

RESEARCH ARTICLE



Noise intensity modulates the responses of mantled howler monkeys to anthropophony

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Abstract

Anthropogenic noise is *a major* global pollutant but its effects on primates are poorly understood, limiting our ability to develop mitigation actions that favor their welfare and conservation. In this study, we used an experimental approach to determine the impact of variation in noise intensity on mantled howler monkeys (*Alouatta palliata*). We conducted the study at Los Tuxtlas (México), where we studied the physiological stress (proxied via fecal glucocorticoid metabolites, fGCM) and behavioral responses of 16 males. We played back chainsaw noise at two intensities (40 and 80 dB) and used days in which groups were not exposed to noise as matched controls. With increased noise intensity fGCM increased, vigilance and vocalizations were longer, and vigilance, vocalizations, and flight occurred quicker. Physiological and behavioral responses occurred even after low-intensity noise playbacks (i.e., 40 dB). Therefore, noise intensity is a significant factor explaining the responses of mantled howler monkeys to anthropogenic noise. These results imply that management actions aimed at eradicating anthropogenic noise are required for the conservation and welfare of mantled howler monkeys at Los Tuxtlas.

KEYWORDS

behavior, glucocorticoids, playback experiments, stress, vigilance, vocalizations

1 | INTRODUCTION

Anthropogenic noise pertains to sounds produced by humans and their activities. Although it is mostly concentrated in areas with high human population density (Katti & Warren, 2004), anthropogenic noise is currently present worldwide, including remote natural regions (Barber et al., 2011; Bowker et al., 2012; Buxton et al., 2017; Gabriele et al., 2018). Exposure to anthropogenic noise can affect the physiology and behavior of wildlife and potentially impact their fitness (Kunc & Schmidt, 2019; Shannon et al., 2016). Therefore, anthropogenic noise is probably a significant contemporary selective pressure for wildlife (Barber et al., 2010; Francis & Barber, 2013; Slabbekoorn et al., 2010; Swaddle et al., 2015). The responses of wildlife to anthropogenic noise are determined by different noise attributes. Overall, noise that is novel, occurs in a sudden and unpredictable manner (i.e., temporality), that acoustically overlaps with biologically relevant sounds or interferes with the organism's hearing capacity (i.e., its spectral content), and is intense (i.e., high amplitude with respect to ambient values) is expected to have strong effects on wildlife (Francis & Barber, 2013; Shannon et al., 2016). Intensity is a particularly salient feature of anthropogenic noise, as increases in intensity add to the severity of impacts, independent of how stimuli are perceived (e.g., threat vs. masking: Francis & Barber, 2013).

The physiological impacts of noise intensity on wildlife range from increased blood pressure to hearing loss whereas behavioral

Abbreviations: fGCM, fecal glucocorticoid metabolites; SPL, sound pressure level.

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responses include avoidance, distraction, and changes in communication patterns (Francis & Barber, 2013; Kight & Swaddle, 2011; Shannon et al., 2016). These impacts are well characterized in several animal groups, such as birds and marine mammals (e.g., Erbe et al., 2019; Halfwerk et al., 2018; Slabbekoorn & Ripmeester, 2008; Wright et al., 2007), but there is a paucity of information for primates. A few studies suggest that noise intensity influences the behavior of primates. First, at noisier locations black-tufted marmosets (Callithrix penicillata) and black-fronted titi monkeys (Callicebus nigrifrons) change the acoustics and temporal patterns of their vocalizations (Duarte et al., 2018; Santos et al., 2017). Second, black-tufted marmosets, Bolivian gray titi monkeys (Plecturocebus donacophilus), and pygmy marmosets (Cebuella pygmaea) change their ranging behavior, by either avoiding or moving less in noisier areas (Duarte et al., 2011; Hernani Lineros et al., 2020; Sheehan & Papworth, 2019). Research in other animal groups suggests that these behavioral changes could impose fitness costs (e.g., Habib et al., 2006; Halfwerk et al., 2011; Kight & Swaddle, 2011), but the available evidence for primates neither informs on the physiological consequences of noise nor conveys information that can be used to design management actions aimed at increasing the welfare of individuals

