

# Temporal but Not Acoustic Plasticity in Hybrid Howler Monkey (*Alouatta palliata × A. pigra*) Loud Calls

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**Abstract** The relatively fixed vocal structure of nonhuman primates stands in stark contrast to humans. However, primate vocal–plasticity studies are particularly limited by ethical and logistic constraints. As an alternative approach, we take advantage of a confirmed howler hybrid zone (*Alouatta palliata* × *A. pigra*) to compare the effects of genetic ancestry and experience on vocal variation. Deviations from a tight phenotype–ancestry correlation can indicate potential plasticity. We also tested whether temporal features (e.g., syllable number, calling rate) show more plasticity than acoustic features (e.g., peak frequency, bandwidth) which might be morphologically constrained. Using 29 microsatellite markers, most hybrid male subjects fell at the extremes of the genetic ancestry distribution, consistent with the entire population's distribution. We then analyzed 182 howling bouts and 231 loud call recordings from 33 male hybrid and purebred subjects from sympatric and allopatric populations. Acoustic features of hybrid calls clustered with calls from genetically similar purebred males, and calls

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from the only genetically intermediate hybrid in our sample fell between the two acoustic extremes, suggesting a strong effect of ancestry. However, temporal features tended to converge in sympatry (e.g., vocalizations from purebred *A. palliata* in the hybrid zone were more *pigra*-like than vocalizations from allopatric *A. palliata*, and indistinguishable from sympatric *palliata*-like and intermediate hybrid vocalizations). Our study shows that, at least for temporal features, primate vocal plasticity can extend beyond intrapopulation variation, consistent with a growing body of research suggesting that primate vocalizations may be more flexible than traditionally assumed.

Keywords Genetic ancestry  $\cdot$  Howling bouts  $\cdot$  Production learning  $\cdot$  Roaring rate  $\cdot$  Usage learning  $\cdot$  Vocal convergence

### Introduction

Humans are an extreme example of vocal production learning and unusual among mammals, where vocal learning has been demonstrated in only a few taxa (bats: Knörnschild 2014; Prat *et al.* 2015; cetaceans: Janik 2014; Tyack and Sayigh 1997; elephants: Poole *et al.* 2005; Stoeger and Manger 2014; pinnipeds: Reichmuth and Casey 2014). Somewhat surprisingly, this list of mammals does not include our closest relatives, the nonhuman primates. Among primates, there is little evidence for novel call development or ontogenetic changes in established vocalizations that could not be attributed to maturation, despite acoustic deprivation (Hammerschmidt *et al.* 2001), isolation (Hammerschmidt *et al.* 2000), and cross-fostering experiments (Owren *et al.* 1993). However, recent studies in birds have shown that vocal learning is not an "all or none" phenomenon (Petkov and Jarvis 2012), and perhaps the same is true in mammals (e.g., Tyack 2008). Indeed, despite a lack of novel sound production, the temporal and acoustic features of nonhuman primate vocalizations do have flexibility (Seyfarth and Cheney 2010a).

Thus, it may be more effective to search for evidence of flexibility in nonhuman primate vocalizations within fairly fixed situations (e.g., Ey and Fischer 2011; Levréro *et al.* 2015). For example, vocal similarities are greater within than between groups or populations in several species (e.g., tamarins, *Saguinus labiatus labiatus*: Maeda and Mastataka 1987; chimpanzees, *Pan troglodytes*: Crockford *et al.* 2004; Marshall *et al.* 1999; Mitani *et al.* 1992, 1999; Barbary macaques, *Macaca sylvanus*: Fischer *et al.* 1998; pygmy marmoset, *Callithrix pygmaea*: de la Torre and Snowdon 2009). Additionally, a relationship has been found between familiarity and vocal features (chimpanzees: Mitani and Gros-Louis 1998; Campbell's monkey, *Cercopithecus campbelli campbelli*: Lemasson *et al.* 2011; but see mandrills, *Mandrillus sphinx*: Levréro *et al.* 2015). However, the influence of genetics is a major confound in many of these studies, and only a few have incorporated relatedness measures to address the problem ( e.g., Crockford *et al.* 2004; Lemasson *et al.* 2011; Levréro *et al.* 2015).

Several studies show signs of social feedback as vocalizations converge over time among introduced animals (e.g., marmosets: Elowson and Snowdon 1994; Snowdon and Elowson, 1999; Wied's marmosets, *Callithrix kuhlii*: Rukstalis *et al.* 2003; and chimpanzees: Marshall *et al.* 1999; Watson *et al.* 2015) or during vocal exchanges (e.g., Japanese macaques, *Macaca fuscata*: Sugiura 1998; Diana monkeys, *Cercopithecus diana*: Candiotti *et al.* 2012; and common marmosets, *Callithrix jacchus*: Chow *et al.* 2015).

Furthermore, baby common marmoset vocalizations develop at different rates based on contingent vocal feedback from their parents (Takahashi *et al.* 2015). However, although important for establishing that primates have vocal flexibility, these studies tell us little about plasticity beyond differences that exist in the range of intraspecific variation.

Hybrid zones are ideal for examining vocal plasticity in more distinct, species-level contexts. Given the broad array of phenotypes living within acoustic range, hybrid zones are particularly useful for teasing apart the influence of genetic ancestry and exposure on vocalizations. A strong correlation between ancestry and vocal phenotype was found in the only three species of hybridizing mammals with vocalization data: gibbons (*Hylobates pileatus* × *H. lar*: Brockelman and Schilling 1984; Geissmann 1984), deer (*Cervus elaphus* × *C. nippon*: Long *et al.* 1998), and fur seals (*Arctocephalus tropicalis* × *A. gazella/A. forsteri*: Page *et al.* 2001). In contrast, captive hybrid squirrel monkeys produce vocalizations like those of their mothers, suggesting either an influence of exposure or a maternal genetic effect (Newman and Symmes 1982). Thus, to date, evidence of vocal variation from primate hybrid zones is too limited for accurate interpretation.

