent of vocal divergence in two howler monkey species and the possible influence of morphology and sexual selection.

The unique loud calls of howler monkeys (*Alouatta* spp.) have generated considerable interest among vocal communication researchers. Male members of this genus produce long howling bouts, during which loud bark and roar vocalizations are most conspicuous [e.g., Baldwin and Baldwin, 1976; Carpenter, 1934; Whitehead, 1995]. Individual males can be recognized by distinctive features of their roars and barks [Briseño-Jaramillo et al., 2015]. Howling bouts play a role in competition within and between groups, and perhaps function in mate choice [reviewed in Kitchen et al., 2015]. Females also participate in howling bouts [Van Belle, 2015], but their calls are not as loud, long, or low in frequency because they do not have the exaggerated hyoid bones with accompanying bulla and air sacs (hereafter, hyoid apparatus) seen in males [da Cunha et al., 2015]. These differences led Darwin [1871] to propose that the hyoid apparatus is sexually selected, a speculation recently supported by cross-species comparisons in howler monkeys [Dunn et al., 2015].

In a comparison of six howler species, Whitehead [1995] suggested that roar vocalizations fall into two distinct groups—*A. palliata* versus all others—separated primarily by the duration of sustained calling and the bandwidth of the calls. Similarly, Dunn and colleagues [2015] found that *A. palliata* is somewhat of an outlier, with a smaller hyoid and wider formant dispersion than the other members of the genus, including *A. pigra*. However, a recent review [da Cunha et al., 2015] suggests that the

two Mesoamerican howler species, *A. pigra* and *A. palliata*, are overall more similar to each other and distinct from the South American species in terms of temporal features of their vocalizations. In their qualitative comparison, da Cunha et al. [2015] suggest that the Mesoamerican species have shorter roars but longer and more varied bouts (in terms of vocal types) than the South American species. The hypothesis of da Cunha and colleagues is more aligned with genetic evidence that indicates the Mesoamerican species are sister taxa, sharing a common ancestor approximately 3 mya [Cortés-Ortiz et al., 2003], but empirical data are sparse.

Here, we extend previous research on these two species in three important ways. First, we expand the number of temporal and acoustic features analyzed and make comparisons across a larger sample size than was possible for others [da Cunha et al., 2015; Dunn et al., 2015; Whitehead, 1995]. As a result, we will better understand the acoustic evolution that has occurred since their common ancestor. Second, based on recent studies [e.g., Cortés-Ortiz, unpubl. data; Dunn et al., 2015; Kelaita et al., 2011; Kelaita and Cortés-Ortiz, 2013; Youlatos et al., 2015], we now know the extent of morphological differences between *A. pigra* and *A. palliata*, providing an opportunity to understand how morphology translates to acoustic parameters. Third, the contact zone between *A. pigra* and *A. palliata* in southern Mexico is now well documented and generations of hybrids have been observed [Cortés-Ortiz et al., 2007, 2015; Ho et al., 2014; Kelaita and Cortés-Ortiz, 2013]. Clarifying interspecific acoustic differences in allopatric populations sets the stage for further exploration of how vocalizations might contribute to either reproductive isolation or introgression.

We compare 15 variables (Table I) that describe the temporal pattern of howling bouts and the acoustic structure of individual roars and test the following predictions: (i) Building on the findings of Dunn and colleagues [2015] from a single recording in each species, we predict that *A. pigra* has a lower fundamental frequency and less formant dispersion than *A. palliata* given their larger body size and larger hyoid apparatus; (ii) *A. pigra* invests in more intense howling displays—longer roars, longer bouts, and faster calling rates—than *A. palliata* given that the former species has higher levels of between-group competition. This prediction is based on the fact that approaches, chases, and physical aggression between groups are reported more frequently in *A. pigra* [Horwich et al., 2000; Kitchen, 2000; Van Belle et al., 2008] than in *A. palliata* [Glander 1992; Hopkins, 2013; Ryan et al., 2008] and that long-distance, intergroup competition in *A. pigra* is common, whereas most competition in *A. palliata* is at close range, within the group [Sekulic and Chivers, 1986]; (iii) Given the presumed higher competition in *A. pigra*, we predicted more

TABLE I. Variables Measured From Roars and Howling Bouts

Temporal Patterns of Howling Bouts	
Bout duration (min)	Duration of continuous loud calling (including breaks of <1 min)
Time spent silent (%)	Percent of a 3 min sample (from section of high intensity calling, see text) spent in silent periods of >5 sec
Roaring rate (#/min)	Rate of roaring produced during above sample
Barking rate (#/min)	Rate of barking produced during above sample
Acoustic Features of Roar Vocalizations*	
Fundamental frequency (Hz)	From Praat's automatic pitch query
First formant (Hz)	From Praat's automatic first formant query
Highest frequency (Hz)	The 8th formant in <i>A. pigra</i> and 6th formant in <i>A. palliata</i> (see supplementary figures in Dunn et al. [2015])
Formant dispersion (Hz)	Average distance [Fitch, 1997] between the lowest six formant frequencies [Dunn et al., 2015]
Emphasized frequency (Hz)	Frequency with highest relative energy (Fig. 2)
Emphasized frequency range (Hz)	Bandwidth that includes highest and lowest frequency components that contribute the most energy to the roar (arbitrarily chose >60% of maximum energy in spectral slice) [Staicer, 1996]
Harmonic-to-noise ratio (dB)	Relative energy given to tonal versus atonal noise [Riede et al., 2001] from Praat's voice report query
Temporal Patterns of Roar Vocalizations	
Roar duration (sec)	Overall duration including inhaled and exhaled syllables (Fig. 2)
Number of syllables (#)	Each inhaled and exhaled portions of a roar counted separately
Longest syllable duration (sec)	Duration of the longest syllable in roar (Fig. 2)
Time at maximum amplitude (%)	Portion of syllable with darkest frequency bands, significant energy >2,000 Hz, and intensity contour line oscillating around peak intensity (lowest point in oscillation >90% of maximum intensity and higher than remainder of contour line; Fig. 2)

*All acoustic features were measured within portion defined by "time at maximum amplitude."