Howler monkeys (Alouatta) are arboreal platyrrhines with a wide geographical distribution. As other primates (Estrada et al., 2017) they are increasingly affected by anthropogenic disturbance, mainly due to habitat loss and fragmentation (Arroyo-Rodríguez & Dias, 2010; Bicca-Marques et al., 2020). As a result, 14 of the 21 taxa recognized by the IUCN are threatened by extinction (IUCN, 2023). There is very scant information on the impact of anthropogenic noise on howler monkeys, but we have documented physiological and behavioral variation in mantled howler monkeys (Alouatta palliata) related to noise attributes. First, individuals have stronger physiological stress and behavioral responses to anthropogenic noise than to changes in habitat spatial patterns (e.g., land cover type; Cañadas-Santiago et al., 2020). For instance, fecal glucocorticoid metabolite concentrations and time spent in vigilance are more influenced by the occurrence of anthropogenic noise than by the amount of available forest. Second, most anthropogenic noises are not associated with a behavioral response by mantled howler monkeys, but the response likelihood depends on noise type, frequency, and intensity such that, for instance, vigilance and vocalizations are more frequent with increasing noise intensity (Gómez-Espinosa et al., 2022). Mantled howler monkeys seem therefore to be reactive to anthropogenic noise, although the available correlational data does not allow establishing which noise attributes underly their physiological and behavioral responses. In this study, we experimentally tested the hypothesis that intensity is a major factor determining the responses of wild mantled howler monkeys to anthropogenic noise. We predicted stronger physiological and behavioral reactions toward increased noise intensity, specifically, high physiological stress concentrations and both quick and long behavioral responses.

2 | METHODS

2.1 | Study sites and subjects

We conducted the study in four forest fragments located in the Los Tuxtlas Biosphere Reserve. Over the past 60 years the area has been highly disturbed by human activities and consists of a mosaic of original and secondary forests, agricultural fields, and human settlements (Von Thaden et al., 2020). We focused on five groups of mantled howler monkeys that we had studied for at least 6 years (mean ± standard deviation [SD] = 16.6 ± 6.8 years; Gómez-Espinosa et al., 2022). All groups were habituated to the presence of researchers, and we identified subjects by natural markings in their fur and other physical traits, such as scars, broken fingers, and facial features. We studied 16 resident adult males from the five groups (mean ± SD number of males per group = 3.2 ± 0.4). We focused on males because the behavior and physiology of female mantled howler monkeys vary across reproductive states (e.g., Dias et al., 2017; Rangel Negrín et al., 2021).

2.2 | Sampling of howler monkey behavior and anthropogenic noise (nonexperimental)

From January to December 2020 (240 fieldwork days) we visited each group for a mean (±SD) of 4 (±2) days per month and a mean of 7.3 (±4) consecutive hours (7:00–8:00 to 14:00–15:00, depending on the time of the year). We used focal animal sampling and 10 min continuous recordings (Altmann, 1974) to study the following behaviors: flight (movements \geq 135° from the direction of a stimulus: Van Belle and Estrada, 2019), vigilance (visual exploration of the environment directed beyond the reach of the animal's arm: Treves, 2000), vocalize (barks and roars: da Cunha et al., 2015). We recorded all instances of anthropogenic noise (i.e., aerial traffic, human voice, recreation, tools/machinery, traffic, and unknown noises: Gómez-Espinosa et al., 2022). We observed the study groups for a total of 1754 h. During this period, we also collected fecal samples from males as described in section 2.6.