To better understand the extent of primate vocal flexibility, we conducted a genetic and vocal study of free-ranging hybrid howlers (Alouatta palliata × A. pigra) in Mexico. In addition to genetic (Cortés-Ortiz et al. 2007), morphological (Cortés-Ortiz et al. 2015; Kelaita and Cortés-Ortiz 2013), and social differences (Ho et al. 2014), these species have very distinct vocalizations, particularly in terms of the loud calls that are the hallmark of the genus (Kitchen et al. 2015). Roar vocalizations are the loudest, most salient howler monkey calls and in purebred A. pigra these typically comprise two syllables, with the longest syllable reaching a crescendo in increasing amplitude (Bergman et al. 2016). In contrast, the roar vocalizations in purebred A. palliata are typically multiple short syllables with constant amplitude (Bergman et al. 2016). No one has yet described the vocalizations of these two species in sympatry, where ongoing hybridization has produced a patchwork of pure and admixed individuals living in acoustic contact (Cortés-Ortiz et al. 2007). Although aspects of social behavior correlate strongly with ancestry despite geographic overlap in the hybrid zone (even in the same forest fragment: Ho et al. 2014), we do not yet know how call variation maps onto genetic ancestry and proximity.

As suggested in gibbons (Brockelman and Schilling 1984; Geissmann 1984), the only other primate hybrid system tested for vocal variation, we hypothesized genetic background would determine vocal structure. Using a panel of 29 microsatellite markers to assess ancestry (Cortés-Ortiz *et al.* 2015), we predicted we would find a strong phenotype–ancestry correlation among admixed and pure (both sympatric and allopatric) individual howlers. Alternatively, if results indicated deviations from a strong genetic correlation, we hypothesized that one of two patterns would emerge: divergence or convergence. Although divergence in sympatry can be an emergent property of developmental processes such as learning bias for novelty ("peak shift": ten Cate and Rowe 2007), it is more typically driven by reinforcement of conspecific mating when hybridization is maladaptive (reviewed in: Grant and Grant 1997; Noor 1999; Pfennig and Pfennig 2009). Such character displacement has been reported in some birds (e.g., antbirds, Thamnophilidae family: Seddon 2005; tinkerbirds, *Pogoniulus subsulphureus* 

and *P. bilineatus*: Kirschel *et al.* 2009). Convergence in sympatry, in contrast, suggests a social component to vocalizations, as seen in vocal-learning birds (e.g., warblers, *Hippolais polyglotta* and *H. icterina*: Secondi *et al.* 2003; flycatchers, *Ficedula hypoleuca* and *F. albicollis*: Haavie *et al.* 2004; ringneck parrots, *Platycercus zonarius* spp.: Baker 2008; warblers, *Oporornis tolmiei* and *O. philadelphia*: Kenyon *et al.* 2011).

We also hypothesized (based on Janik and Slater 1997, 2000) that temporal features would be more flexible than acoustic features. Of the three components of sound production, respiration is most likely to affect temporal features and is under direct motor control by the caller (Janik and Slater 1997, 2000), which makes the influence of learning more plausible. Conversely, the larynx ("source") and vocal tract ("filter") control acoustic features (cf. Riede *et al.* 2005) and are more morphologically constrained, making it harder to adjust many acoustic properties of a call (Janik and Slater 1997, 2000; Lameira *et al.* 2014). We therefore tested the prediction that temporal features (e.g., syllable number, calling bout duration) of howler vocalizations would show a weaker relationship to ancestry than acoustic features (e.g., peak frequency, bandwidth).

### Methods

#### **Study Subjects**

We collected recordings of hybrid *A. palliata* × *A. pigra* hybrid howlers during one sampling expedition (June 2008) and during >1068 h of behavioral observation (February–July 2011 and February–June 2012) on 12 groups in a confirmed hybrid zone (Cortés-Ortiz *et al.* 2007, 2015), in the Mexican state of Tabasco (Fig. 1). We have intermittently followed these groups since 2007; thus, we are able to distinguish individuals within and between groups based on characteristic fur/skin color, scarring patterns, uniquely colored ankle bracelets, and a photographic record of some individuals from prior capture (e.g., Cortés-Ortiz *et al.* 2015; Ho *et al.* 2014). Because it is not always possible to discriminate between purebred and admixed individuals in the hybrid zone (Kelaita and Cortés-Ortiz 2013) and because our analyses of molecular markers were completed after onset of the current study, we chose focal groups containing adult members that could be placed into one of two phenotypic categories: more similar to either *A. pigra* (hereafter, *pigra*-like) or *A. palliata* (hereafter, *palliata*-like).

The hybrid zone is a heterogeneous mix of small forest patches surrounded by ranches and villages. Although only one to six groups occupy each forest fragment, all study subjects could hear loud calls from other subjects of both phenotypes (Cortés-Ortiz, Bergman, and Kitchen *unpubl. data*). Additionally, howlers move between fragments by descending to the ground (Bicca-Marques and Calegaro-Marques 1995), and our groups occasionally encounter solitary individuals.