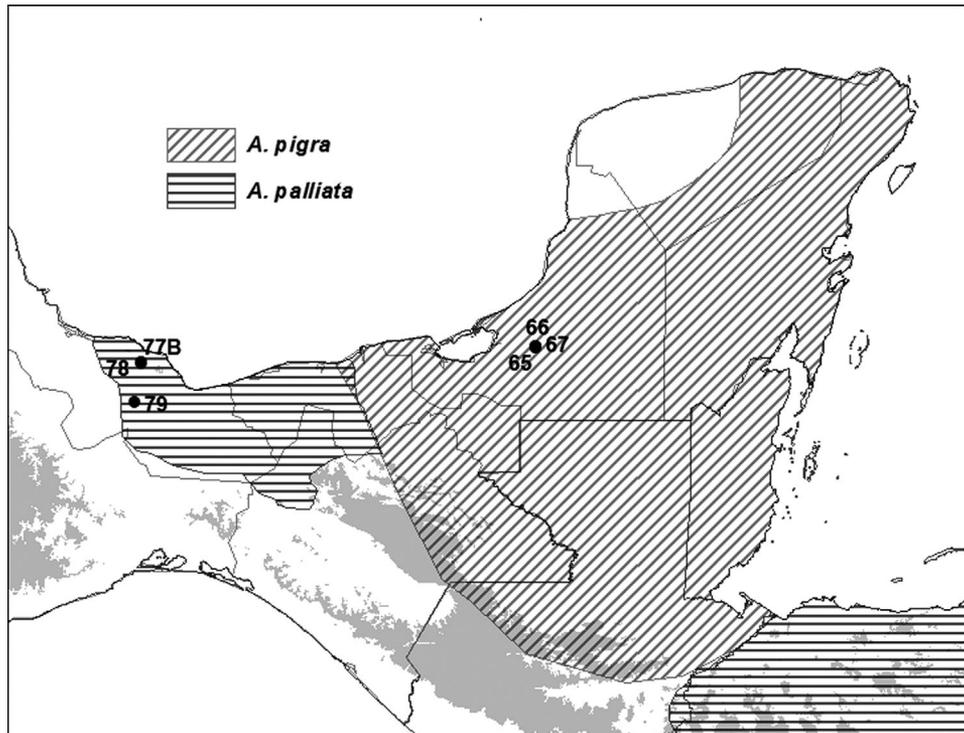


Fig. 1. Range of *A. palliata* and *A. pigra* in southern Mexico (modified from [IUCN, 2015]), with identification numbers representing focal groups [Ho et al., 2014].

exaggerated call features related to vocal effort such as higher emphasized frequencies and more “deterministic chaos” (i.e., broadband, noisy energy with residual harmonics [Wilden et al., 1998]) in *A. pigra* roars. Deterministic chaos, a type of nonlinear phenomena [Wilden et al., 1998], may have attention-getting or intimidation functions [reviewed in Fitch et al., 2002].

METHODS

Study Populations

Recordings were collected during behavioral studies on three *A. pigra* groups in the Mexican state of Campeche (groups 65, 66, and 67; Fig. 1) from

February to March and June to August 2011 and on three *A. palliata* groups in the state of Veracruz (groups 77b, 78, and 79; Fig. 1) from February to May 2012 (for details on groups and habitats, see [Ho et al., 2014]). We spent 699 hr of observation on these six focal groups (average: 117 hr/group; range 112–125 hr over 12–15 days/group) and also recorded some vocal data from four nonfocal *A. pigra* and two nonfocal *A. palliata* groups. Because multiple groups in these populations have been intermittently followed since 2008, we are able to distinguish individuals from both focal and surrounding groups based on distinctive color and scarring patterns, as well as uniquely colored ankle bracelets and a photographic record of some animals from prior

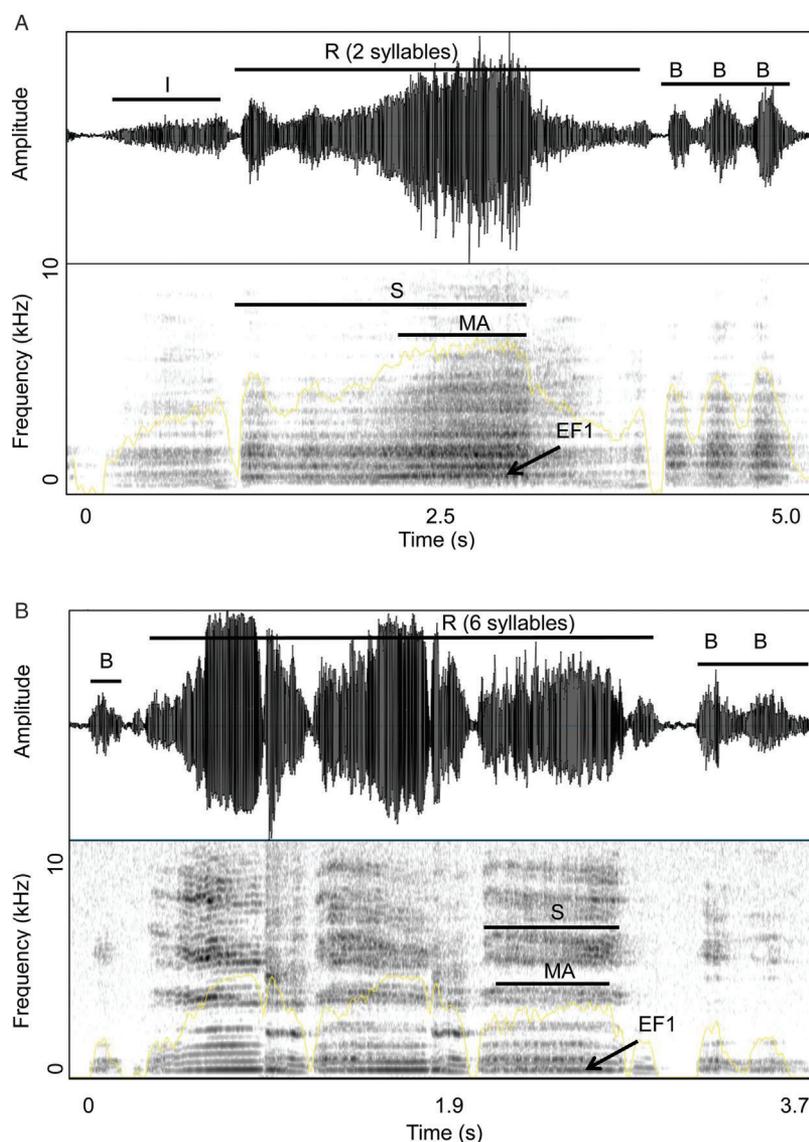


Fig. 2. Example A) *A. pigra* and B) *A. palliata* loud calling periods (including pauses of <5 sec) taken from longer howling bouts. Top panes: oscillograms (amplitude vs. time) with bars labeling components (I: inhalation; R: roars; B: barks). Bottom panes: spectrograms (frequency vs. time) with bars labeling acoustic features (S: longest syllable duration; MA: time at maximum amplitude; EF1: emphasized frequency).

capture [Cortés-Ortiz et al., 2007, 2015; Ho et al., 2014; Kelaita and Cortés-Ortiz, 2013].

Recordings

Observers carried Sennheiser ME66 directional microphones (Wennebostel, Germany) and Marantz PMD660 compact flash recorders (Tokyo, Japan). We used all occurrence sampling [Altmann, 1974] for calling bouts by focal groups and ad libitum sampling for bouts by nonfocal groups. Observers noted time of day, location, context (i.e., close encounters, distant interactions, or spontaneous vocalizations; see Statistics), bout duration, identity and behavioral changes of caller(s), and direction and vocal behavior of other groups. Two calling bouts from the same group were considered independent if separated by silence from all group members for at least 10 min (following [Hopkins, 2013; Van Belle et al., 2013]). Based on previous studies of howler vocalizations [Briseño-Jaramillo et al., 2015; Dunn et al., 2015; Kitchen, 2000; Whitehead, 1995] and similar vocalizations in other species [Ey et al., 2007; Fitch, 1997; Gamba and Giacoma, 2008; Reby and McComb, 2003; Riede et al., 2001], we measured 11 temporal and acoustic features of individual roars and four features of howling bouts (described below).

