Primates (2024) 65:183–190
https://doi.org/10.1007/s10329-024-01120-0

ORIGINAL ARTICLE

Mantled howler monkey males assess their rivals through formant spacing of long-distance calls

Natalia Maya Lastra[1] · **Ariadna Rangel Negrín**[1] · **Alejandro Coyohua Fuentes**[1] · **Pedro A. D. Dias**[1]

Received: 2 August 2023 / Accepted: 1 February 2024 / Published online: 21 February 2024

Abstract

Formant frequency spacing of long-distance vocalizations is allometrically related to body size and could represent an honest signal of fighting potential. There is, however, only limited evidence that primates use formant spacing to assess the competitive potential of rivals during interactions with extragroup males, a risky context. We hypothesized that if formant spacing of long-distance calls is inversely related to the fighting potential of male mantled howler monkeys (*Alouatta palliata*), then males should: (1) be more likely and (2) faster to display vocal responses to calling rivals; (3) be more likely and (4) faster to approach calling rivals; and have higher fecal (5) glucocorticoid and (6) testosterone metabolite concentrations in response to rivals calling at intermediate and high formant spacing than to those with low formant spacing. We studied the behavioral responses of 11 adult males to playback experiments of long-distance calls from unknown individuals with low (i.e., emulating large individuals), intermediate, and high (i.e., small individuals) formant spacing ($n = 36$ experiments). We assayed fecal glucocorticoid and testosterone metabolite concentrations ($n = 174$). Playbacks always elicited vocal responses, but males responded quicker to intermediate than to low formant spacing playbacks. Low formant spacing calls were less likely to elicit approaches whereas high formant spacing calls resulted in quicker approaches. Males showed stronger hormonal responses to low than to both intermediate and high formant spacing calls. It is possible that males do not escalate conflicts with rivals with low formant spacing calls if these are perceived as large, and against whom winning probabilities should decrease and confrontation costs increase; but are willing to escalate conflicts with rivals of high formant spacing. Formant spacing may therefore be an important signal for rival assessment in this species.

Keywords Acoustic assessment · Androgens · Glucocorticoids · Hormones · Playback experiments

Introduction

Competition for limited resources leads to conflict, which entails several costs, such as increased energy expenditure, decreased reproduction, and risk of physical injury and death (Enquist and Leimar 1983; Maynard Smith and Price 1973). To avoid these costs, animals have evolved conflict-avoidance and -resolution mechanisms (Aureli and de Waal 2000), such as rival assessment (Maynard Smith 1982). In this context, signals that reflect motivation and/or fighting ability allow for mutual assessment and, thus, may prevent the escalation of conflicts and the costs associated with those conflicts (Vehrencamp 2000).

A widely used signal in animal communication is vocalizations. The acoustic characteristics of vocalizations depend on the size and shape of the phonatory apparatus (Bowling et al. 2017; Riede y Fitch 1999). Specifically, formant frequency dispersion (formant spacing, hereafter), which is a measure of the spacing between resonance peaks in a vocalization (Fitch 1997), varies as a function of vocal tract size (i.e., longer vocal tracts have higher resonance capacity and formants tend to have lower frequencies, decreasing formant spacing; Ey et al. 2007). Formant spacing also is allometrically related to body size (Garcia et al. 2017). Thus, the spacing between frequency formants may represent an honest signal of the size of the caller (Taylor and Reby 2010). The ability to recognize variation in formant spacing is widespread across primates (e.g., *Macaca mulatta:* Fitch and Fritz 2006, *Eulemur rubriventer*: Gamba et al. 2012,

---

✉ Pedro A. D. Dias
pedroaddias@gmail.com

[1] Primate Behavioral Ecology Lab, Instituto de Neuro-etología, Universidad Veracruzana, Av. Dr. Luis Castelazo Ayala S/N, CP 91190 Xalapa, México

Colobus guereza: Harris et al. 2006, *Papio anubis*: Hienz et al. 2004, *Cercopithecus aethiops*: Owren 1990, *Papio cyncephalus ursinus*: Owren et al. 1997, *Macaca fuscata*: Sommers et al. 1992), implying that it may be a functionally relevant acoustic trait of vocal signals (Fitch and Fritz 2006). It is unclear, however, if individuals use information conveyed by formant spacing to adjust their behavior and physiology in a competitive context, such as interactions with extragroup conspecifics.

Howler monkeys (genus *Alouatta*) produce potent long-distance calls that can be heard over 1 km (Whitehead 1995). Their production is linked to several morphological traits, including enlarged hyoid bone and larynx, air sacs, and long vocal folds (Schön 1971). The behavioral responses of males to long-distance calls seem to result from the assessment of their current context (e.g. food availability: Hopkins 2013, Van Belle and Estrada 2020; presence of vulnerable offspring: Kitchen 2004; location: da Cunha and Byrne 2006, Maya Lastra et al. 2023) and interaction history with the callers (e.g., familiarity: Briseño-Jaramillo et al. 2015; Ceccarelli et al. 2021). For instance, black howler monkey males (*A. pigra*) do not answer long-distance calls from intruders when numeric odds are against their group, unless vulnerable offspring is present (Kitchen 2004). Given that in howler monkeys variation in formant spacing of long-distance calls is correlated with body size (Dunn et al. 2015), it is also possible that this characteristic could be used to assess the fighting potential of rivals, thus complementing information on context and interaction history.