To understand how well estimates of genetic contribution from each parental species correlated with vocal characteristics, we compared vocalizations of hybrid zone subjects to those of allopatric purebred individuals (Table I) using data from a prior publication (Bergman *et al.* 2016). These vocalizations were recorded during >700 h of behavioral observations on purebred *A. pigra* in Campeche



Fig. 1 Distribution of *A. palliata*, *A. pigra*, and their hybrids in southern Mexico (based on Cortés-Ortiz *et al.* 2015; IUCN 2017), along with general locations of study groups contributing roar vocalizations: allopatric locations of *A. palliata* (La Flor and Jalapilla, Veracruz) and *A. pigra* (El Tormento, Campeche) from Bergman *et al.* (2016). Inset shows groups sampled in the hybrid zone in 2008 and 2011–2012: 1) Calicanto, 2) Minto, 3) Vázquez, 4) Diecisiete, 5) Dago, 6) Roco, 7) Doce, 8) Acahual, 9) Puente, 10) Félix, 11) Consuelo, 12) Flores.

(February–March and June–August 2011) and purebred *A. palliata* in Veracruz (February–May 2012; Fig. 1).

	Allopatric (Veracruz)	Sympatric (Tabasco)	/hybrid			Allopatric (Campeche)
	Purebred A. palliata	Purebred A. palliata	A. palliata- like hybrid	Intermediate hybrid	A. pigra- like hybrid	Purebred A. pigra
Bout duration in seconds (N=182  bouts)	31/3	30/3	42/5	0/0	51/7	28/8
Roaring rate per minute $(N=65 \text{ bouts})$	10/5	8/3	10/5	1/1	22/6	14/7
% Time silent in bout ( $N = 65$ bouts)	10/5	8/3	10/5	1/1	22/6	14/7
Features of roars $(N=231 \text{ roars})$	23/10/6/4	26/6/3/3	45/14/7/5	29/1/1/1	72/28/9/6	36/14/7/7

**Table I** Total sample sizes used for analysis of howling bouts (N= bouts/groups) and roar vocalizations (N= calls/bouts/males/groups) to determine differences between categories of howlers from our 2008 and 2011–2012 study in southern Mexico

**Data Availability** The datasets analyzed during the current study are available from the corresponding author on reasonable request.

### Individual Genetic Admixture in the Hybrid Zone

As part of an ongoing genetics project across the hybrid zone (e.g., Cortés-Ortiz *et al.* 2007, 2015; *unpubl. data*), members of our team collected blood samples from 254 howlers between 1998 and 2012 (Fig. 2). Using techniques described elsewhere (Cortés-Ortiz *et al.* 2015; *unpubl. data*), our team calculated a hybrid index (HI, Buerkle 2005) for each sample based on 29 microsatellite markers (28 autosomal and one on the X chromosome). Our results demonstrated that some individuals living in the hybrid zone are "pure" *A. palliata* (HI: 0.00) or "pure" *A. pigra* (HI: 1.00), with most remaining hybrids (HI: 0.01–0.99) biased toward each end of the spectrum, i.e., strongly *palliata*-like or strongly *pigra*-like hybrids, due to multiple generations of backcrossing. Only a few individuals (and only a single male) captured in the population were genetically intermediate hybrids (HI: ca. 0.50).

### **Howling Bout Analysis**

During behavioral follows, observers used all-occurrence sampling (Altmann 1974) to record vocalizations and relevant data including caller identity from all loud calling "bouts" (strings of roars, barks, and other loud vocalizations, following Bergman *et al.* 2016). Two calling bouts in the same group were considered independent if separated by  $\geq 10$  min of silence from all group members (Hopkins 2013; Van Belle *et al.* 2013). We



**Fig. 2** The hybrid index distribution of 254 pure and admixed *Alouata palliata* and *A. pigra* individuals captured and sampled in a genetic study in a hybrid zone in Tabasco, Mexico (adapted from *unpubl. data*). Arrows indicate the hybrid index of 20 males that produced roar vocalizations in 2008 and 2011–2012 that were of high enough quality for inclusion in our acoustic analysis (numbers above each arrow represent the number of males with that hybrid index).

recorded vocalizations with Sennheiser ME66 directional microphones (Wennebostel, Germany) and Marantz PMD660 compact flash recorders (Tokyo, Japan).

Howling bouts of purebred, allopatric howler populations differ in three ways (Bergman et al. 2016): A. palliata have shorter overall howling bouts, slower roaring rates, and spend more time silent during a bout than A. pigra. To determine how well ancestry predicts these temporal features, we examined bouts in hybrid zone individuals and then compared them to bouts from purebred individuals of the same phenotype (Table I). First, we measured duration of all howling bouts excluding breaks of >1 min (Kitchen 2000; Van Belle et al. 2013). Second, we measured roaring rate. Roars are the loudest and longest individual calls produced during loud-call bouts (Fig. 3). A 3-min sample was taken from the first half of each bout (mean: 10% into the bout; range: 0-42%), typically starting at the first clearly recorded roar. Because calling rates tend to slow toward the end of a bout in both species, using 3 min of calling from early in the bout ensures a comparable sample and avoids confounding overall rate measures with bout duration (Cortés-Ortiz, Bergman, and Kitchen unpubl. data). Only bouts with minimal overlap among callers could be measured accurately (Table I). Third, from these 3-min samples, we calculated the percent of time spent silent rather than loud calling (loud calling periods are a subsection of the howling bout made up of roars, barks, other loud vocalizations, and pauses <5 s: Kitchen 2000). Unlike for roar analyses, we scored the three howling bout measures by group (following Bergman et al. 2016). Two of our hybrid zone groups contained both a purebred A. palliata (HI: 0) and a *palliata*-like hybrid male (HI: 0.05 or 0.08). Whenever the purebred male was part of a chorus or the sole contributor, we labeled the bout after him to improve sample-size spread between howler categories. However, results did not change if we labeled those choruses as coming from the *palliata*-like hybrid male.