Bout Analysis

Howling bouts were analyzed in three ways. First, because context has been shown to affect vocalizations in other populations of *A. pigra* [Kitchen, 2000; Van Belle et al., 2013] and *A. palliata* [Chivers, 1969], we examined whether distance to another group prompted different responses in our two populations. During daily follows of focal groups, we noted whether or not the focal group responded vocally to other groups or extragroup individuals seen or heard within 50 m of our focal group (hereafter, close encounters following [Hopkins, 2013; Van Belle et al., 2013]) or heard calling from distances of >50 m (hereafter, distant interactions). If multiple calling groups from different directions were heard within 10 min, they were lumped as one stimulus. If both a close and a distant stimulus occurred within 10 min, we categorized the encounter as close.

Second, we measured the duration of all recorded bouts (including close, distant, and spontaneous contexts) (*A. pigra*: $N=28$ bouts by seven groups; *A. palliata*: $N=31$ bouts by five groups). Following previous authors [Kitchen 2000; Van Belle et al., 2013], breaks of >1 min were not included in the duration of a call even though calls on either side of the break were considered part of the same bout.

Third, from the highest quality of these bouts (recorded at close recordist-caller distance, facing caller, with minimal background noise or overlap among callers) in which individual callers could be

isolated (*A. pigra*: $N=14$ bouts by seven groups; *A. palliata*: $N=10$ by five groups), we measured roaring and barking rates as well as time spent silent (Table I). Following Kitchen [2000], we used a three-minute-long sample from the first half of the bout (mean = 20% into the bout; range 2–54%). By using the first half of all bouts analyzed we ensured that we were obtaining a representative sample because calling tends to slow down at the end of a bout in both species [unpubl. data]. The three-minute sample started with a loud call period (subsection of bout made up of roars, barks, other vocalizations, and pauses <5 sec [Kitchen, 2000]) containing at least one high quality roar.

Roar Analysis

From the highest quality howling bouts (regardless of context), we sampled 25 *A. palliata* roars (from 12 bouts by eight males in five groups) and 36 *A. pigra* roars (from 14 bouts by seven males in seven groups) for analysis. We included no more than five roars per bout (mean = $2.3 \pm \text{SE } 0.2$ roars/bout), and we chose roars distributed from the beginning, middle, and end of each calling bout (separated by mean = $236.1 \pm \text{SE } 90.6$ sec). We used Audacity software [Audacity Team, 2015] to isolate individual roars as .wav audio files. Roars were digitized at a sample rate of 44.1 kHz (16-bit resolution, mono format) and analyzed using Praat software [Boersma and Weenink, 2013]. Spectrograms (Fig. 2) were created with fast Fourier transformations, a Gaussian window shape, a 0.1 sec window length, a 50 dB dynamic range, a maximum formant of 4,000 Hz, and resolutions of 1,500 time steps and 250 frequency steps. The pitch function in Praat was set to cross-correlation when calculating harmonic-to-noise ratio and to auto-correlation for all other analyses.

The hyoid apparatus of howlers is responsible for additions and shifts of formant frequencies [de Boer 2008, 2009; Riede et al., 2008]. Additionally, all *Alouatta* species apparently produce nonlinear phenomena, including subharmonics and biphonation (see spectrograms in Whitehead [1995]). For these reasons, we follow Whitehead [1995] in examining the “emphasized frequency” (frequency with the most energy; Table I), recognizing that this is likely a harmonic or subharmonic frequency. Although we follow Dunn and colleagues [2015] in calling the prominent frequency bands “formants,” it is not known if these represent true formants in howler monkeys [Fitch and Fritz, 2006]. We used Praat’s formant query to search for the highest number of formants clearly defined on the spectrogram in each species and used the lowest six to determine formant dispersion [following Dunn et al., 2015], based on the equation developed by Fitch [1997].

Following Riede et al. [2001], [see also Tokuda et al., 2002], we assessed deterministic chaos by

measuring harmonic-to-noise ratios (HNR) using Praat's voice report, with high HNR (e.g., syllable 1 in Fig. 2b) being more tonal than low HNR (e.g., syllable 3 in Fig. 2b). Chaos is also characterized by having energy distributed across a broad bandwidth [Fitch et al., 2002], so we also measured the range of emphasized frequencies (defined in Table I).

The presence of chaos in roar vocalizations can make it difficult to calculate the true fundamental frequency (the base vibration rate of the vocal cords) [Dunn et al., 2015]. To improve accuracy, we set the voice threshold to 0.05 Hz, used a Gaussian window, and set the pitch range to 15–150 Hz based on values estimated in previous studies [Dunn et al., 2015; Whitehead, 1995].

Statistics

We used a crosstabs analysis to confirm that focal groups in our populations responded differently to close versus distant stimuli. Then for all variables in Table I, we used an analysis of variance (ANOVA) to test for an effect of species and included the potentially confounding effects of context (close vs. distant/spontaneous calls, lumping the latter two categories following results in Van Belle et al. [2013]) and species-context interaction. A linear mixed model with caller identity as a random effect also produced nearly identical results, but these data are not shown because we were uncertain about identity in some cases (ten roars during four bouts). To avoid a Type I error due to multiple comparisons (i.e., testing the roar and the bout data sets each multiple times), we lowered our alpha using a sequential Bonferroni correction [Holm, 1979]. To identify which of the multiple acoustic or temporal features most clearly differentiate *A. pigra* and *A. palliata* roars, we performed two stepwise Discriminant Function

Analyses (DFA). We entered variables in the DFA using the criteria of minimizing Wilks' Lambda (partial *F* to enter = 3.84, partial *F* to remove = 2.71). We also applied a leave-one-out cross-validation (i.e., jackknife), which subsamples the data to test the robustness of the classification. All analyses were performed in SPSS version 22 [IBM, 2013].

Protocol Statement

Research complied with protocols approved by The Ohio State University's Animal Care and Use Committee (IACUC) and the University of Michigan's Committee on Use and Care of Animals (UCUCA), as well as the American Society of Primatologists' Principles for Ethical Treatment of Non-Human Primates, and all Mexican legal requirements.

RESULTS

Species Differences in Howling Bouts

Using all recorded bouts, we found that *A. pigra* produced calling bouts that were more than twice as long as *A. palliata* (Table II). Our findings are similar to those reported in other populations (*A. palliata*: average approximately 6 min [Hopkins, 2013]; *A. pigra*: average approximately 15 min [Van Belle et al., 2013]).