Interactions with extragroup males (solitary or from other groups) are a strong selective pressure for mantled howler monkeys (*A. palliata*), as they may result in injury and death (Cristóbal-Azkarate et al. 2004; DeGusta and Milton 1998), infanticide (Crockett 2003), and loss of reproductive opportunities (Glander 1992). Additionally, howler monkeys have high energy expenditure compared with similar-sized primates (Pontzer et al. 2014), which may further constrain their participation in costly interactions with extragroup males. Besides behavioral responses, males show hormonal modulation in this context involving increases in testosterone concentrations with increasing intruder pressure (proxied via the number and density of solitary males and number of groups in the habitat: Cristóbal-Azkarate et al. 2006) and the frequency of physical, visual, and vocal encounters with extragroup males: Dias et al. 2022). This modulation may be linked to the involvement of testosterone in preparative mechanisms for subsequent interaction (e.g., expression of aggressive behavior: Booth et al. 2006). Interestingly, glucocorticoid concentrations, which are a robust hormonal marker of the physiological stress response (Sapolsky et al. 2000), do not vary as a function of interactions with extragroup males (actual or potential: Cristóbal-Azkarate et al. 2006; Dias et al. 2022). The fact that individual participation in intragroup agonistic interactions elicits glucocorticoid secretion (a probable consequence of psychosocial stress; Dias et al. 2017, 2022; Gómez-Espinosa et al. 2014) raises the question of whether these hormones are only involved in very specific competitive contexts, which is unlikely (e.g., Abbott et al. 2003), or if previous studies have not used suitable metrics of extragroup competition. Currently, covariation between the acoustic attributes of long-distance calls from rivals and the hormonal responses of listeners has not been assessed in howler monkeys.

Here, we examine the behavioral and hormonal responses of mantled howler monkey males to experimental variation in formant spacing of long-distance calls, while controlling for numeric odds and familiarity with the callers. Given that individuals are more likely to escalate conflicts with weaker contestants or with opponents with similar power (Maynard Smith and Parker 1976), we hypothesized that, if formant spacing of long-distance calls is inversely related to the fighting potential of male mantled howler monkeys then, males should: (1) be more likely and (2) faster to answer vocally to calling rivals; (3) be more likely and (4) faster to approach calling rivals; and also to show higher fecal (5) glucocorticoid and (6) testosterone metabolite concentrations in response to rival long-distance calls with intermediate and high formant spacing than to calls with low formant spacing.

Methods

Study site and subjects

We studied 11 adult males belonging to four groups of mantled howler monkeys that lived in two forest fragments in the Los Tuxtlas Biosphere Reserve (Veracruz, México; Table 1). These groups have been studied for several years (Rangel-Negrín et al. 2021) and do not react to the presence of researchers. Subjects were individually recognized via physical attributes, such as patches of yellow fur in the tail and feet, scars, and facial features.

Playback stimuli

We recorded naturally occurring long-distance calls ad libitum from adult males belonging to six groups with a Sennheiser MKE600 directional microphone and a Marantz PMD660 digital recorder. Sixty-five recordings corresponded to calls produced by a single male and were both complete (i.e., recorded from beginning to end of the calling bout) and free from background noise. These calls consisted of barks and roars, corresponding to vocalization types A1 and C1 in Baldwin and Baldwin (1976). To modify formant spacing, we produced spectrograms for

Table 1 Attributes of study sites and groups

Attribute	Group 1	Group 2	Group 3	Group 4
Site	Balzapote	Balzapote	La Flor de Catemaco	La Flor de Catemaco
Location	18° 36′30.80″ N 95° 04′15.69″ W	18° 36′36.50″ N 95° 04′11.16″ W	18°26′29.63″ N 95°03′01.75″ W	18°26′39.27″ N 95°03′08.88″ W
Fragment size (ha)	12	8	100	100
Groups	2	2	3	3
Adult males	2	2	3	4
Adult females	2	2	5	6
Juveniles	1	1	2	2
Infants	1	2	2	2

each call in Praat 6.1.15 (Boersma and Weenink 2020) which we edited to a 75 to 4000-Hz frequency and selected the first six formants (Dunn et al. 2015). We then used the "change gender" function with a formant shift ratio of 1.05 and 0.95 to generate calls with high and low formant spacing, respectively, compared to non-modified calls. With these shift ratios, modified calls had formant frequencies within the natural range (305.4–3612.4 Hz) and sounded natural to experienced human listeners. Mean ± SD formant spacing of roars extracted in Praat using linear predictive coding (LPC) via the 'LPC: To Formants (Burg)' command was 610.3 ± 13.5 Hz in low formant calls, 638.9 ± 14.3 Hz in intermediate calls, and 674.0 ± 14.4 Hz in high formant calls (extraction parameters: time-step, 0.01 s; maximum number of formants, 8–10; maximum formant frequencies, 3500–4000 Hz; window of analysis, 0.1 s). We prepared a set of playbacks for each group consisting of three low, three intermediate, and three high formant spacing calls, with no source calls being repeated within groups. All playbacks were composed by roars and barks. We tried to standardize the duration of playbacks to 5 min, which, during the recording of naturally occurring long-distance calls, was the period in which males were more likely to display behavioral responses to neighbor calls. The mean ± SD duration of playbacks was 5 ± 0.007 min (range = 4:40–5:19 min).

To account for the effect of numerical odds on the responses of males to long-distance calls (Kitchen 2004; Van Belle and Scarry 2015) we combined multiple calls from the same individual with the multitrack function of Adobe Audition 12.1.4.5 (Adobe 2019) so that the number of males in each playback matched that of the study group that would be exposed to it. Study groups were exposed to playbacks prepared with calls from unfamiliar males (i.e., males that lived in different forest fragments that were at a distance of at least 20 km) to account for the influence of familiarity with callers on behavioral responses (Briseño-Jaramillo et al. 2015; Ceccarelli et al. 2021; Kitchen 2004).