### **Roar Vocalization Analysis**

We used Audacity software (Audacity Team 2015) to isolate individual roars (Fig. 3) from howling bouts as .wav audio files. We extracted calls throughout the beginning, middle, and end of the highest quality bouts (mean: 323 s into bout; range: 2–5524 s). Calls sampled within the same bout were a mean of 139 s apart (range: 3–3146 s). Roars selected for acoustic analysis had minimal background noise, no call overlap, unambiguous caller identity, and known hybrid index for the caller (Table I).

We digitized roars at a sample rate of 44.1 kHz (16-bit resolution, mono format) and analyzed using Praat software (Boersma and Weenink, 2013). We created spectrograms



**Fig. 3** Example oscillograms (top pane: time vs. amplitude) and spectrograms (bottom pane: frequency vs. time; each pane is 3.56 s; dark bands represent frequencies with high intensity) of single roars from a purebred *A. palliata* (far left; HI: 0.00), *palliata*-like hybrid (HI: 0.05), intermediate hybrid (center; HI: 0.46), *pigra*-like hybrid (HI: 0.87), and purebred *A. pigra* (far right; HI: 1.00) that we recorded in southern Mexico in 2008 and 2011–2012.

(Fig. 3) with fast Fourier transformations, a Gaussian window shape, a 0.1 s window length, a 50 dB dynamic range, a maximum formant of 4000 Hz, and resolutions of 1500 time steps and 250 frequency steps. We set the pitch function in Praat to cross-correlation when calculating harmonic-to-noise ratio and to autocorrelation for all other analyses. To improve accuracy of fundamental frequency calculations, 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).

From roars, we measured the following four temporal features (following Bergman et al. 2016): 1) duration of the longest syllable; 2) total number of syllables (counting each inhaled and exhaled portion of a roar separately); 3) percent time at maximum amplitude (portion of syllable with darkest frequency bands and an intensity contour line that oscillates around peak intensity: Bergman et al. 2016); and 4) call duration (including all inhaled and exhaled syllables). We also measured seven acoustic features of roars based on those found to vary in allopatric purebred populations (Bergman et al. 2016): 1) fundamental frequency (base vibration rate of vocal cords); 2) first formant (lowest prominent frequency band: Dunn et al. 2015; cf. Fitch and Fritz 2006); 3) highest frequency band (eighth formant in pigra-like intermediate males and sixth formant in *palliata*-like males: Dunn et al. 2015); 4) formant dispersion (mean distance between the lowest six formant frequencies: Dunn et al. 2015; Fitch 1997); 5) emphasized frequency (frequency with highest relative energy: Whitehead 1995); 6) emphasized frequency range (calls with more of the nonlinear phenomenon called "chaos" should have energy distributed across a broader bandwidth: Fitch et al. 2002; we measured bandwidth of frequencies that contributed >60% of maximum energy in spectral slices); 7) harmonic-to-noise ratio (relative energy given to tonal vs. atonal noise, with low values indicating noisier/atonal/chaotic calls: Riede et al. 2001).

#### **Statistical Analysis**

We used Q–Q plots to ensure data were normally distributed. In the case of howling bout duration, data were normally distributed after they were natural-log transformed.

To compare the temporal characteristics of howling bouts (i.e., bout duration, roaring rate, and percent time spent silent) we used a linear mixed model (LMM), which allows repeated tests on the same individuals. The random factor in the model was group identity and the fixed factor was howler category (i.e., allopatric purebred *A. palliata* roars; sympatric purebred *A. palliata*, *palliata*-like, intermediate hybrids, and *pigra*-like individuals; and allopatric purebred *A. pigra*).

To identify which of the multiple characteristics most clearly differentiate roars among the six howler categories, we performed stepwise discriminant function analyses (DFA) separately on temporal and acoustic features. Running DFA on just hybrid zone individuals resulted in the same patterns as those using only allopatric populations (Bergman *et al.* 2016), so we combined all six categories. We entered variables in the stepwise DFA using the criterion of minimizing Wilks' lambda (partial *F* to enter=3.84, partial F to remove=2.71) and applied a leave-one-out cross-validation (i.e., jackknife), which subsamples the data to test classification robustness.

To examine intercategory differences in discriminant scores, we used an LMM with caller and group identity as random factors and howler category and hybrid index as fixed factors. We also used an analysis of variance (ANOVA) to compare intramale coefficients of variation (CV%: standard deviation/mean  $\times$  100) among howler categories and between acoustic and temporal features.

All analyses were two-tailed and performed in SPSS version 24 (IBM 2016). We set  $\alpha$  at 0.05. For all LMMs, we used estimated marginal means (EMMs: mean responses adjusted for other variables in the model; raw EMM values provided in Electronic Supplementary Material [ESM] Table SI) for post hoc, pairwise comparisons, and we calculated Cohen's *d* statistics (Nakagawa and Cuthill 2007) to ensure that all significant pairwise results reported had at least a moderate effect size (d > 0.50; Cohen 1992). We used a likelihood ratio test (LRT: Dunteman and Ho 2006) to ensure that the addition of fixed effects to our LMM was an improvement over a model based on just intercept and random effects.

# **Ethical Note**

Our 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). Our research adhered to all USA and Mexican legal requirements.

The authors declare that they have no conflict of interest.

# Results

### **Genetic Data**

In all cases, the hybrid index confirmed our a priori classification of individual phenotypes based on morphological and behavioral characteristics. Although we chose individuals for the current study before the completion of this genetic analysis, subjects (including a genetically intermediate subject) are representative of the global distribution of hybrid individuals in the hybrid zone (Fig. 2). However, data that follow represent six different howler categories instead of seven because we did not get recordings from any pure male *A. pigra* living in the hybrid zone.