Within howling bouts, we found that *A. pigra* spent little time taking silent breaks (>5 sec) between loud calling periods, whereas *A. palliata* spent almost half their time silent (Table II). Although the barking rate of the two species did not differ, *A. pigra* produced roars at nearly double the rate of *A. palliata* (Table II). Results were nearly identical to roaring rates published on other populations of these species (*A. pigra*: mean = 4.8/min; *N* = 19 bouts by 13 males [Kitchen 2000]; *A. palliata*:

TABLE II. Mean ± SE and ANOVA Results Comparing Roars and Howling Bouts by Species

Dependent variable	<i>A. pigra</i>	<i>A. palliata</i>	<i>N</i>	df	<i>F</i>	<i>P</i> ^a	α ^b
Bout duration (min)	20.0 ± 2.5	9.3 ± 2.2	59 bouts	1,55	7.6	<0.010	<0.025
Time spent silent (%)	5.5 ± 2.5	48.6 ± 8.1	24 bouts	1,20	30.3	<0.001	<0.010
Roaring rate (roars/min)	4.5 ± 0.6	2.0 ± 0.5	24 bouts	1,20	10.3	<0.005	<0.025
Barking rate (barks/min)	35.2 ± 6.7	29.9 ± 5.3	24 bouts	1,20	0.6	0.432	<0.050
Fundamental frequency (Hz)	86 ± 5	112 ± 4	61 roars	1,57	12.7	<0.001	<0.017
First formant (Hz)	566 ± 6	413 ± 9	61 roars	1,57	188.2	<0.001	<0.005
Highest frequency (Hz)	3,405 ± 18	3,535 ± 24	61 roars	1,57	24.1	<0.001	<0.012
Formant dispersion (Hz)	371 ± 3	624 ± 5	61 roars	1,57	2,400.2	<0.001	<0.004
Emphasized frequency (Hz)	754 ± 25	499 ± 44	61 roars	1,57	35.1	<0.001	<0.008
Emphasized frequency range (Hz)	3,933 ± 159	2,648 ± 326	61 roars	1,57	14.4	<0.001	<0.017
Harmonic-to-noise ratio (dB)	2.4 ± 0.1	7.9 ± 0.9	61 roars	1,57	95.7	<0.001	<0.006
Roar duration (sec)	2.5 ± 0.1	2.2 ± 0.2	61 roars	1,57	1.4	0.243	<0.050
Number of syllables	2.2 ± 0.1	6.1 ± 0.7	61 roars	1,57	75.0	<0.001	<0.007
Longest syllable duration (sec)	1.8 ± 0.1	0.74 ± 0.0	61 roars	1,57	156.2	<0.001	<0.006
Time at maximum amplitude (%)	47.5 ± 2.5	73.5 ± 4.3	61 roars	1,57	22.9	<0.001	<0.012

^aStatistically significant results are in bold.

^bAlpha values for the 11 tests of roars and 4 tests of bouts adjusted using a sequential Bonferroni correction [Holm, 1979].

1.7/min; $N=702$ bouts by four groups [Hopkins, 2013]).

Species Differences in Roars

Focusing only on roar vocalizations, there were significant species differences in all acoustic and temporal features except roar duration (Table II). *Alouatta pigra* roars typically contained two syllables, with the longest syllable building in amplitude over time, whereas *A. palliata* roars contained many short syllables, with the long syllables sustained at non-modulating amplitude (Fig. 2; Table II; see also Supplementary Materials). As predicted based on body size, *A. pigra* had a lower fundamental frequency and smaller formant dispersion than *A. palliata* (Table II). However, first formant and emphasized frequency were higher in *A. pigra* (Table II). Under 4,000 Hz, we found six clearly defined formants in *A. palliata* and eight in *A. pigra* [see also supplementary figures in Dunn et al., 2015]. Despite having fewer distinct bands, the highest frequency was higher in *A. palliata* than in *A. pigra* (Table II), resulting in a wider overall bandwidth (i.e., highest minus fundamental frequency) in *A. palliata* (mean \pm SE = $3,423 \pm 25$ Hz) than *A. pigra* ($3,319 \pm 17$ Hz), as proposed by Whitehead [1995]. However, *A. pigra* had the widest emphasized frequency range and lowest harmonic-to-noise ratio, both characteristics of chaos [Fitch et al., 2002] (Table II).

Because we measured many variables from roars (Table I), we used two stepwise DFAs to identify the acoustic and temporal variables that most clearly differ between the two species. Within the temporal variables, the stepwise DFA entered the longest syllable duration followed by the number of syllables, whereas within acoustic variables, the stepwise DFA entered formant dispersion followed by highest frequency (temporal: Wilks' Lambda = 0.223, $F=100.91$, $P<0.001$, $N=61$; acoustic: Wilks' Lambda = 0.014, $F=2080.47$, $P<0.001$, $N=61$; Table III). With the exception of the temporal features of a single roar, the two species had non-overlapping values for the function (Fig. 3a,b) and all other calls were classified correctly according to species (leave-one-out validation: 97% for temporal features and 100% for acoustic features).

Contextual Differences in Bouts and Roars

In both species, close encounters with other groups prompted loud calling responses in focal groups more often (*A. pigra*: 80.0% of 15 cases; *A. palliata*: 70.0% of 10 cases) than the sound of other groups calling in the distance (Fisher's Exact Test: *A. pigra*: 4.0% of 175 cases, $P<0.001$; *A. palliata*: 23.8% of 80 cases, $P=0.002$), similar to findings in other studies [Chivers, 1969; Van Belle et al., 2013]. However, no features of howling bouts or roars were different based on context or species-context interaction (Table IV).

DISCUSSION

Although vocal differences between *A. pigra* and *A. palliata* are salient to experienced observers, no prior study had systematically assessed what makes the vocalizations and calling bouts of these species so distinct. Of the 15 features measured, we found that only roar duration and barking rate did not differ between the two species. Below, we examine this variation and suggest that vocal differences are largely driven by social differences and appear to be the result of sexual selection.

A. pigra combine nearly continuous vocalizing over long time periods with fast roaring rates. As the loudest and most salient vocalizations, roars are thought to be the most effective and energetically demanding calls [Baldwin and Baldwin, 1976; Kitchen et al., 2015]. Taken together, these results suggest that the calling bouts of *A. pigra* should be more successful than *A. palliata* bouts at intimidating rivals. It remains to be seen how the howlers themselves perceive differences in calling rate and bout duration and whether responses vary between the two species, questions best addressed using playback experiments.

To human observers, differences in the temporal features of roars are the most conspicuous: *A. pigra* roars typically contain two sustained syllables, whereas *A. palliata* roars contain many short syllables. Syllable duration was also the best temporal feature for differentiating roars in the DFA, but we do not yet know the functional significance of shorter or longer syllables. Because all other members of *Alouatta* have longer syllables, the short

TABLE III. Coefficients for the Five Variables Entered in the Stepwise DFA

DFA	Variable ^a	Function 1 coefficient
Temporal	Longest syllable duration	0.88
Temporal	Number of syllables	-0.41
Acoustic	Formant dispersion	1.41
Acoustic	Highest frequency	-0.93

^aVariables are listed in the order they were entered by the stepwise DFA, with the most discriminating variable at the top.