Playback design and behavioral data collection

We conducted playback experiments between March 2020 and December 2021, by exposing each group thrice to each formant spacing treatment (i.e., low, intermediate, and high formant spacing calls), with a median of 7 days between consecutive experiments in the same group (range = 2–14 days, $n = 36$ experiments). The order in which each treatment was administered was randomized. Playbacks began once the first feeding bout of the morning ended, and all adults were resting. We installed a speaker (Bose 151SE) at 100 m from the nearest subject and raised it on a 8-m collapsible fiberglass pole. The speaker was connected to a JBL A6002 amplifier powered by a 12 V/7 A Powersonic PS-1270 F2 battery and we played recordings from a Motorola Moto E5 Play cellular phone.

At the onset of playbacks, we started a 1-h focal animal sample (Altmann 1974) of the first male that displayed long-distance calls or movement responses (i.e., 36 h of focal sampling). Regarding movement, we specifically recorded approaches defined as any movement > 1 m by the focal male that was less than 45° in the direction of the speaker.

Fecal sample collection and hormonal assays

To assess the hormonal responses of males to variation in formant spacing of long-distance calls we measured fecal glucocorticoid (fGCM) and fecal testosterone metabolite (fTM) concentrations. Given that there is a time lag of approximately 24 h between hormone secretion and excretion in feces in this species (Aguilar-Cucurachi et al. 2010; Cañadas-Santiago et al. 2020), we aimed at collecting fecal samples from all males during the morning of playback days ($n = 84$, mean ± SD = 8 ± 2 samples per male), to assess baseline hormonal status (i.e., not associated with playbacks), and during the next day ($n = 90$, 8 ± 2 samples per male), to investigate hormonal responses to playbacks. The mean ± SD latency between the time of experiment onset and the time of collection of fecal samples used to assess hormonal responses of males was 25.8 ± 1.7 h (range 20.9–29.1 h).

We collected fecal samples from the forest floor immediately after deposition when we could unambiguously match them to a male. We deposited samples in polyethylene bags labeled with the identity of each individual and stored them in a cooler with ice packs while in the field and in a freezer at − 20 ℃ once back at the field station. We dried feces in an oven (Cole-Parmer OVG-400–56-120 Gravity Convection Drying Oven) at 60 ℃ and extracted steroids following a modification of the method by Wasser et al. (2000). Briefly, we shook 0.6 g of homogenized, dried, and pulverized feces for 30 min in 4.0-ml analytical-grade methanol. We centrifuged extracts (460 g for 30 min) and recovered the supernatant. After complete evaporation of the solvent in a water bath at 60 ℃ for 24 h, we reconstituted pellets with 2-ml albumin buffer which we used for assays.

We determined fGCM and fTM concentrations in 174 samples with chemiluminescent immunoassays using commercial kits (Cortisol, Immulite, Siemens, Los Angeles, CA, USA; sensitivity = 5.5 nmol/l; calibration range = 28–1380 nmol/l; Testosterone, Immulite, Siemens, Los Angeles, CA, USA; sensitivity = 0.5 nmol/l; calibration range = 0.7–55 nmol/l) and an automated immunoassay system (Immulite 1000 analyzer, Siemens, Munich, Germany). The antibodies in these kits are highly specific to cortisol and testosterone, showing low (< 9%) cross-reactivity with other compounds. Pooled fecal extracts, when added to standard curve points, exhibited similar slopes (fGCM: $R^2 = 0.95$, $n = 8$, $P < 0.001$; fTM: $R^2 = 0.88$, $n = 8$, $P < 0.001$), and serial dilutions of a fecal pool yielded results that were parallel to kits' standards (fGCM: $t = 0.9$, $n = 4$, $P = 0.402$; fTM: $t = 1.2$, $n = 4$, $P = 0.534$). For fGCM, intra-assay variation (coefficient of variation) averaged 7% ($n = 3$ samples) and inter-assay variation was 14% ($n = 4$ samples), whereas for fTM intra-assay variation was 3% ($n = 3$ samples) and inter-assay variation was 9% ($n = 4$ samples). These assays had been previously biologically validated (Cañadas-Santiago et al. 2020; Dias et al. 2022).

Data analysis

We assessed the behavioral responses of males via the occurrence of vocal and movement responses (binary variable, yes/no) and the latency to the first vocal and movement response (i.e., 0 to 3600 s) per experiment. We used generalized linear models to analyze the effect of formant spacing (i.e., low, intermediate, high) on male behavior. For occurrence data we built models with binomial error distribution and a logit link function whereas for latencies we used models with negative binomial error distribution and log link function.

We calculated variation in fGCM and fTM as the subtraction between post- and pre-experiment hormone concentrations per treatment per male. We then assessed the influence of formant spacing on hormonal variation with linear mixed models on log transformed hormonal values (following the addition of a constant to produce positive values). In these models we added subject and group identity as random factors to account for the repeated sampling of males and groups, respectively. We compared complete models (i.e., with fixed and random predictors) with a null model including only the random factors with likelihood ratio tests to determine whether the random factors accounted for a larger proportion of variation in response variables than the fixed factor (Pinheiro and Bates 2000). We found significant differences ($P < 0.001$) in both comparisons, indicating that formant spacing was more influential in the response variables than the random factors. In all models, we used Tukey contrasts as post-hoc tests. We ran all models in R 4.3.0 (R Core Team 2023).