### **Differences in Howling Bouts**

An LMM with howler category as the fixed effect (full LMM:  $F_{1,13,1} = 3373.98$ , P < 0.001) was better at explaining howling bout results than a model based on only intercept and random effects (LRT: -20.0, P < 0.001). Within the full model, we found an overall difference in bout duration between howler categories (LMM:  $F_{4,20.5} = 3.45$ , P = 0.026, N = 182 bouts; Table II). Specifically, *pigra*-like males converged with *A. palliata* and *palliata*-like males in the hybrid zone; the *pigra*-like individuals had shorter howling bouts than allopatric *A. pigra* (EMM: P = 0.038, d = 0.68) and did not differ from *palliata*-like hybrids (EMM: P = 0.178) or from either sympatric (EMM: P = 0.706) or allopatric purebred *A. palliata* (EMM: P = 0.204). Allopatric *A. pigra* had

Feature Allopatric Purebred						
Purebred	tric (Veracruz)	Sympatric/hybrid z	one (Tabasco)			Allopatric (Campeche)
	ed A. <i>palliata</i>	Purebred A. palliata	<i>A. palliata</i> -like hybrid	Intermediate hybrid	<i>A. pigra</i> -like hybrid	Purebred A. pigra
Temporal features of howling bouts						
Natural log of bout duration (s) $5.8 \pm 0.2$	.2	$6.0\pm0.2$	$5.8\pm0.2$	n/a	$6.2\pm0.2$	$6.8\pm0.1$
Roaring rate (roars/min) $2.0 \pm 0.5$	S	$1.8\pm0.4$	$1.7 \pm 0.4$	4.3	$4.3\pm0.4$	$4.5 \pm 0.6$
Silent periods (%) $48.6 \pm 8.1$	8.1	$32.2 \pm 5.1$	$45.4\pm8.2$	50.3	$21.7 \pm 5.0$	$5.5 \pm 2.5$
Temporal features of roar vocalizations						
Duration longest syllable (s) $0.7 \pm 0.0$	0.	$1.0\pm0.0$	$1.0\pm0.1$	$1.0\pm0.0$	$2.1\pm0.1$	$1.8\pm0.1$
Total syllables (no.) $6.3 \pm 0.7$	L.	$3.2\pm0.3$	$3.8\pm0.2$	$3.4\pm0.3$	$2.1\pm0.1$	$2.2 \pm 0.1$
Time at maximum amplitude (%) $74.2 \pm 4.6$	4.6	$76.1 \pm 4.4$	$60.2\pm3.2$	$78.0\pm3.8$	$42.5\pm1.5$	$47.5 \pm 2.5$
Call duration (s) $2.3 \pm 0.2$	.2	$2.0\pm0.2$	$2.0\pm0.1$	$2.1\pm0.2$	$2.7 \pm 0.1$	$2.5\pm0.1$
Temporal DF1scores $-2.50 \pm 0$ .	± 0.22	$-1.09\pm0.10$	$-1.09\pm2.0$	$-1.13\pm0.12$	$1.76\pm0.12$	$1.14 \pm 0.13$
Temporal DF2 scores $1.21 \pm 0.4$	0.43	$-0.89\pm0.17$	$0.05\pm0.13$	$-0.67\pm0.13$	$0.25\pm0.09$	$-0.15\pm0.12$
Acoustic features of roar vocalizations						
Formant dispersion (Hz) $625 \pm 5$	10	$607 \pm 5$	$640 \pm 4$	$442\pm 2$	$366 \pm 2$	$371 \pm 3$
Highest frequency (Hz) $3534 \pm 26$	26	$3471 \pm 24$	$3642 \pm 19$	$3560\pm 20$	$3311\pm10$	$3405\pm18$
First formant (Hz) $408 \pm 9$		$434\pm 6$	$444 \pm 3$	$490 \pm 4$	$557 \pm 5$	$566\pm 6$
Harmonic-to-noise ratio (dB) $8.1 \pm 1.0$	0.	$5.4\pm0.3$	$7.6 \pm 0.7$	$2.7\pm0.2$	$3.0\pm0.2$	$2.4 \pm 0.1$
Acoustic DF1 scores $8.87 \pm 0.1$	0.17	$8.12\pm0.16$	$8.96\pm0.12$	$-3.46 \pm 0.15$	$-6.50\pm0.15$	$-6.94 \pm 0.17$

significantly longer howling bouts than allopatric *A. palliata* (EMM: P = 0.005, d = 1.44), pure *A. palliata* from the hybrid zone (EMM: P = 0.032, d = 0.96), and *palliata*-like hybrids (EMM: P = 0.003, d = 1.02). Although *A. pigra* had the lowest variability (CV = 10% vs. range of 16–24% for other categories), coefficients of variation in howling bout duration did not differ among howler categories (ANOVA:  $F_{4,20} = 1.58$ , P = 0.229, N = 21).

Within howling bouts, an LMM with howler category as the fixed effect (full LMM:  $F_{1,27,7} = 52.14$ , P < 0.001) was better at explaining roaring rate than a model based on intercept and random effects only (LRT: -47.9, P < 0.001). Within the full model, we found differences among howler categories in roaring rate (LMM:  $F_{5,25.0} = 3.64$ , P = 0.013, N = 65 bouts; Table II), but no evidence of convergence. In other words, there were no differences between genotypically similar animals (all EMMs: P > 0.804) but substantial differences between genotypically dissimilar animals (all EMMs: P < 0.016, d > 1.38), with *pigra*-like males roaring rate obtained from the only truly intermediate hybrid male most closely resembled those of *A. pigra* and *pigra*-like hybrids (Table II), it was not significantly different from any howler category (all EMMs: P > 0.178). *A. palliata* had the highest average coefficients of variation (allopatric: CV = 63%; sympatric: CV = 56%), hybrids intermediate variation (palliata-like: CV = 47%; *pigra*-like: CV = 28%), and *A. pigra* least variation (CV = 13%); however, these differences were not statistically significant (ANOVA:  $F_{4.17} = 2.27$ , P = 0.117, N = 18).