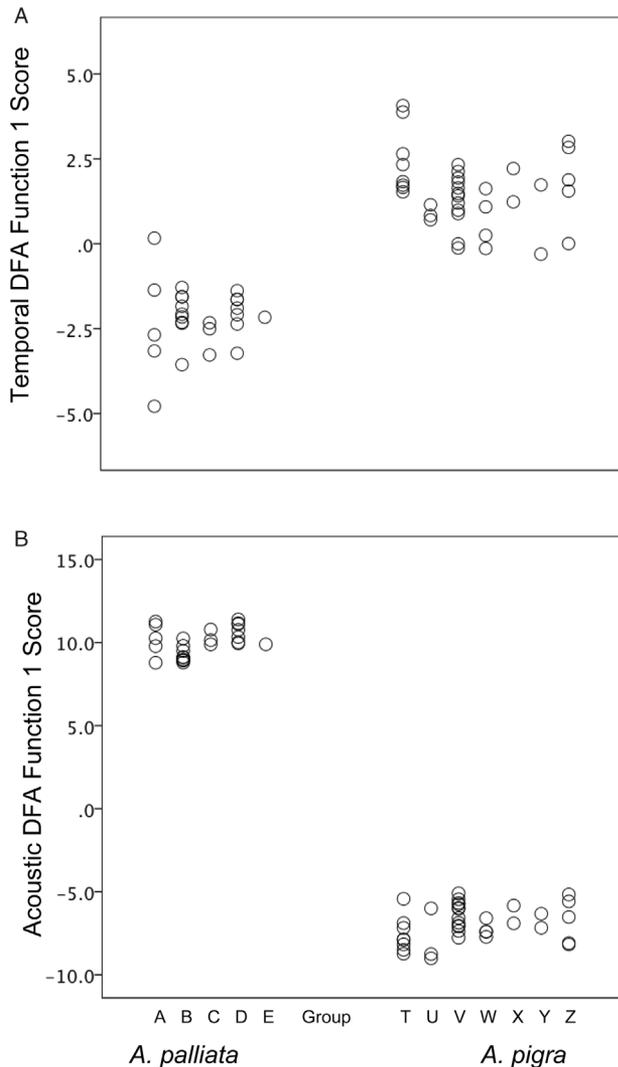


Fig. 3. Function 1 values for callers from five groups of *A. palliata* and seven groups of *A. pigra* resulting from A) the stepwise DFA with temporal features and B) the stepwise DFA with acoustic features.

syllables of *A. palliata* probably evolved following the recent split between *A. pigra* and *A. palliata* (thought to have occurred 3 mya [Cortés-Ortiz et al., 2003]). If so, selection seems to have been acting most strongly to decrease syllable duration in *A. palliata*. Interspecific morphological differences (*A. pigra* have shorter limbs, larger bodies, coarser, and darker hair [Cortés-Ortiz unpubl. data; Kelaita and Cortés-Ortiz, 2013]) suggest that *A. pigra* spent time in a colder, higher altitude environment than *A. palliata* during speciation, even though they live in similar habitats today. Selection favoring body size differences in these different habitats might have indirectly affected spectral and structural differences in calls. Due to lung capacity alone, larger species should have longer call elements than smaller species [Fitch and Hauser, 2003]. However, given the large, cross-genus variation in syllable duration

uncorrelated with body size [da Cunha et al., 2015; Youlatos et al., 2015], it is unlikely that the small-sized *A. palliata* are physically unable to produce longer syllables.

Unlike the subjective human ear, our DFA analyses revealed that acoustic features were better than temporal features at distinguishing the two species. Likewise, in a review of vocal learning, Janik and Slater [1997] suggested that frequency components of vocalizations seem to be less flexible than temporal changes (e.g., amplitude and duration) in mammals, including primates. To directly test whether the howler monkeys attend to these differences, we are using playback experiments to examine the intra- and interspecific reactions to altered syllable length when frequency components remain unaltered.

The most notable interspecific differences in acoustic features of roars are consistent with *A. pigra*'s larger body size and/or larger hyoid apparatus—fundamental frequency and formant dispersion. All members of *Alouatta* have relatively long vocal folds for their body size (more than twice as long as in humans [Dunn et al., 2015; Titze, 1994]), which contributes to their relatively low fundamental frequency (equivalent to animals as large as tigers and reindeer [Dunn et al., 2015]). Here, we found that *A. pigra* have a lower fundamental frequency than *A. palliata*, a size relationship seen in some other mammals [reviewed in Garcia et al., 2013]. Likewise, formant dispersion (the best acoustic feature for differentiating roars in the DFA) was lower in *A. pigra* than in *A. palliata*, consistent with patterns found within other mammal species [e.g., Fitch, 1997; Reby and McComb, 2003; Riede and Fitch, 1999] and supporting the idea that formant dispersion is a direct consequence of the size of the vocal tract [Fitch, 1997]. Although *A. pigra* individuals are both larger in body size and have a larger hyoid apparatus than *A. palliata*, there is some evidence that hyoid differences are more important in this case. Even though body size and formant dispersion are correlated among individuals within howler species [e.g., Dunn et al., 2015], this relationship seems to be obscured by variation in hyoid size among the members of the genus *Alouatta* [Dunn et al., 2015; Youlatos et al., 2015] and only hyoid size correlates with formant dispersion across species [Dunn et al., 2015]. Despite their small body size, the vocal tract lengths (VTL) of members of the *Alouatta* genus are approximately the size of a gorilla's [Schön Ybarra, 1995]. However, our measures of formant dispersion for *A. palliata* and *A. pigra* would predict a VTL of 27 and 45 cm, respectively [using equation in Fitch, 1997], and this is impossible given that the sitting height of each species is only 41 and 48 cm [Kelaita et al., 2011]. Our findings are similar to Dunn and colleagues [2015] who found that the predicted VTL based on

TABLE IV. ANOVA Results of Comparing Roars and Howling Bouts by Context

Variable	Context			Species-context interaction		
	<i>F</i>	<i>P</i>	α^a	<i>F</i>	<i>P</i>	α^a
Bout duration	2.1	0.153	<0.008	0.5	0.468	<0.017
Time spent silent	1.9	0.180	<0.010	0.5	0.467	<0.012
Roaring rate	2.3	0.146	<0.007	5.6	0.027	<0.005
Barking rate	1.6	0.213	<0.012	5.0	0.036	<0.006
Fundamental frequency	0.8	0.382	<0.017	1.0	0.993	<0.012
First formant	0.0	0.871	<0.050	2.7	0.105	<0.006
Highest frequency	6.2	0.016	<0.005	0.0	0.949	<0.025
Formant dispersion	5.0	0.030	<0.006	1.6	0.207	<0.008
Emphasized frequency	0.7	0.409	<0.025	0.0	0.990	<0.050
Emphasized frequency range	8.6	0.005	<0.004	8.2	0.006	<0.004
Harmonic-to-noise ratio	0.8	0.379	<0.017	0.1	0.788	<0.025
Roar duration	0.3	0.559	<0.050	1.6	0.209	<0.010
Number of syllables	2.6	0.115	<0.006	2.6	0.115	<0.007
Longest syllable duration	0.7	0.400	<0.025	0.0	0.952	<0.050
Time at maximum amplitude	1.6	0.204	<0.012	0.1	0.701	<0.017

^aAlpha values for the 11 tests of roars and 4 tests of bouts adjusted using a sequential Bonferroni correction [Holm, 1979].

formant dispersion was longer than the actual VTL measured in *A. caraya* and *A. sara* and they hypothesize that large hyoids may have evolved to enhance the perceived body size. Others [de Boer 2008, 2009; Riede et al., 2008] have used models to simulate howler monkey vocal tracts and demonstrate that size exaggeration might be caused by the additions and shifts in the frequency bands by the hyoid apparatus.