Results

Males displayed vocal responses to all playbacks and had quicker vocal responses toward playbacks with intermediate formant spacing than to those with high formant spacing ($R^2 = 0.33$, $\chi^2_{2,35} = 16.5$, $P < 0.05$; Fig. 1a). Males were more likely to move following intermediate and high formant spacing playbacks than after low formant spacing playbacks ($R^2 = 0.22$, $\chi^2_{2,35} = 9.6$, $P < 0.01$; Fig. 1b), and moved quicker after high than both intermediate and low formant spacing playbacks ($R^2 = 0.24$, $\chi^2_{2,35} = 10.8$, $P < 0.05$; Fig. 1c). Both fGCM ($R^2 = 0.41$, $\chi^2_{2,89} = 49.6$, $P < 0.05$; Fig. 1d) and fTM ($R^2 = 0.15$, $\chi^2_{2,89} = 12.8$, $P < 0.05$; Fig. 1e) concentrations increased after low formant spacing calls compared to both intermediate and high formant spacing calls.

Discussion

In this study, we experimentally examined the influence of variation in the formant spacing of long-distance calls on the behavior and hormonal modulation of listeners to test the hypothesis that formant spacing of long-distance calls is inversely related to the fighting potential of mantled howler monkey males. Contrary to our prediction, playback experiments always elicited vocal responses by listeners, independently of formant spacing, but males responded quicker to intermediate than to low formant spacing playbacks. Low formant spacing calls were less likely to elicit approaches whereas high formant spacing calls resulted in quicker approaches by males, who additionally showed stronger hormonal responses to low than to both intermediate and

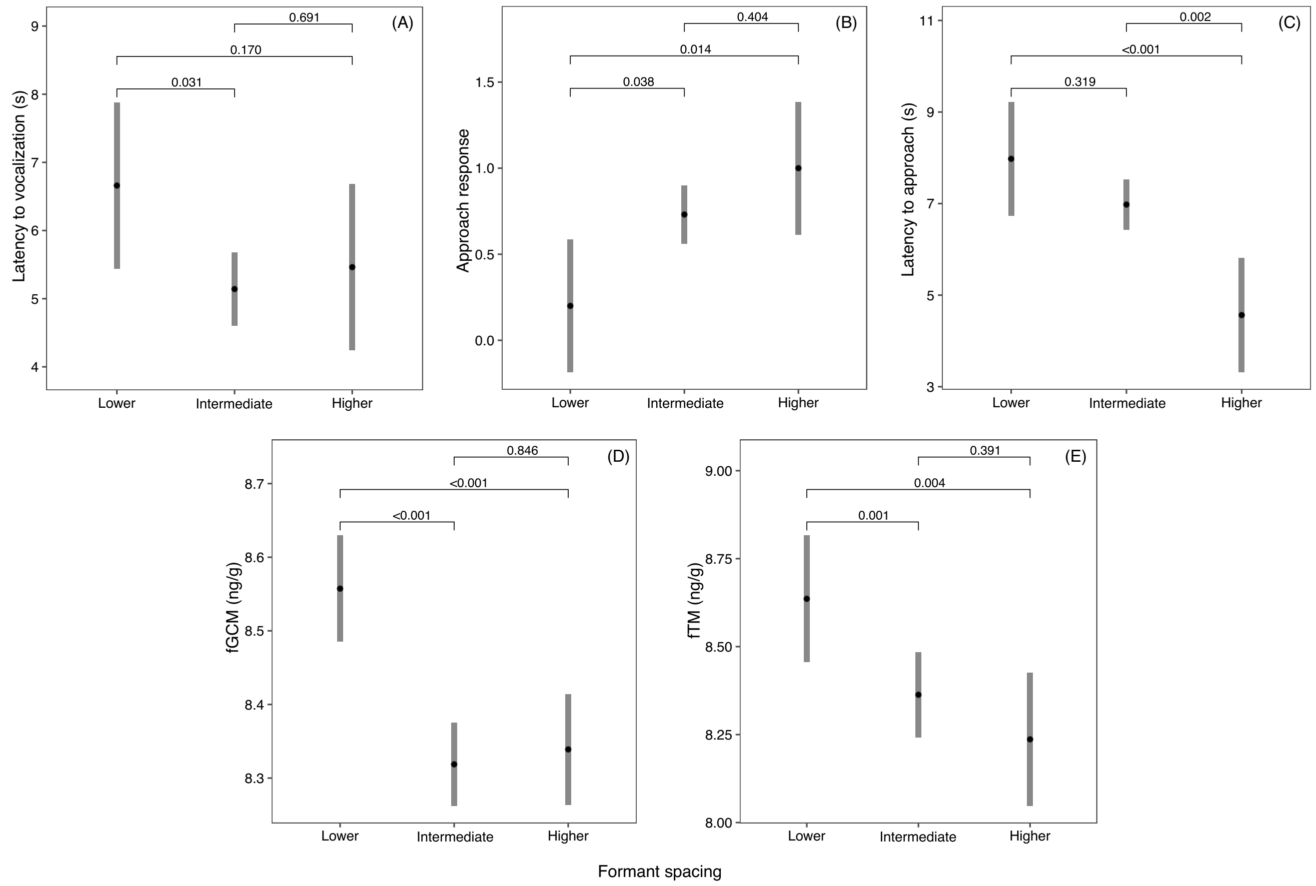

Fig. 1 Estimated marginal means (*black dots*) and 95% confidence intervals (*gray rectangles*) of generalized linear models (**A** to **C**) and linear mixed models (**D** and **E**) on the influence of formant spacing of simulated long-distance calls on the behavior and hormonal modulation of mantled howler monkey males: **A** latency to first vocalization; **B** occurrence of movement; **C** latency to first movement; **D** variation in fecal glucocorticoid hormone metabolites (fGCM); and **E**) variation in fecal testosterone metabolites (fTM). Eleven males belonging to four groups were exposed to playbacks of long-distance calls with low, intermediate, and high formant frequency ($n = 36$ experiments). Significance results of post hoc pairwise comparisons (with Tukey adjustment) are indicated above horizontal lines on top of each panel

high formant spacing calls. Although our study is based on a small set of playback experiments, mantled howler monkeys seem to have non-random responses to variation in formant spacing of conspecific long-distance calls, which could be related to vocal assessment of rival competitive potential.