An LMM with howler category as the fixed effect (full LMM:  $F_{1.59.0} = 64.94$ , P < 0.001) was better at explaining time spent taking silent breaks (>5 s) within howling bouts than a model based on intercept and random effects only (LRT: -114.0, P < 0.001). Within the full model, we found differences among howler categories in time spent silent (LMM:  $F_{559} = 7.14$ , P < 0.001, N = 65 bouts; Table II), with *pigra*-like males converging with *palliata*-like males in the hybrid zone. As with roaring rate, *palliata*-like males did not differ from allopatric (EMM: P = 0.733) or sympatric A. palliata (EMM: P = 0.195) and these three all differed from allopatric A. pigra (all EMMs: P < 0.006, d > 2.90). However, other patterns differed from the roaring rate results. First, *pigra*-like individuals spent significantly more time silent than allopatric A. pigra (EMM: P = 0.029, d = 1.09). Second, although pigra-like males differed from allopatric A. palliata (EMM: P = 0.001, d = 1.51) and palliata-like hybrids (EMM: P = 0.005, d = 1.32), they did not differ from sympatric, purebred A. palliata (EMM: P = 0.229). Additionally, the only intermediate hybrid male was significantly different from allopatric A. pigra (EMM: P = 0.044, d = 5.19) but was not significantly different from the other groups including *pigra*-like hybrids (all EMMs: P > 0.188). There was no difference in coefficients of variation in the percentage of time spent silent during a bout among howler categories (ANOVA:  $F_{4,17} = 1.22$ , P =0.351, N = 18), with allopatric A. *pigra* having an intermediate level of variation (CV = 65% vs. range of 31–88% for other categories).

### **Differences in Roars**

All four variables remained in the final stepwise DFA of the temporal features of roars (DFA: Wilks' lambda = 0.206,  $F_{20,737.2}$  = 22.5, P < 0.001, N = 231), with longest syllable duration (DFA structure matrix in ESM Table SII; individual caller data in ESM

Fig. S1) the most discriminating variable in the first function (hereafter, DF1; canonical coefficient: 0.8) and number of syllables per roar most important in the second function (hereafter, DF2; canonical coefficient: 1.6). The temporal DF1 had an eigenvalue of 2.4 and explained 85.3% of the variance, while DF2 had an eigenvalue of 0.3 and explained another 11.7% of the variance.

Four of seven variables remained in the final stepwise DFA of the acoustic features of roars (DFA: Wilks' lambda = 0.008,  $F_{20,737,2}$  = 118.4, P < 0.001, N = 231), with formant dispersion the most discriminating variable in DF1 (canonical coefficient: 1.4) and highest frequency most important in DF2 (canonical coefficient: 1.1). The acoustic DF1 had an eigenvalue of 54.5 and explained 98.4% of the variance. Because DF2 had an eigenvalue of 0.6 and only explained another 1.1% of the variance, we did not analyze this function further.

Cross-validated (leave-one-out) classification (classification count in ESM Table SIII) was more accurate for acoustic features (64.9% correct) than temporal features (45.9% correct). In temporal features, there was extensive overlap between categories of howlers in addition to misclassifications among individuals with similar genotypes (Fig. 4a). For example, 11.2% of allopatric *A. pigra* were misclassified with either pure *A. palliata* from the hybrid zone or *palliata*-like hybrids and 15.5% of *palliata*-like hybrids were misclassified as either pure *A. pigra* or as *pigra*-like hybrids. In temporal features, the intermediate hybrid tended to cluster with pure *A. palliata* and *palliata*-like genotypes in and outside the hybrid zone (44.8% of miscalculations), although it was also misclassified as a pure *A. pigra* 6.9% of the time.

Conversely, males that were misclassified in acoustic features clustered only with individuals of similar genotype (Fig. 4b). For example, allopatric *A. pigra* were misclassified with *pigra*-like individuals 36.1% of the time, while the reverse occurred 38.9% of the time. However, calls of *A. pigra* were never misclassified with *A. palliata* or *palliata*-like animals. Likewise, allopatric *A. palliata*, pure *A. palliata* from the



**Fig. 4** First and second discriminant functions (DF1 vs. DF2) from our analysis of **(a)** temporal and **(b)** acoustic characteristics of howler roars recorded in southern Mexico in 2008 and 2011–2012. Triangles represent allopatric and hybrid zone (HZ) *A. palliata* males and HZ *palliata*-like hybrids; diamonds represent an intermediate hybrid; and circles represent allopatric *A. pigra* and HZ *pigra*-like males.

hybrid zone, and *palliata*-like animals were misclassified with each other 3.8–39.1% of the time, but they never clustered with the *pigra*-like individuals. Calls from the one truly intermediate hybrid individual were the most accurately classified (96.6% of the time) and misclassified only as pure *A. pigra*.