2.3 | Experimental noise

We used chainsaw noise as the experimental stimulus in this study because all groups had previously been exposed to it and noise produced by tools and machinery frequently elicits behavioral responses by mantled howler monkeys at Los Tuxtlas (Gómez-Espinosa et al., 2022). We recorded the sound of a chainsaw at 2 m with a Marantz PMD 660 recorder and a Sennheiser MKE-600 microphone. We used Audacity (Audacity Team, 2020) to isolate chainsaw sound from background noise and to prepare audio playbacks. Each audio had a 10 min duration and consisted of 5 min of silence followed by five 30 s chainsaw sounds with 5 to 10 s silence intervals between them so that in total each chainsaw playback included 150 s of noise. The initial silence allowed us to move away from the speaker and position ourselves closer to the group to sample the behavioral responses of males to playbacks. To avoid pseudoreplication, we prepared different exemplars of each playback, which we randomly used as playback stimuli in the experiments.

We used a KSR speaker (KSA-6915, 13,000 W PMPO, 250 W RMS) to broadcast the chainsaw noise. Before the playback experiments, we determined the distance between the speaker and the study subjects as well as the speaker volume that would be required for the chainsaw noise to reach mantled howler monkeys at two sound pressure level (SPL) treatments, 40 and 80 dB. SPL is the pressure of sound waves within a certain frequency range in the air relative to a reference pressure. The two SPL treatments correspond to the minimum and maximum values of naturally occurring chainsaw noise recorded in a previous study (Gómez-Espinosa et al., 2022). In a similar environment to those where we would conduct the experiments, we placed the speaker at ground level and recorded SLP with a sound meter (TN-ST106, Tenmars, Taiwan; measuring range = 30–130 dB; sampling frequency = 20.8 µS (48 kHz); frequency band = 10Hz-16 kHz) at increasing distances (assessed with a measuring tape) from the speaker while regulating the speaker's volume so that chainsaw noise sounded natural.

2.4 | Experimental protocol and behavioral sampling (experimental)

We exposed the five study groups to chainsaw playbacks from January to June 2021. We located groups on the early morning and started the experiments (i.e., either the 40 dB or the 80 dB treatment) after the focal group had its first feeding bout of the day and all adult individuals were resting (i.e., sleep or static without interaction) for 10 min. The mean ± SD starting time of the experiments was 9:14 ± 2:53 h. Once the speaker's volume and distance from the group were set, we began the playback experiments. At the onset of chainsaw playbacks we performed a 10 min behavioral sampling that consisted of two parts: (i) we scanned all group males for the occurrence of flight, vigilance, and vocalizations, which are the typical behavioral responses of mantled howler monkey males to noise produced by tools/machinery (Cañadas-Santiago et al., 2020; Gómez-Espinosa et al., 2022); (ii) when a male displayed any of the target behaviors, besides noting his identity, we recorded the time and duration of the behavior.

After the end of the playback experiments, we followed groups for the rest of the day. If before, during, or after the experiments we observed any of the following events, which are stimuli with the potential to affect mantled howler monkey behavior and physiology, we discarded the experiment and rescheduled it: aggression (Dias et al., 2017; n = 1 experiment); noise produced by aerial traffic, human voice (not produced by researchers), and tools/machinery (e.g., chainsaw, lawnmower: Gómez-Espinosa et al., 2022; n = 8experiments); mating (Dias et al., 2022; n = 1 experiment). All 3 of 9

experiments were conducted under similar environmental conditions: no rain, absent to gentle wind (Beaufort Scale categories 0–2), mean SPL of 40.1 ± 2.1 dB. Each group was exposed five times to each SLP treatment, 40 and 80 dB, resulting in 10 experiments per group and a total of 50 experiments. A minimum of 15 days elapsed between consecutive experiments conducted on each group.

2.5 | Hormonal sampling

Glucocorticoid hormones are released by the hypothalamo-pituitaryadrenocortical axis in response to psychological and energetic demands (Sapolsky et al., 2000). We have previously demonstrated that the fecal concentrations of glucocorticoid metabolites (fGCM) of mantled howler monkeys are responsive to social, ecological, and anthropogenic challenges (e.g., Cañadas-Santiago et al., 2020; Dias et al., 2017, 2022; Gómez-Espinosa et al., 2014). Furthermore, there is a ca. 24-h delay between the exposure of mantled howler monkeys to an acute challenge (i.e., capture, anesthesia, and handling) and a peak in fGCM concentrations (Cañadas-Santiago et al., 2020). We therefore assessed the physiological responses of mantled howler monkey males to experimental chainsaw noise by measuring fGCM in fecal samples collected the day after playback experiments.