The fact that we recorded male vocal responses to all playback experiments suggests that the factors that were standardized across groups, or a combination of them, are critical for eliciting long-distance calling in this species: unknown callers, even numerical odds, and presence of young infants. Regarding the first, assessment is particularly important during first encounters, as it allows information gathering between unknown rivals (Archer and Huntingford 1994; Arnott and Elwood 2009; Preuschoft and van Schaik 2000; van Rhijn and Vodegel 1980). This is especially important when meeting strangers who can attempt to take over groups and commit infanticide (Kitchen 2004). Second, as not all group males participate in all long-distance calling bouts, reciprocating long-distance calls may be a tactic to elicit vocal behavior by silent opponents (Kitchen 2004). In this way, males may confirm group size and reduce uncertainty about conflict outcome (Maynard Smith and Price 1973; Parker 1974; Van Belle and Scarry 2015), which should be highest at matched numerical odds, a situation that normally leads to the need of further assessment or escalation (Clutton-Brock et al. 1979). In our study, it is plausible to assume that uncertainty was the highest in the intermediate formant spacing treatment, as it involved matched numerical odds and formant spacing did not deviate from average values. This could explain why males were quicker in vocally responding intermediate than low and high formant spacing playbacks. Third, it is possible that males always answer extragroup calls when infants are present due to the importance of preventing takeover attempts that could lead to infanticidal attacks (Crockett 2003; Kitchen 2004). Future experimental playback studies will be necessary to disentangle the relative effects of these factors.

In contrast with the occurrence of vocal responses, other behavioral responses varied as a function of formant spacing. Overall, decreased likelihood of approach and delayed vocal and approach responses toward low formant spacing calls could result from males perceiving such calls as more threatening, and thus be less willing to escalate interactions, as proposed by theoretical models (Enquist and Leimar 1983; Maynard Smith 1982; Parker 1974). Given that both vocalizations and approaches are likely energetically costly to howler monkeys (Kitchen 2004), the mentioned evidence on behavioral responses to low formant spacing playbacks (i.e., decreased likelihood of approach and delayed vocal and approach responses) suggests that, as observed in other species, formant spacing may be an honest signal of the caller's body size, and thus, of its competitive potential (Bowling et al. 2017; Reby and McComb 2003), with males avoiding conflicts with stronger opponents.

Vocal and movement responses by males, which were in general stronger toward calls with intermediate and high formant spacing, were not accompanied by increases in fGCM concentrations, suggesting that these activities did not require significant mobilization of energy stores (Sapolsky et al. 2000). Therefore, the increase in fGCM concentrations in response to lower formant spacing calls probably results from psychological stress associated with the assessment of such calls as threatening, whereas higher fTM concentrations are likely related to the anticipation of reproductive challenges (Cristóbal-Azkarate et al. 2006; Dias et al. 2022; Rangel-Negrín et al. 2011). While it is possible that our behavioral sampling overlooked individual variation in responses to playbacks (i.e., we recorded the behavior of a single male per experiment), there was no remarkable interindividual variation in hormonal responses to playbacks, suggesting that all males react to formant spacing independently of their intrinsic attributes (e.g., age, body size). Previous research has demonstrated that primate males, including howler monkeys, cope with challenges from extragroup rivals via hormonal mechanisms (e.g., Brockman et al. 1998; Cristóbal-Azkarate et al. 2006; Jaeggi et al. 2018; Rangel-Negrín et al. 2011; Ross et al. 2004; Teichroeb and Sicotte 2008), but this is the first study to report positive glucocorticoid and testosterone responses to such challenges that are not dependent on dominance status (see Schoof and Jack 2013), as well as the first to link hormonal modulation in this context with vocal assessment.

Three main factors may affect the likelihood of conflict escalation: motivation, which is a function of the value of the resource being disputed; assessment of winning probabilities; and the costs participants are willing to incur during confrontation (Dunbar 1988; Preuschoft and van Schaik 2000). The present study does not allow addressing the first, but it suggests that mantled howler monkeys use acoustic information to assess the other two: they escalate conflicts with rivals producing high formant spacing calls, which are likely perceived as small, and against whom winning probabilities should increase and confrontation costs decrease. Given the evidence of plasticity in vocal production in this species (e.g., calls with lower formant frequencies toward unfamiliar intruders than those emitted naturally: Whitehead 1994), future research analyzing variation in the vocal responses of males to long-distance calls that convey information on caller motivation (e.g., approaching vs. retreating callers: Whitehead 1994; call duration: Sekulic and Chivers 1986) should provide further insight on the value of acoustic signals for rival assessment in mantled howler monkeys and other primates.

Acknowledgements We thank D. Canales Espinosa, P. Cruz-Miros, and J. Landa for their support during fieldwork and Ing. J. L. Ponce Puente and property owners for allowing the work at La Flor de Catemaco S.A. and Balzapote, respectively. We thank J. C. Dunn and F. Aureli for stimulating discussions during the development of the research. We also thank Dr. J. C. Bicca-Marques (Associate Editor) and two anonymous reviewers for their very helpful comments and suggestions. The study was financed by Consejo Nacional de Ciencia y Tecnología (CONACyT grant 726265), Consejo Veracruzano de Ciencia y Tecnología (COVEICyDET project 15 1529/21), Posgrado en Neuroetología, Instituto de Neuro-etología (Universidad Veracruzana), and Leakey Foundation. We complied with the ethical standards in the treatment of primates as described in the guidelines of the Primate Society of Japan and followed the Mexican Law (permits SGPA/DGVS/13528/19 and SGPA/DGVS/04015/21 from Secretaria de Medio Ambiente y Recursos Naturales). A Rangel Negrín and PAD Dias thank Mariana and Fernando for continued inspiration to understand primate behavior.