An LMM with fixed effects of howler category and hybrid index (full LMM: DF1:  $F_{1,35.0} = 0.22$ , P = 0.643; DF2:  $F_{1,15.6} = 0.02$ , P = 0.888) was better at explaining temporal results than models without the howler category term (LRT: DF1: -111.3, P < 0.001; DF2: -49.8, P < 0.001) or models based on only intercept and random effects (LRT: DF1: -42.2, P<0.001; DF2: -47.6, P<0.001). Within the full models, howler category predicted differences in temporal features of roars (LMM: DF1:  $F_{5,20,4} = 4.13, P = 0.009; DF2: F_{5,15,8} = 4.86, P = 0.007, N = 231; Table II; Fig. 5), with$ convergence by sympatric A. palliata and palliata-like individuals toward A. pigra. Specifically in DF1, purebred A. *palliata* in the hybrid zone clustered with all hybrids (all EMMs: P > 0.156) as well as with pure A. pigra (EMM: P = 0.287), but not with purebred A. palliata outside the hybrid zone (EMM: P = 0.016; d = 2.09; Fig. 5). DF2 converged in a similar way (Table II); purebred, allopatric A. palliata were significantly different from purebred A. palliata (EMM: P < 0.001, d = 1.69) and palliata-like hybrids in the hybrid zone (EMM: P = 0.015, d = 1.06), sympatric A. palliata (EMM: P = 0.877) and *palliata*-like hybrids (EMM: P = 0.905) did not differ significantly from *pigra*-like hybrids, and neither *palliata*-like hybrids (EMM: P = 0.778) or purebred A. palliata in the hybrid zone (EMM: P = 0.980) differed significantly from pure A. pigra.

There was no difference among howler categories in intramale coefficients of variation (CV% range: 17–25%) in the most discriminating variable of DF1, longest syllable duration (ANOVA:  $F_{5,27} = 0.62$ , P = 0.687, N = 33 males). However, *A. palliata* (allopatric: CV = 31%; sympatric: CV = 40%) and *palliata-like* males (CV = 33%) exhibited more intramale variation in total syllable number (most



Fig. 5 Mean  $\pm$  SE of the first discriminant function (DF1) based on temporal features of roars that we recorded from six categories of *A. palliata*, *A. pigra*, and hybrid howlers in southern Mexico (HZ: hybrid zone) in 2008 and 2011–2012.



**Fig. 6** Five example oscillograms (top pane: time vs. amplitude) and spectrograms (bottom pane: frequency vs. time; each pane is 4.58 s; dark bands represent frequencies with high intensity) of single roars from one *palliata*-like hybrid male (HI: 0.07) that we recorded in Tabasco, Mexico in 2012 (calls from left: 7 syllables; 5 syllables; 4 syllables; 3 syllables; 2 syllables).

discriminating in DF2) than pigra-like (CV = 14%) and male *A. pigra* (CV = 5%; ANOVA:  $F_{5,27} = 8.77$ , *P* < 0.001, *N* = 33; Fig. 6).

An LMM with fixed effects of howler category and hybrid index (full LMM:  $F_{1,13.6} = 0.04$ , P = 0.839) was better at explaining acoustic results than a model without the howler category term (LRT: -116.6, P < 0.001) or a model based on only intercept and random effects (LRT: -248.7, P < 0.001). Within this model, acoustic features differed between howler categories (LMM:  $F_{5,15.8} = 26.2$ , P < 0.001; Table II; Fig. 7). However, unlike with temporal features, the acoustic features of roars from hybrid zone individuals clustered with allopatric populations of the most similar genotype categories (all EMMs: P > 0.108). The calls from the genetically intermediate hybrid were statistically different and intermediate to the genotype categories on the two extreme ends of the continuum (all EMMs: P < 0.011; d > 3.57; Fig. 7). There was no difference among howler categories in intramale coefficients of variation (CV% range: 2.3–2.5%) in the most discriminating variable, formant dispersion (ANOVA:  $F_{5,27} = 0.05$ , P = 0.999, N = 33 males). Overall (i.e., comparing all individual measures listed in Table I), temporal features (mean CV = 31%) had higher coefficients of variation than acoustic features (mean CV = 9%; ANOVA:  $F_{5,9} = 5.06$ , P = 0.051, N = 11 features).



**Fig. 7** Mean  $\pm$  SE of the first discriminant function (DF1) based on acoustic features of roars that we recorded from six categories of *A. palliata*, *A. pigra*, and hybrid howlers in southern Mexico (HZ: hybrid zone) in 2008 and 2011–2012.

### Discussion

Acoustic features of howler vocalizations were strongly associated with individual ancestry in terms of howler category (see also Bergman *et al.* 2016). In contrast to this suggested heritability in acoustic features, we found evidence of plasticity in several temporal features. Bout duration of *pigra*-like individuals from the hybrid zone differed from allopatric *A. pigra*. Additionally, fewer than half of roars were correctly classified based on temporal features and some misclassifications crossed genotype categories (e.g., *palliata*-like confused with *A. pigra* individuals). Similarly, the only truly intermediate hybrid tended to cluster with *palliata*-like males in temporal features of roars, but fell midway between the two genotypic extremes in terms of acoustic features (as predicted if features were strongly tied to ancestry).

In sympatry, temporal features converged and no features diverged. For example, purebred *A. palliata* in the hybrid zone differed significantly from allopatric *A. palliata* in temporal features of roars, converging toward values for *A. pigra* and not differing from intermediate or *palliata*-like hybrids. Likewise, *pigra*-like hybrids differed significantly in howling bout duration and time spent silent from purebred *A. pigra* but not from purebred and hybrid *palliata*-like individuals. Roaring rate was the only temporal feature measured that followed genotype category rather than convergence patterns. Overall, these results suggest fairly extensive temporal plasticity in the calls of animals in the contact zone given they appear to be modifying their calls to match others around them.