We collected fecal samples from the forest floor immediately after deposition when we could unambiguously match them to male identity. 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° C once back at the field station. We collected 224 fecal samples during the nonexperimental stage of the study (mean ± SD = 44.8 ± 3.9 samples per group, 14 ± 1.8 samples per male) and 185 samples during the experimental stage (mean ± SD = 18.5 ± 2.5 samples per group, 11.5 ± 0.9 samples per male).

We freeze-dried (FreeZone 18; Labconco) all fecal samples within a maximum of 6 months after collection. We extracted fGCM from dried samples following a modification of the method by Wasser et al. (2000). Briefly, we shook 0.6 g of homogenized, lyophilized, and pulverized feces for 20 h 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°C for 20 h, we reconstituted pellets with 3-mL albumin buffer which we used for fGCM assays.

We determined fGCM concentrations with a chemiluminescent immunoassay using a commercial kit (Cortisol, Immulite, Siemens; sensitivity = 5.5 nmol/L; calibration range = 28–1380 nmol/L) and an automated immunoassay system (Immulite 1000 analyzer, Siemens, Munich, Germany). The antibody in this kit is highly specific to cortisol, showing low (8.6%) cross-reactivity with corticosterone. Pooled fecal extracts, when added to the standard curve points, exhibited a similar slope (R^2 = 0.95, n = 8, p < 0.001), and serial dilutions of a fecal pool yielded results that were parallel to the kit's standards (t = 0.9, n = 4, p = 0.402). Intra-assay variation (coefficient of variation) averaged 12.1% (n = 4 samples) and inter-assay variation was 13.7% (n = 4 samples). We report fGCM values as ng/g (dry feces).

2.6 | Data organization and analysis

We defined baseline conditions as days in which groups were not exposed to noise produced by chainsaws or other tools/machinery as well as to the stimuli described in section 2.5 during the nonexperimental stage of the study. We used these baseline days as matched controls (MC) to assess the effects of experimental chainsaw noise on the behavior and fGCM of males. For the statistical analysis of male behavior, we randomly selected focal animal samples in our baseline dataset from the first male that responded to each experimental playback as MC (i.e., 50 focal animal samples in baseline days matched with observations of the same males in the 50 playback experiments). For the statistical analysis of fGCM responses, we selected as MC fecal samples that we collected during the nonexperimental stage from all males (n = 224) following a baseline day (i.e., when in the day preceding sample collection males were not exposed to the above-described stimuli).

We calculated the latency of behavioral responses of males as the time elapsed between the beginning of a focal sample (for MC) or the beginning of the playback experiments and the first displayed behavioral response. Latency could vary between 0 s, when males responded immediately, and 10 min, when they did not display any of the target behaviors. We calculated the duration of behavioral responses of males as the sum of time allocated to each of the target behaviors in the 10 min sampling periods. Duration could vary between 0 s, when males did not display behavioral responses, and 10 min, when they spent the complete sampling period displaying the target behaviors.

We used linear mixed models to test our predictions. First, we built a model in which mean fGCM concentrations per male per treatment (n = 48) were the response variable, treatment (i.e., MC, 40 dB playbacks, 80 dB playbacks) was the fixed predictor, and both male (n = 16) and group (n = 5) identity were random factors to account for the repeated measuring of males and groups. Second, we ran six models with the same fixed and random predictors and both the latency and duration of vigilance, vocalizations, and flight per treatment as response variables in each model. We log-transformed fGCM and durations to improve model fit and we checked that the assumptions of normally distributed and homogeneous residuals were fulfilled by visually inspecting Q–Q plots and residuals plotted against fitted values. Model residuals did not deviate significantly from normality (all Kolmogorov–Smirnov tests p > 0.05). We calculated post hoc pairwise comparisons with a Tukey adjustment.