In contrast, neither body size nor hyoid size explains the first formant and the emphasized frequency results, which are both higher in the larger *A. pigra*. In fact, looking across the genus *Alouatta*, there seems to be no relationship between morphology and emphasized frequency [Dunn et al., 2015; Whitehead, 1995; Youlatos et al., 2015]. Instead, higher emphasized frequencies might reflect vocal effort. In mammals with [de Boer, 2009; Riede et al., 2008] and without air sacs (humans: Liénard and Di Benedetto, [1999]; see also Garnier et al., [2008]), vocal effort can shift the first formant and fundamental frequency, with higher subglottal pressure resulting in higher values for one or both. Studies in red deer [Reby and McComb, 2003] and baboons [Fischer et al., 2004] have suggested that such differences among individuals within a species might be caused by amplitude differences and might, therefore, be honest indicators of motivation and/or competitive abilities. Similarly, differences between the two howler species might reliably reflect greater vocal effort invested by the seemingly more aggressive *A. pigra* males. Unlike *A. palliata*, *A. pigra* individuals also modulate amplitude during the longest syllable of their roars (Fig. 2), and perhaps the crescendo functions to highlight vocal effort.

Another acoustic feature potentially linked to vocal effort is the nonlinear phenomenon called deterministic chaos [Wilden et al., 1998]. Chaos results in calls that sound harsh or noisy, a characteristic correlated with high arousal [Morton, 1977]. Such calls are not known to correlate with body size, and are perceived as more threatening or provocative than tonal sounds [e.g., Blumstein and Récapet, 2009; Garcia et al., 2014; Gouzoules et al., 1984; Townsend and Manser, 2011]. Although one possible function of the hyoid apparatus in the *Alouatta* genus is to increase the noisiness—and therefore the competitive effectiveness—of the roars, it is unclear why selection has favored calls in *A. pigra* to be so much noisier and harsher than in *A. palliata*.

One likely possibility is that the marked differences in vocalizations are related to social differences between the two species. Since their recent common ancestor [Cortés-Ortiz et al., 2003], differences in social behavior have arisen [e.g., Ho et al., 2014] that may have, in turn, created different selective environments. *A. pigra* males, living in groups with zero to two other males, appear more adapted to direct, individual physical confrontation with extra-group males. This social system may have meant stronger intrasexual selection for more intimidating vocalizations (e.g., with more chaos and higher emphasized frequencies). In contrast, *A. palliata* live in large, multi-male groups and may be more strongly affected by intragroup competition [Sekulic and Chivers, 1986] that often does not involve roaring. Their roars may instead attract mates to their groups [e.g., Whitehead, 1989]. For example, Fitch and colleagues [2002] suggested that individuals with the ability to control chaos (which is caused

by right and left vocal cords vibrating out of sync) and increase the tonal quality of their calls might convey their superior symmetry and quality to mates and rivals. In support of this hypothesis, only *A. palliata* were observed controlling vocal chaos in our study (see switch from atonal to tonal within Fig. 2) and female immigration into established groups is relatively common in *A. palliata* but rarely observed in *A. pigra* [reviewed in Ho et al., 2014]. In future tests, we will be able to differentiate between intra- and intersexual hypotheses in the two howler species by examining emphasized frequencies and harmonic-to-noise ratios in individuals of known sizes in different contexts, as well as male and female reactions to calls that vary in these traits.

An alternative explanation for the observed interspecific call differences is that they result from selection for transmission of call properties with high fidelity over longer distances (e.g., [Wiley and Richards, 1978]; reviewed in [Ey and Fischer, 2009]). However, genus-wide comparisons found no role for habitat productivity in shaping howler vocalizations [Dunn et al., 2015], and we found no evidence that call transmission is superior in either species (although only playback experiments could test this hypothesis [e.g., Maciej et al., 2011]). Furthermore, it is difficult to find a feature of the relatively similar habitats occupied by these two species [Baumgarten and Williamson, 2007] that might select for such conspicuous vocal differences. However, we cannot completely rule out the influence of the potential habitat differences where the two species originally evolved.

Despite extensive differences, there are some similarities between *A. pigra* and *A. palliata* vocalizations, particularly compared with other members of the genus. For example, the total roar duration was similar between *A. pigra* and *A. palliata*, despite the fact that *A. palliata* break their roars into multiple syllables. The ~2 sec roar durations for both *A. pigra* and *A. palliata* [see also Briseño-Jaramillo et al., 2015; Kitchen, 2000] may represent a physiological maximum based on lung capacity, although it stands in sharp contrast to roars lasting several minutes in South American howler monkeys [da Cunha et al., 2015], some of which are smaller than *A. pigra*. Alternatively, *A. palliata* lack the flexible, lateral air sacs seen in some South American howlers [Youlatos et al., 2015] (no such data exist on *A. pigra*). Perhaps inflatable air sacs contribute to the ability to sustain individual vocalizations [e.g., Hewitt et al., 2002]. Conversely, the overall howling bouts of South American species are substantially shorter and lack the variety of vocal types included in the bouts of both Mesoamerican species [reviewed in da Cunha et al., 2015]. For example, *A. pigra* and *A. palliata* bark at approximately the same rate during howling bouts, yet South American howlers rarely roar and bark within the same bout.

In sum, there is little evidence that the striking differences in *A. pigra* and *A. palliata* vocalizations are a direct result of selection for propagation. Rather, for most features, sexual selection likely shaped vocalizations in different ways. We found that 13 of 15 features varied between the two species and 11 of these differed in a way that may cause *A. pigra* to sound more intimidating than *A. palliata* by exaggerating bout length, roaring rate, roar intensity, vocal effort, nonlinear phenomena, and indicators of larger body size.

We focused here on allopatric populations, far from the small zone of secondary contact in southern Mexico [Cortés-Ortiz et al., 2007]. Given the extent of interspecific differences uncovered, it is perhaps surprising that the two species hybridize at all, yet they do extensively [Cortés-Ortiz et al., 2015]. Armed with a quantitative understanding of the vocal features of the purebred species, we are now in a good position to examine how the two species respond to each other's calls, how calls converge or diverge in sympatry, and how vocalizations contribute to hybridization dynamics.

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REFERENCES

- Altmann J. 1974. Observational study of behavior: sampling methods. *Behaviour* 49:227–266.
- Audacity Team. 2015. Audacity(R): free audio C editor C and recorder, version 2.1.0. Retrieved April 1, 2015 from <http://web.audacityteam.org/copyright>
- Baldwin JD, Baldwin JI. 1976. Vocalizations of howler monkeys (*Alouatta palliata*) in southwestern Panama. *Folia Primatologica* 26:81–108.
- Baumgarten A, Williamson GB. 2007. The distributions of howling monkeys (*Alouatta pigra* and *A. palliata*) in southeastern Mexico and Central America. *Primates* 48: 310–315.
- Blumstein DT, Récapet C. 2009. The sound of arousal: the addition of novel non-linearities increases responsiveness in marmot alarm calls. *Ethology* 115:1074–1081.
- Boersma P, Weenink D. 2013. Praat: doing phonetics by computer, version 5.3.51. Retrieved April 1, 2015 from <http://www.praat.org/>