Funding Consejo Nacional de Ciencia y Tecnología, 726265, Natalia Maya Lastra, Consejo Veracruzano de Ciencia y Tecnología, 15 1529, Ariadna Rangel Negrín, Leakey Foundation

Data availability The data that support the findings of this study are available from the corresponding author upon reasonable request.

References

Abbott DH, Keverne EB, Bercovitch FB, Shively CA, Mendoza SP, Saltzman W, Snowdon CT, Ziegler TE, Banjevic M, Garland T Jr, Sapolsky RM (2003) Are subordinates always stressed? A comparative analysis of rank differences in cortisol levels among primates. Horm Behav 43:67–82. https://doi.org/10.1016/s0018-506x(02)00037-5

Adobe (2019) Adobe Audition CC (12.1.4.5) [Software]. https://www.adobe.com/mx/products/audition.html. Accessed 4 Apr 2023

Aguilar-Cucurachi MAS, Dias PAD, Rangel-Negrín A, Chavira R, Boeck L, Canales-Espinosa D (2010) Preliminary evidence of accumulation of stress during translocation in mantled howlers. Am J Primatol 72:805–810. https://doi.org/10.1002/ajp.20841

Altmann J (1974) Observational study of behavior: sampling methods. Behaviour 49:227–267. https://doi.org/10.1002/zamm.19730531271

Archer J, Huntingford F (1994) Game theory models and escalation of animal fights. In: Potegal M, Knutson JF (eds) The dynamics of aggression. Lawrence Erlbaum Associates, Hillsdale, pp 3–31

Arnott G, Elwood RW (2009) Assessment of fighting ability in animal contests. Anim Behav 77:991–1004. https://doi.org/10.1016/j.anbehav.2009.02.010

Aureli F, de Waal F (2000) Natural conflict resolution. University of California Press, Berkeley

Baldwin JD, Baldwin JI (1976) Vocalizations of howler monkeys (*Alouatta palliata*) in southwestern Panama. Folia Primatol 26:81–108. https://doi.org/10.1159/000155733

Boersma P, Weenink D (2020) PRAAT: Doing phonetics by computer (6.1.16) [Software]. http://www.praat.org/. Accessed 4 Apr 2023

Booth A, Granger DA, Mazur A, Kivlighan KT (2006) Testosterone and social behavior. Soc Forces 85:166–192. https://doi.org/10.1353/sof.2006.0116

Bowling DL, Garcia M, Dunn JC, Ruprecht R, Stewart A, Frommolt KH, Fitch WT (2017) Body size and vocalization in primates and carnivores. Sci Rep 7:1–11. https://doi.org/10.1038/srep41070

Briseño-Jaramillo M, Estrada A, Lemasson A (2015) Individual voice recognition and an auditory map of neighbours in free-ranging black howler monkeys (*Alouatta pigra*). Behav Ecol Sociobiol 69:13–25. https://doi.org/10.1007/s00265-014-1813-9491

Brockman DK, Whitten PL, Richard AF, Schneider A (1998) Reproduction in free-ranging male *Propithecus verreauxi*: The hormonal correlated of mating and aggression. Am J Phys Anthropol 105:137–151. https://doi.org/10.1002/(SICI)1096-8644(199802)105:2%3c137::AID-AJPA3%3e3.0.CO;2-S

Cañadas-Santiago S, Dias PAD, Garau S, Coyohua Fuentes A, Chavira-Ramírez DR, Canales Espinosa D, Rangel-Negrín A (2020) Behavioral and physiological stress responses to local spatial disturbance and human activities by howler monkeys at Los Tuxtlas, Mexico. Anim Conserv 23:297–306. https://doi.org/10.1111/acv.12541

Ceccarelli E, Rangel-Negrín A, Coyohua-Fuentes A, Canales-Espinosa D, Dias PAD (2021) Vocal and movement responses of mantled howler monkeys (*Alouatta palliata*) to natural loud calls from neighbors. Am J Primatol 83:e23252. https://doi.org/10.1002/ajp.23252

Clutton-Brock TH, Albon SD, Gibson RM, Guiness FE (1979) The logical stag: adaptive aspects of fighting behaviour in red deer. Anirn Behav 2722:1–225. https://doi.org/10.1016/0003-3472(79)90141-6

Cristóbal-Azkarate J, Dias PAD, Veà J (2004) Causes of intraspecific aggression in the mantled howler monkey (*Alouatta palliata mexicana*): evidence from injuries, demography, and habitat. Int J Primatol 25:939–953. https://doi.org/10.1023/B:IJOP.0000029130.10312.63

Cristóbal-Azkarate J, Chavira R, Boeck L, Rodríguez-Luna E, Veà JJ (2006) Testosterone levels of free-ranging resident mantled howler monkey males in relation to the number and density of solitary males: a test of the challenge hypothesis. Horm Behav 49:261–267. https://doi.org/10.1016/j.yhbeh.2005.07.015

Crockett CM (2003) Re-evaluating the sexual selection hypothesis for infanticide by *Alouatta* males. In: Jones CB (ed) Sexual selection and reproductive competition in primates: new perspectives and directions. American Society of Primatologists, Norman, pp 327–365

da Cunha RGT, Byrne RW (2006) Roars of black howler monkeys: evidence for a function in intergroup spacing. Behaviour 143:1169–1199. https://doi.org/10.1163/156853906778691568