We compared complete models (i.e., with fixed and random predictors) with a null model including only the random factor with likelihood ratio tests to determine whether the random factor accounted for a larger proportion of variation in response variables than the fixed factors (Pinheiro & Bates, 2000). In all cases, we found significant differences (p < 0.001 in all tests, i.e., fixed factors were

more influential in the response variables than the random factor). We calculated marginal pseudo-coefficients of determination for each model to assess the deviance in response variables explained by each model (i.e., goodness-of-fit). We performed all statistical analyses in R (R Core Team, 2023).

3 | RESULTS

fGCM of mantled howler monkey males increased with increasing intensity of chainsaw noise (Tables 1 and 2). Specifically, compared to MC there was a 112% increase and a 245% increase in mean hormone concentrations in response to 40 and 80 dB playbacks, respectively, which in turn differed by 63% (p < 0.05 in all pairwise post hoc comparisons; Figure 1a). Regarding behavioral responses to playbacks, there were significant differences between MC and experimental treatments in the latency and duration of vigilance (Figure 1b,c) and vocalizations (Figure 1d,e). Males displayed vigilance and vocalizations quicker and for longer with increasing stimuli intensity (p < 0.05 in all pairwise post hoc comparisons; Table 1

TABLE 1 Linear mixed model results of the effect of chainsaw noise on the fecal glucocorticoid metabolite concentrations (fGCM) and behavior of mantled howler monkey males.

Variable	R ² m (R ² c) ^a	χ²	Р
fGCM	0.47 (0.50)	44.9	<0.001
Latency to vigilance	0.64 (0.65)	183.1	<0.001
Vigilance duration	0.41 (0.47)	76.9	<0.001
Latency to vocalization	0.46 (0.48)	87.7	<0.001
Vocalization duration	0.58 (0.61)	144.9	<0.001
Latency to flight	0.11 (0.12)	12.8	0.002
Flight duration	0.01 (0.01)	1.0	0.594

^aMarginal coefficients of determination (R^2m) indicate the proportion of variance explained by the fixed factor whereas conditional coefficients of determination (R^2c) account for both the effects of fixed and random factors.

TABLE 2 Descriptive statistics (mean ± SD) of the variation in fecal glucocorticoid metabolite concentrations and behavior of mantled howler monkey males in response to chainsaw noise.

Variable	МС	40 dB	80 dB
fGCM (ng/g)	425 ± 250	901 ± 609	1466 ± 418
Latency to vigilance (min)	6.8 ± 2.3	2.4 ± 2.4	0.9 ± 1.0
Vigilance duration (min)	2.4 ± 1.9	4.6 ± 1.9	6.7 ± 1.5
Latency to vocalization (min)	6.8 ± 2.8	4.2 ± 3.0	1.1 ± 1.1
Vocalization duration (min)	1.7 ± 1.9	4.8 ± 2.6	7.2 ± 1.3
Latency to flight (min)	8.0 ± 2.2	7.6 ± 2.7	5.9 ± 2.7
Flight duration (min)	0.7 ± 1.2	0.8 ± 1.2	1.0 ± 1.4



FIGURE 1 Estimates (black dots) and 95% confidence intervals (gray rectangles) of linear mixed models on the influence of chainsaw noise on the physiological stress and behavior of mantled howler monkey males: (a) fecal glucocorticoid metabolites (fGCM); (b) latency to first vigilance; (c) duration of vigilance; (d) latency to first vocalization; (e) duration of vocalizations; (f) latency to first flight. Males were exposed to playbacks of chainsaw noise at two sound intensities (40 and 80 dB) whereas in MC (matched control samples) males were not exposed to noise. Significance results of post hoc pairwise comparisons (with Tukey adjustment) are indicated above horizontal lines on the top of each panel.

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and 2). No variation was observed in the duration of flight, although 80 dB playbacks elicited quicker flight responses than MC (p < 0.05 in the post hoc comparison of MC vs. 80 dB; Table 1, Figure 1e).