- Braune P, Schmidt S, Zimmermann E. 2008. Acoustic divergence in the communication of cryptic species of nocturnal primates (*Microcebus* spp.). *BMC Biology* 6:19.
- Briseno-Jaramillo M, Estrada A, Lemasson A. 2015. Individual voice recognition and an auditory map of neighbours in free-ranging black howler monkeys (*Alouatta pigra*). *Behavioral Ecology and Sociobiology* 69:13–25.
- Carpenter CR. 1934. A field study of the behavior and social relations of howling monkeys (*Alouatta palliata*). *Comparative Psychology Monographs* 10:1–168.
- Charlton BD, Zhihe Z, Snyder RJ. 2009. The information content of giant panda, *Ailuropoda melanoleuca*, bleats: acoustic cues to sex, age and size. *Animal Behaviour* 78: 893–898.
- Chivers DJ. 1969. On the daily behaviour and spacing of howling monkey groups. *Folia Primatologica* 10:48–102.
- Cortés-Ortiz L, Agostini I, Aguiar LM, et al. 2015. Hybridization in howler monkeys: current understanding and future directions. In: Kowalewski MM, Garber PA, Cortés-Ortiz L, Urbani B, Youlatos D, editors. *Howler monkeys: adaptive radiation, systematics, and morphology*. New York: Springer Press. p 107–132.
- Cortés-Ortiz L, Bermingham E, Rico C, Rodriguez-Luna E, Sampaio I, Ruiz-García M. 2003. Molecular systematics and biogeography of the Neotropical monkey genus, *Alouatta*. *Molecular Phylogenetics and Evolution* 26:64–81.
- Cortés-Ortiz L, Duda TJ, Jr, Canales-Espinosa F, et al. 2007. Hybridization in large-bodied New World primates. *Genetics* 176:2421–2425.
- da Cunha RGT, de Oliveira DAG, Holzmann I, Kitchen DM. 2015. Production of loud and quiet calls in howler monkeys. In: Kowalewski MM, Garber PA, Cortés-Ortiz L, Urbani B, Youlatos D, editors. *Howler monkeys: adaptive radiation, systematics, and morphology*. New York: Springer Press. p 337–368.
- de Boer B. 2009. Acoustic analysis of primate air sacs and their effect on vocalization. *Journal of the Acoustical Society of America* 126:3329–3343.
- de Boer B. 2008. The acoustic role of supralaryngeal air sacs. *Journal of the Acoustical Society of America* 123: 3732–3733.
- de Kort SR, ten Cate FC. 2004. Repeated decrease in vocal repertoire size in *Streptopelia* doves. *Animal Behaviour* 67:549–557.
- Darwin C. 1871. *The descent of man and selection in relation to sex*. London: John Murray.
- Dunn JC, Halenar LB, Davies TG, et al. 2015. Evolutionary trade-off between vocal tract and testes dimensions in howler monkeys. *Current Biology* 25:2839–2844.
- Ey E, Pfefferle D, Fischer J. 2007. Do age- and sex-related variations reliably reflect body size in non-human primate vocalizations? A review. *Primates* 48:253–267.
- Ey E, Fischer J. 2009. The “acoustic adaptation hypothesis”—a review of the evidence from birds, anurans and mammals. *Bioacoustics* 19:21–48.
- Fitch WT. 1997. Vocal tract length and formant frequency dispersion correlate with body size in rhesus macaques. *Journal of the Acoustical Society of America* 102:1213–1222.
- Fitch WT, Fritz JB. 2006. Rhesus macaques spontaneously perceive formants in conspecific vocalizations. *Journal of the Acoustical Society of America* 120:2132–2141.
- Fitch WT, Hauser MD. 2003. Unpacking “honesty”: vertebrate vocal production and the evolution of acoustic signals. In: Simmons A, Fay RR, Popper AN, editors. *Acoustic communication*. New York: Springer Press. p 65–137.
- Fitch WT, Neubauer J, Herzel H. 2002. Calls out of chaos: the adaptive significance of nonlinear phenomena in mammalian vocal production. *Animal Behaviour* 63:407–418.
- Fichtel C. 2014. Acoustic differences in loud calls of Decken’s and crowned sifakas (*Propithecus deckenii* and *P. coronatus*) at two sites in Madagascar. *Primate Conservation* 28:85–91.
- Fischer J, Kitchen DM, Seyfarth RM, Cheney DL. 2004. Baboon loud calls advertise male quality: acoustic features and their relation to rank, age, and exhaustion. *Behavioral Ecology and Sociobiology* 56:140–148.
- Gamba M, Giacoma C. 2008. Subspecific divergence in the black lemur’s low-pitched vocalizations. *Open Acoustics Journal* 1:49–53.
- Garcia M, Charlton BD, Wyman MT, Fitch WT, Reby D. 2013. Do red deer stags (*Cervus elaphus*) use roar fundamental frequency (F0) to assess rivals? *PLoS ONE* 8:e83946.
- Garcia M, Wyman MT, Charlton BD, Fitch WT, Reby D. 2014. Response of red deer stags (*Cervus elaphus*) to playback of harsh versus common roars. *Naturwissenschaften* 101: 851–854.
- Garnier M, Wolfe J, Henrich N, Smith J. 2008. Interrelationship between vocal effort and vocal tract acoustics: a pilot study. *Interspeech* 2008:2302–2305.
- Ghazanfar AA, Turesson HK, Maier JX, et al. 2007. Vocal-tract resonances as indexical cues in rhesus monkeys. *Current Biology* 17:425–430.
- Glander KE. 1992. Dispersal patterns in Costa Rican mantled howling monkeys. *International Journal of Primatology* 13:415–436.
- Gouzoules S, Gouzoules H, Marler P. 1984. Rhesus monkey (*Macaca mulatta*) screams: representational signalling in the recruitment of agonistic aid. *Animal Behaviour* 32: 182–193.
- Hewitt GP, MacLarnon A, Jones KE. 2002. The functions of laryngeal air sacs in primates: a new hypothesis. *Folia Primatologica* 73:70–94.
- Ho L, Cortés-Ortiz L, Dias PAD, et al. 2014. Effect of ancestry on behavioral variation in two species of howler monkeys (*Alouatta pigra* and *A. palliata*) and their hybrids. *American Journal of Primatology* 76:855–867.
- Holm S. 1979. A simple sequentially rejective multiple test procedure. *Scandinavian Journal of Statistics* 6:65–70.
- Hopkins ME. 2013. Relative dominance and resource availability mediate mantled howler (*Alouatta palliata*) spatial responses to neighbors’ loud calls. *International Journal of Primatology* 34:1032–1054.
- Horwich RH, Brockett RC, Jones CB. 2000. Alternative male reproductive behaviors in the Belizean black howler monkey (*Alouatta pigra*). *Neotropical Primates* 8:95–98.
- Huber SK, Podos J. 2006. Beak morphology and song features covary in a population of Darwin’s finches (*Geospiza fortis*). *Biological Journal of the Linnean Society* 88:489–498.
- Irisarri I, Vences M, San Mauro D, Glaw F, Zardoya R. 2011. Reversal to air-driven sound production revealed by a molecular phylogeny of tongueless frogs, family Pipidae. *BMC Evolutionary Biology* 11:114.
- IUCN. 2015. The IUCN red list of threatened species, version 2015-3. Retrieved September 9, 2015 from <http://www.iucnredlist.org>
- Janik VM, Slater PJ. 1997. Vocal learning in mammals. *Advances in the Study of Behaviour* 26:59–100.
- Kelaita M, Cortés-Ortiz L. 2013. Morphology of genetically-confirmed *Alouatta pigra* × *A. palliata* hybrids from a natural hybrid zone in Tabasco, Mexico. *American Journal of Physical Anthropology* 150:223–234.
- Kelaita MA, Dias PAD, Aguilar-Cucurachi MS, Canales-Espinosa D, Cortés-Ortiz L. 2011. Impact of intrasexual selection on sexual dimorphism and testes size in the Mexican howler monkeys *Alouatta palliata* and *A. pigra*. *American Journal of Physical Anthropology* 146:179–187.
- Kitchen DM. 2000. Aggression and assessment among social groups of Belizean black howler monkeys (*Alouatta pigra*) [dissertation]. St. Paul (MN): University of Minnesota. p 286. UMI Dissertation Express, Ann Arbor, MI: 9983584.
- Kitchen DM, da Cunha RGT, Holzmann I, de Oliveira DAG. 2015. Function of loud calling in howler monkeys. In: Kowalewski MM, Garber PA, Cortés-Ortiz L, Urbani B,