DeGusta D, Milton K (1998) Skeletal pathologies in a population of *Alouatta palliata*: behavioral, ecological, and evolutionary implications. Int J Primatol 19:615–650. https://doi.org/10.1023/A:1020372825031

Dias PAD, Coyohua-Fuentes A, Canales-Espinosa D, Chavira Ramírez DR, Rangel-Negrín A (2017) Hormonal correlates of energetic condition in mantled howler monkeys. Horm Behav 94:13–20. https://doi.org/10.1016/j.yhbeh.2017.06.003

Dias PAD, Coyohua-Fuentes A, Canales-Espinosa D, Chavira-Ramírez DR, Rangel-Negrín A (2022) Correlates of hormonal variation in mantled howler monkey males, *Alouatta palliata*. Am J Phys Anthropol 178:17–28. https://doi.org/10.1002/ajpa.24464

Dunbar RIM (1988) Primate Social Systems. Cornell University Press, Ithaca

Dunn JC, Halenar LB, Davies TG, Cristobal-Azkarate J, Reby D, Sykes D, Dengg S, Fitch WT, Knapp LA (2015) Evolutionary trade-off between vocal tract and testes dimensions in howler monkeys. Curr Biol 25:2839–2844. https://doi.org/10.1016/j.cub.2015.09.029

Enquist M, Leimar O (1983) Evolution of fighting behaviour: decision rules and assessment of relative strength. J Theor Biol 102:387–410. https://doi.org/10.1016/0022-5193(83)90376-4

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. https://doi.org/10.1007/s10329-006-0033-y

Fitch WT (1997) Vocal tract length and formant frequency dispersion correlate with body size in rhesus macaques. J Acoust Soc Am 102(2):1213–1221. https://doi.org/10.1121/1.421048

Fitch WT, Fritz JB (2006) Rhesus macaques spontaneously perceive formants in conspecific vocalizations. J Acoust Soc Am 120:2132–2141. https://doi.org/10.1121/1.2258499

Gamba M, Colombo C, Giacoma C (2012) Acoustic cues to caller identity in lemurs: a case study. J Ethol 30:191–196. https://doi.org/10.1007/s10164-577011-0291-z

Garcia M, Herbst CT, Bowling DL, Dunn JC, Fitch WT (2017) Acoustic allometry revisited: morphological determinants of fundamental frequency in primate vocal production. Sci Rep 7:10450. https://doi.org/10.1038/s41598-017-11000-x

Glander KE (1992) Dispersal patterns in Costa Rican mantled howling monkeys. Int J Primatol 13:415–436. https://doi.org/10.1007/BF02547826

Gómez-Espinosa E, Rangel-Negrín A, Chavira R, Canales-Espinosa D, Dias PAD (2014) The effect of energetic and psychosocial stressors on glucocorticoids in mantled howlers (*Alouatta palliata*). Am J Primatol 76:362–373. https://doi.org/10.1002/ajp.22240

Harris TR, Fitch WT, Goldstein LM, Fashing PJ (2006) Black and white colobus monkey (*Colobus guereza*) roars as a source of both honest and exaggerated information about body mass. Ethol 112:911–920. https://doi.org/10.1111/j.1439-0310.2006.01247.x

Hienz RD, Jones AM, Weerts EM (2004) The discrimination of baboon grunt calls and human vowel sounds by baboons. J Acoust Soc Am 116:1692–1697. https://doi.org/10.1121/1.1778902

Hopkins ME (2013) Relative dominance and resource availability mediate mantled howler (*Alouatta palliata*) spatial responses to neighbors' loud calls. Int J Primatol 34:1032–1054. https://doi.org/10.1007/s10764-013-9713-9

Jaeggi AV, Trumble BC, Brown M (2018) Group-level competition influences urinary steroid hormones among wild red-tailed monkeys, indicating energetic costs. Am J Primatol 80:e22757. https://doi.org/10.1002/ajp.22757

Kitchen DM (2004) Alpha male black howler monkey responses to loud calls. Anim Behav 67:125–139. https://doi.org/10.1016/j.anbehav.2003.03.007

Maya Lastra N, Rangel-Negrín A, Canales-Espinosa D, Coyohua-Fuentes A, Dias PAD (2023) Behavioral responses of mantled howler monkeys to neighbor long-distance vocalizations. Am J Biol Anthropol 182:59–68. https://doi.org/10.1002/ajpa.24810

Maynard Smith J (1982) Do animals convey information about their intentions? J Theor Biol 97:1–5. https://doi.org/10.1016/0022-5193(82)90271-5

Maynard Smith J, Parker GA (1976) The logic of asymmetric contests. Behaviour 24:159–175. https://doi.org/10.1016/S0003-3472(76)80110-8

Maynard Smith J, Price GR (1973) The logic of animal conflict. Nature 246:15–18. https://doi.org/10.1038/246015a0

Owren MJ (1990) Acoustic classification of alarm calls by vervet monkeys (*Cercopithecus aethiops*) and humans (*Homo sapiens*): I. Natural Calls J Comp Psychol 104:20–28. https://doi.org/10.1037/0735-7036.104.1.20

Owren MJ, Seyfarth RM, Cheney DL (1997) The acoustic features of vowel-like grunt calls in chacma baboons (*Papio cyncephalus ursinus*): implications for production processes and functions. J Acoust Soc Am 101:2951–2963. https://doi.org/10.1121/1.418523

Parker GA (1974) Assessment strategy and evolution of fighting behavior. J Theor Biol 47:223–243. https://doi.org/10.1016/0022-5193(74)90111-8

Pinheiro J, Bates D (2000) Mixed-effects models in s and S-plus. Springer, New York