4 | DISCUSSION

In this study, we used playback experiments to demonstrate that the intensity of anthropogenic noise affects the physiology and behavior of wild mantled howler monkeys. As predicted, with increased noise intensity the physiological stress (fGCM) of males increased, vigilance and vocalizations were longer, and vigilance, vocalizations, and flight occurred quicker. Therefore, we confirm the hypothesis that intensity is *a major* factor determining the responses of wild mantled howler monkeys to anthropogenic noise.

Our study is not the first to assess the effects of anthropogenic noise on wild primates. Besides previous correlational evidence on fGCM and behavioral responses of mantled howler monkeys to noise (Cañadas-Santiago et al., 2020; Gómez-Espinosa et al., 2022), other species have been reported to change vocalization patterns and avoid areas with more noise (e.g., Duarte et al., 2011; Sheehan & Papworth, 2019). Those studies, however, did not establish which noise attribute was linked to primate responses (e.g., noise intensity vs. frequency), precluding precise interpretations. For instance, the decreased frequency of vocalizations by black-fronted titi monkeys in noisier locations (Duarte et al., 2018) could result from either startling caused by intense noise or spectral overlap between anthropogenic noise and vocalizations that does not allow listening, and thus answering, to conspecific calls (i.e., masking). By simulating a single type of noise reproduced at a constant duration and frequency we could parse the effects of intensity from other noise attributes. Although our experiments probably do not capture the complexity of all factors at stake (e.g., sounds produced by single loudspeakers may be unrealistic: Harding et al., 2019), these results offer direct evidence of the effects of anthropogenic noise intensity on mantled howler monkeys that can be used to inform conservation and management actions. Future research focused on variations in noise duration and frequency may provide further understanding of noise impacts on these primates.

The physiological and behavioral responses of males were proportional to the intensity of anthropogenic noise, a result that confirms previous observations in this species (Cañadas-Santiago et al., 2020) and overall evidence of noise gradient effects on wildlife responses (e.g., Guo et al., 2016; Mendes et al., 2011). Our study, however, demonstrates that even low intensity noise (40 dB) affects mantled howler monkey males. In humans it is well established that low intensity noise is perceived as annoying and has both physiological and psychological consequences (Ouis, 2001), although comparative evidence for terrestrial animals is scarce. Owls (California spotted owls, *Strix occidentalis*; Mexican spotted owls, *Strix occidentalis lucida*), for instance, do not show significant behavioral changes nor increases in physiological stress following playbacks of chainsaw noise at <60 dB (Delaney et al., 1999; Tempel & Gutiérrez, 2003), a

contrast that could result from differences in auditory perception between birds and primates (Ball & Balthazart, 2021; Weisman et al., 2014). However, pygmy marmoset behavior is also not influenced by the intensity of simulated human speech (played back at 30, 60, and 78 dB: Sheehan & Papworth, 2019) and in Bolivian gray titi monkeys, from a total of eight response variables (including fGCM and social proximity), only time spent moving was negatively associated with noise intensity (Hernani Lineros et al., 2020). Considering that mantled howler monkeys have enhanced auditory sensitivity at lower frequencies compared to other primate species (Ramsier et al., 2019), they may be particularly susceptible to anthropogenic noise, which is typically low-frequency (Barber et al., 2010; Francis et al., 2009). Further understanding of the effects of anthropogenic noise on mantled howler monkeys will require deeper knowledge of the sense of hearing of this species, which remains practically unstudied (Hernández-Salazar et al., 2015).