- Youlatos D, editors. Howler monkeys: adaptive radiation, systematics, and morphology. New York: Springer Press. p 369–402.
- Liénard JS, Di Benedetto MG. 1999. Effect of vocal effort on spectral properties of vowels. *Journal of the Acoustical Society of America* 106:411–422.
- Maciej P, Fischer J, Hammerschmidt K. 2011. Transmission characteristics of primate vocalizations: implications for acoustic analyses. *PLoS ONE* 6:e23015.
- Masters JC. 1991. Loud calls of *Galago crassicaudatus* and *G. garnettii* and their relation to habitat structure. *Primates* 32:153–167.
- May-Collado LJ, Agnarsson I, Wartzok D. 2007. Reexamining the relationship between body size and tonal signals frequency in whales: a comparative approach using a novel phylogeny. *Marine Mammal Science* 23:524–552.
- McComb K, Semple S. 2005. Coevolution of vocal communication and sociality in primates. *Biology Letters* 1:381–385.
- Mitani JC, Stuht J. 1998. The evolution of nonhuman primate loud calls: acoustic adaptation for long-distance transmission. *Primates* 39:171–182.
- Morton ES. 1977. On the occurrence and significance of motivation-structural rules in some bird and mammal sounds. *American Naturalist* 111:855–869.
- Price JJ, Lanyon SM. 2002. Reconstructing the evolution of complex bird song in the oropendolas. *Evolution* 56:1514–1529.
- Reby D, McComb K. 2003. Anatomical constraints generate honesty: acoustic cues to age and weight in the roars of red deer stags. *Animal Behaviour* 65:519–530.
- Reby D, McComb K, Cargnelutti B, et al. 2005. Red deer stags use formants as assessment cues during intrasexual agonistic interactions. *Proceedings of the Royal Society of London B: Biological Sciences* 272:941–947.
- Riede T, Fitch WT. 1999. Vocal tract length and acoustics of vocalization in the domestic dog, *Canis familiaris*. *Journal of Experimental Biology* 202:2859–2869.
- Riede T, Herzog H, Hammerschmidt K, Brunnerberg L, Tembrock G. 2001. The harmonic-to-noise-ratio applied to dog barks. *Journal of the Acoustical Society of America* 110:2191–2197.
- Riede T, Tokuda IT, Munger JB, Thomson SL. 2008. Mammalian laryngeal air sacs add variability to the vocal tract impedance: physical and computational modeling. *Journal of the Acoustical Society of America* 124:634–647.
- Ryan SJ, Starks PT, Milton K, Getz WM. 2008. Intersexual conflict and group size in *Alouatta palliata*: a 23-year evaluation. *International Journal of Primatology* 29:405–420.
- SchönYbarra MA. 1995. A comparative approach to the nonhuman primate vocal tract: implications for sound production. In: Zimmerman E, Newman JD, editors. *Frontiers in primate vocal communication*. New York: Plenum Press. p 185–198.
- Sekulic R, Chivers DJ. 1986. The significance of call duration in howler monkeys. *International Journal of Primatology* 7:183–190.
- Stachowicz JB, Vannoni E, Pitcher BJ, et al. 2014. Acoustic divergence in the rut vocalizations of Persian and European fallow deer. *Journal of Zoology* 292:1–9.
- Staicer CA. 1996. Acoustical features of song categories of the Adelaide's warbler (*Dendroica adelaidae*). *The Auk* 113: 771–783.
- Thinh VN, Hallam C, Roos C, Hammerschmidt K. 2011. Concordance between vocal and genetic diversity in crested gibbons. *BMC Evolutionary Biology* 11:36.
- Titze I. 1994. *Principles of voice production*. New Jersey: Prentice Hall.
- Tokuda I, Riede T, Neubauer J, Owren MJ, Herzog H. 2002. Nonlinear analysis of irregular animal vocalizations. *Journal of the Acoustical Society of America* 111:2908–2919.
- Townsend SW, Manser MB. 2011. The function of nonlinear phenomena in meerkat alarm calls. *Biology Letters* 7: 47–49.
- Van Belle S. 2015. Female participation in collective group defense in black howler monkeys (*Alouatta pigra*). *American Journal of Primatology* 77:595–604.
- Van Belle S, Estrada A, Garber PA. 2013. Spatial and diurnal distribution of loud calling in black howlers (*Alouatta pigra*). *International Journal of Primatology* 34:1209–1224.
- Van Belle S, Estrada A, Strier KB. 2008. Social relationships among male *Alouatta pigra*. *International Journal of Primatology* 29:1481–1498.
- Whitehead JM. 1989. The effect of the location of a simulated intruder on responses to long-distance vocalizations of mantled howling monkeys, *Alouatta palliata palliata*. *Behavior* 108:73–103.
- Whitehead JM. 1995. Vox Alouattinae: a preliminary survey of the acoustic characteristics of long-distance calls of howling monkeys. *International Journal of Primatology* 16:121–144.
- Whittaker DJ, Morales JC, Melnick DJ. 2007. Resolution of the Hylobates phylogeny: congruence of mitochondrial D-loop sequences with molecular, behavioral, and morphological data sets. *Molecular Phylogenetics and Evolution* 45:620–628.
- Wich SA, Nunn CL. 2002. Do male “long-distance calls” function in mate defense? A comparative study of long-distance calls in primates. *Behavioral Ecology and Sociobiology* 52:474–484.
- Wiley RH, Richards DG. 1978. Physical constraints on acoustic communication in the atmosphere: implications for the evolution of animal vocalizations. *Behavioral Ecology and Sociobiology* 3:69–94.
- Wilden I, Herzog H, Peters G, Tembrock G. 1998. Subharmonics, biphonation, and deterministic chaos in mammal vocalization. *Bioacoustics* 9:171–196.
- Youlatos D, Couette S, Halenar LB. 2015. Morphology of howler monkeys: a review and quantitative analyses. In: Kowalewski MM, Garber PA, Cortés-Ortiz L, Urbani B, Youlatos D, editors. *Howler monkeys: adaptive radiation, systematics, and morphology*. New York: Springer Press. p 133–176.

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