Pontzer H, Raichlen DA, Gordon AD, Schroepfer-Walker KK, Hare BA, O'Neill MC, Muldoon KM, Dunsworth HM, Wood BM, Isler K, Burkart J, Irwin M, Shumaker RW, Lonsdorf EV, Ross SR (2014) Primate energy expenditure and life history. Proc Natl Acad Sci USA 111:1433–1437. https://doi.org/10.1073/pnas.1316940111

Preuschoft S, van Schaik CP (2000) Dominance and communication. In: Aureli F, de Waal FBM (eds) Natural conflict resolution. University of California Press, Berkeley, pp 77–105

R Core Team (2023) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/. Accessed 4 Apr 2023

Rangel-Negrín A, Dias PAD, Chavira R, Canales-Espinosa D (2011) Social modulation of testosterone levels in male black howlers (*Alouatta pigra*). Horm Behav 59:159–166. https://doi.org/10.1016/j.yhbeh.2010.11.005

Rangel-Negrín A, Coyohua-Fuentes A, de la Torre HA, Cano-Huertes B, Reynoso-Cruz E, Ceccarelli E, Gómez Espinosa E, Chavira Ramírez DR, Moreno-Espinoza D, Canales-Espinosa D, Maya-Lastra N, Cruz-Miros P, Cañadas Santiago S, Garau S, Dias PAD (2021) Female reproductive energetics in mantled howler monkeys (*Alouatta palliata*): a follow-up study. Am J Phys Anthropol 174:396–406. https://doi.org/10.1002/ajpa.24222

Reby D, McComb K (2003) Anatomical constraints generate honesty: Acoustic cues to age and weight in the roars of red deer stags. Anim Behav 65:519–530. https://doi.org/10.1006/anbe.2003.2078

Riede T, Fitch WT (1999) Vocal tract length and acoustics of vocalization in the domestic dog (*Canis familiaris*). J Exp Biol 202:2859–2867. https://doi.org/10.1242/jeb.202.20.2859

Ross CN, French JA, Patera KJ (2004) Intensity of aggressive interactions modulates testosterone in male marmosets. Physiol Behav 83:437–445. https://doi.org/10.1016/j.physbeh.2004.08.036

Sapolsky RM, Romero M, Munck AU (2000) How do glucocorticoids influence stress responses? Integrating permissive, suppressive, stimulatory, and preparative actions. Endocr Res 21:55–89. https://doi.org/10.1210/edrv.21.1.0389

Schön MA (1971) The anatomy of the resonating mechanism in howling monkeys. Folia Primatol 15:117–132. https://doi.org/10.1159/000155371

Schoof VM, Jack KM (2013) The association of intergroup encounters, dominance status, and fecal androgen and glucocorticoid profiles in wild male white-faced capuchins (*Cebus capucinus*). Am J Primatol 75:107–115. https://doi.org/10.1002/ajp.22089

Sekulic R, Chivers DJ (1986) The significance of call duration in howler monkeys. Int J Primatol 7:183–190. https://doi.org/10.1007/BF02692317

Sommers MS, Moody DB, Prosen CA, Stebbins WC (1992) Formant frequency discrimination by Japanese macaques (*Macaca fuscata*). J Acoust Soc Am 91:3499–3510. https://doi.org/10.1121/1.402839

Taylor AM, Reby D (2010) The contribution of source-filter theory to mammal vocal communication research. J Zool 280:221–236. https://doi.org/10.1111/j.1469-7998.2009.00661.x

Teichroeb JA, Sicotte P (2008) Social correlates of fecal testosterone in male ursine colobus monkeys (*Colobus vellerosus*): The effect of male reproductive competition in aseasonal breeders. Horm Behav 54:417–423. https://doi.org/10.1016/j.yhbeh.2008.04.006

Van Belle S, Estrada A (2020) The influence of loud calls on intergroup spacing mechanism in black howler monkeys (*Alouatta pigra*). Int J Primatol 41:265–286. https://doi.org/10.1007/s10764-019-00121-x

Van Belle S, Scarry CJ (2015) Individual participation in intergroup contests is mediated by numerical assessment strategies in black howler and tufted capuchin monkeys. Philos Trans R Soc Lond B 370:20150007. https://doi.org/10.1098/rstb.2015.0007

van Rhijn JG, Vodegel R (1980) Being honest about one's intentions: an evolutionary strategy for animal conflicts. J Theor Biol 85:623–641. https://doi.org/10.1016/0022-5193(80)90261-1

Vehrencamp SL (2000) Handicap, index, and conventional signal elements of bird song. In: Espmark Y, Amundsen T, Rosenqvist G (eds) Animal signals: Signalling and signal design in animal communication. Tapir Academic Press, Norway, pp 277–300

Wasser SK, Hunt KE, Brown JL, Cooper K, Crockett CM, Bechert U, Millspaugh JJ, Larson S, Monfort SL (2000) A generalized fecal glucocorticoid assay for use in a diverse array of nondomestic mammalian and avian species. Gen Comp Endocrinol 120:260–275. https://doi.org/10.1006/gcen.2000.7557

Whitehead JM (1994) Acoustic correlates of internal states in free-ranging primates: the example of the mantled howling monkey *Alouatta palliata*. In: Roeder JJ, Thierry B, Anderson JR, Herrenschmidt N (eds) Current primatology, vol II. Social development, learning and behaviour. Université Louis Pasteur, Strasbourg, pp 221–226

Whitehead J (1995) Vox Alouattinae: A preliminary survey of the acoustic characteristics of long-distance calls of howling monkeys. Int J Primatol 16:121–144. https://doi.org/10.1007/BF02700156