Unlike other studies of convergence or divergence within groups or between communities, our reliance on a hybrid zone allowed us to demonstrate convergence on a larger scale, involving traits that are plastic beyond the range of simple individual variation. Although the number of syllables (in which *A. palliata* tended to converge with *A. pigra* in sympatry) was a highly variable character in allopatric roars of *A. palliata*, the mean number in sympatric *A. palliata* (3.2: Table I) was outside the range of means in allopatric *A. palliata* (3.8 to 9.2). Additionally, we found that other convergence patterns were not the result of extensive variability in the allopatric species; for example, howling bout duration of *A. pigra* converged in sympatry but allopatric *A. pigra* were very consistent in this temporal feature.

The only other known cases that demonstrate such natural convergence, i.e., not conditioned, not involving humans, between two separate mammal species is a case of mimicry between captive African and Asian elephants (Poole *et al.* 2005) and anecdotal evidence between howler monkeys (*Alouatta caraya* and *A. clamitans*: Aguiar 2010). Convergence can be the result of experience or context, as demonstrated in vocallearning animals such as birds, pinnipeds, and cetaceans (Tyack 2008). However, whether cases of convergence represent true production learning rather than usage/ contextual learning remains debated (Ey and Fischer 2011; Fitch 2017; Hammerschmidt and Fischer 2008; Janik and Slater 2000; Seyfarth and Cheney 2010b; Tyack 2008).

Our findings also support Janik and Slater's (1997, 2000) hypothesis that temporal vocal features, controlled via respiration, should be more flexible than acoustic features, which are tied morphologically to the vocal tract and likely under different neural control (Janik and Slater 2000). Other studies have noted flexibility in features tied to respiratory control rather than changes to the vocal tract shape in nonhuman primates

(e.g., Ey and Fischer 2011; Levréro et al. 2015). For example, there is evidence of increasing volume to compensate for background noise (Lombard effect) in many primates (e.g., macaques, Sinnott et al. 1975; marmosets, Brumm et al. 2004). Marmosets also increase syllable duration in a noisy environment (as do olive baboons, Papio anubis, in closed habitats: Ey et al. 2009), although marmosets do not alter the number of syllables (Brumm et al. 2004). However, distinguishing respiratory and vocal tract features is complicated by the fact that acoustic features such as fundamental frequencies can be impacted by respiration changes (e.g., Garnier et al. 2008; Hsiao et al. 1994; Liénard and Di Benedetto 1999) brought on by changes in affect (e.g., Janik and Slater 1997; Owren et al. 2011). Additionally, and contrary to traditionally held views (Lieberman et al. 1969), there is growing evidence that individual Old World monkeys are able to modify their vocal tract shapes while vocalizing, producing acoustically variable sounds (Bergman 2013; Boë et al. 2017; Fitch et al. 2016; Riede et al. 2005). Further, there is evidence that at least chimpanzees are capable of volitional control of acoustic features that may be linked to vocal tract shape (Crockford et al. 2004; see also Marshall et al. 1999). These abilities may be reduced in lemurs (Gamba and Giacoma 2006) and remain untested in New World monkeys, with howlers being a particularly difficult test case to model due to the addition of air sacs (e.g., de Boer and Fitch 2010). In sum, we do not yet know the taxonomic breadth of acoustic and temporal flexibility across primates.

The value of being able to discriminate among individuals could be an important pressure for the evolution of flexibility and learning. Whereas divergence between species in mating signals would improve the ability to avoid hybridization in sympatry if hybrids have lower fitness, convergence in signals would improve the ability to recognize rivals and be an advantage when two species compete over food or mates (Cody 1969). Thus, we might expect convergence in contest calls and divergence in mating signals in sympatry (e.g., Leary 2001). It remains unclear if howler monkey loud calls function to attract mates or deter rivals (or both reviewed in: Kitchen et al. 2015). However, we find only convergence and no evidence of character displacement, a pattern more consistent with howling bouts used in interspecific competition rather than as a mating signal (Leary 2001). Only convergence would be predicted if hybridization does not have deleterious effects, but no studies have been conducted to accurately determine hybrid fitness at our site. Although some morphological features (body size and testes volume) may provide fitness advantage to at least some A. palliata  $\times$  A. pigra hybrids (Kelaita and Cortés-Ortiz 2013), the bimodal distribution of admixed individuals and the narrowness of the hybrid zone suggest possible reduced hybrid fitness in this system (Barton and Hewitt 1985; unpubl. data).

Given that we see convergence in temporal but not acoustic features and given the evidence for strong bidirectional backcrossing in the population (Fig. 2), we can make two contrasting predictions for howler responses to other groups living in this hybrid zone. First, if convergence is an adaptive way to ensure that even interspecific rivals respond to competitive calls (Cody 1969) – in that callers with similar temporal patterns are better detected as rivals than those whose vocalizations have different temporal patterns – we predict that matching temporal patterns should elicit stronger responses than matching acoustic patterns. Alternatively, if selection favors rivals that can detect the contest ability of a potential rival, subjects in the contact zone should respond based on acoustic rather than temporal features. Acoustic features may provide accurate

information about the caller's morphology and, presumably, physical threat (e.g., the much larger size of *A. pigra* males); in contrast, temporal features are more labile and, consequently, less reliable indicators of the caller's competitive ability. Playback experiments to test these predictions are currently underway in this howler hybrid zone.

In summary, our study fits with a growing body of research suggesting that nonhuman primate vocalizations may be quite flexible, particularly for temporal features. Contrary to traditional assumptions, we found that such vocal plasticity in howlers can extend beyond the variation seen within a population. However, more studies are needed to determine the taxonomic breadth of such flexibility in nonhuman primates and other mammals.

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