Mantled howler monkeys have high total energy expenditure compared to similarly sized primate species (Pontzer et al., 2014), a probable consequence of the processing costs of hard-to-digest foods (Milton, 1998). A behavioral strategy based on inactivity (e.g., they may spend >80% of daytime resting: Di Fiore & Campbell, 2007) seems to subsidize these costs and, when this strategy is impacted by natural challenges, mantled howler monkeys respond physiologically and behaviorally. For instance, fGCM concentrations increase with involvement in agonistic interactions (Dias et al., 2017); maternal vigilance increases with infant dependency (Dias et al., 2018); the duration of vocalizations increases with decreasing food availability (Ceccarelli et al., 2021); and traveling increases with decreasing ambient temperatures (Ceccarelli et al., 2019). In principle, these are evolved coping mechanisms to acute (e.g., agonism) and predictable (e.g., food seasonality) challenges. Here we show that anthropogenic noise elicits physiological and behavioral responses that emulate those observed in natural contexts. Only the duration of flight did not vary according to noise intensity. It is possible that following assessment (which is perhaps quicker with increasing noise intensity given the lower latencies to vigilance, vocalizations, and flight), males identify chainsaw noise as an annoying, although non-dangerous stimuli, and thus do not leave their current location. This interpretation implies that the energy costs of fleeing exceed those of vocalizations (a displayed behavioral response), an assumption that remains to be directly tested. Indirectly, it is supported by evidence that in face of an immediate threat (domestic dogs, Canis lupus familiaris), mantled howler monkeys do flee (Rangel-Negrín et al., 2023).

Given that anthropogenic disturbance involves novel, mostly unpredictable stimuli, that can be either acute or chronic (Francis & Barber, 2013), the question becomes if in this context the responses of mantled howler monkeys are adaptive. Our study does not allow answering this question, but there is evidence suggesting that they are not. The recurrent activation of the hypothalamic-pituitaryadrenocortical axis could affect growth, reproduction, and survival (Bonier et al., 2009; Breuner et al., 2008; Sapolsky et al., 2000; but see Dantzer et al., 2014), whereas the displaying of vocalizations, through its impact on the behavioral energy-saving strategy of mantled howler monkeys, could disturb their energy balance (Holt et al., 2013; Ilany et al., 2013; Ophir et al., 2010). Given that mantled howler monkeys have been exposed to chainsaw noise and other sources of anthropogenic noise for several decades, and that those noises are generally harmless (i.e., low intensity, do not proxy hazard: Gómez-Espinosa et al., 2022), these physiological and behavioral responses indicate lack of habituation (i.e., decreased responses due to repeated stimulation: Hinde, 1970), which could be maladaptive (Ghalambor et al., 2007). Long-term studies of mantled howler monkeys living in areas with varying degrees of anthropogenic noise should allow addressing this question, but, from a welfare and conservation perspective, we should aim at reducing the exposure of mantled howler monkeys to anthropogenic noise immediately.

We conclude that noise intensity is *a major* factor explaining the responses of mantled howler monkeys to anthropogenic noise. Our sampling regime may be considered low impact, as each playback consisted of only 150s of noise per day, consecutive playbacks in each group were separated by a minimum of 15 days, and the experimental study encompassed 6 months. Yet, males consistently reacted to noise, even to low-intensity playbacks, thus suggesting that management actions aimed at eradicating anthropogenic noise are required for the conservation and welfare of mantled howler monkeys at Los Tuxtlas.

AUTHOR CONTRIBUTIONS

Pedro A. D. Dias: Conceptualization (equal); data curation (equal); formal analysis (equal); funding acquisition (equal); investigation (equal); methodology (equal); project administration (equal); resources (equal); supervision (equal); validation (equal); visualization (equal); writing—original draft (equal); writing—review and editing (equal). **Eugenia Eréndira Gómez Espinosa**: Data curation (equal); formal analysis (equal); investigation (equal); methodology (equal); writing—original draft (equal). **David Roberto Chavira Ramírez**: Data curation (equal); formal analysis (equal); investigation (equal); methodology (equal); resources (equal); writing—original draft (equal). **Ariadna Rangel Negrín**: Conceptualization (equal); data curation (equal); formal analysis (equal); funding acquisition (equal); investigation (equal); methodology (equal); project administration (equal); resources (equal); supervision (equal); validation (equal); visualization (equal); writing—original draft (equal).

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

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

ETHICS STATEMENT

Our research protocols were approved by the Secretaria de Medio Ambiente y Recursos Naturales (permit SGPA/DGVS/04015/21) and complied to the legal requirements of the Mexican law. The research adhered to the American Society of Primatologists Principles for the Ethical Treatment of Nonhuman Primates.

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