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The influence of anthropogenic noise on the behavior of male mantled howler monkeys

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Abstract

Anthropogenic noise is increasingly disturbing natural soundscapes and affecting the physiology, behavior, and fitness of wildlife. However, our knowledge about the impact of anthropogenic noise on wild primates is scant. Here, we assess the effects of anthropogenic noise on the behavior of male mantled howler monkeys (*Alouatta palliata*). Specifically, we describe the types, rates, and sound pressure level (SPL) of anthropogenic noise that occurs in areas inhabited by mantled howler monkeys and determine if the behavioral responses of males to anthropogenic noise are influenced by noise attributes. For 1 year (1753 h), we characterized anthropogenic noise in the Los Tuxtlas Biosphere Reserve (Veracruz, Mexico) and studied the behavior of males belonging to five groups. Anthropogenic noise was common, diverse, and varied among areas in terms of rate, type, and SPL. Males did not display behavioral responses toward most (60%) anthropogenic noises, but were more likely to respond to certain noise types (e.g., aerial traffic) and toward noise with high SPL. Group identity influenced the likelihood of displaying behavioral responses to noise. The most common behavioral responses were vocalizations and vigilance. Males vocalized in response to noise with high SPL, although this relationship depended on group identity. The effect of the number of noises on vocalizations also varied among groups. Males were more likely to display vigilance toward high SPL and infrequent noise, but, again, these relationships varied among groups. In sum, anthropogenic noise is pervasive in areas inhabited by mantled howler monkeys and influences male behavior. Experience and frequency of exposure may modulate the behavioral responses of male mantled howler monkeys to noise and explain the group differences.

KEYWORDS
anthrophony, noise pollution, soundscape ecology, vigilance, vocalizations

1 | INTRODUCTION

Humans have a pervasive influence on the environment through deforestation, biodiversity destruction, and climate change, among others (Ripple et al., 2017). An additional more subtle impact of humans on nature is noise pollution. Man-made noise (anthropogenic noise, hereafter) pertains to the portion of the global soundscape produced by humans and their activities (Slabbekoorn et al., 2018), and includes noise associated with traffic, construction, extractive activities, and energy production. Although anthropogenic noise concentrates mostly

Abbreviations: SPL, sound pressure level; VIP, variance inflation factor.

in urban settings (Mennitt et al., 2013), it is increasingly ubiquitous, even in rural and remote areas (e.g., Barber et al., 2011; Merchan et al., 2014; Rabanal et al., 2010). Consequently, wildlife is being exposed to anthropogenic noise (Barber et al., 2010; Blickley & Patricelli, 2010; Jerem & Mathews, 2021; Shannon et al., 2016; Slabbekoorn et al., 2018; Sordello et al., 2020).

The impact of anthropogenic noise on wildlife may be classified into three main domains (Francis & Barber, 2013). First, it may impact fitness, for instance, through increases in vulnerability to predation (Simpson et al., 2016) or reduced reproductive success (Halfwerk et al., 2011). Second, it may have negative physiological effects, such as auditory damage (e.g., Dooling & Popper, 2007), increases in physiological stress (e.g., Blickley et al., 2012a), and decreased immune function (e.g., Du et al., 2010; Romano et al., 2004). Third, wildlife commonly displays behavioral responses to noise, which mainly relate to changes in diel patterns and time budgets, movement, communication, and mating (Barber et al., 2010; Duquette et al., 2021; Francis & Barber, 2013; Shannon et al., 2016). Both physiological and behavioral responses to noise may have fitness costs (Bonier et al., 2009; Habib et al., 2007; Halfwerk et al., 2011), and the interactions among these domains are extensive and complex (Francis & Barber, 2013). Thus, assessing the extent and nature of the responses of wildlife to anthropogenic noise is important to inform conservation and management strategies (Chen & Koprowski, 2015; Kight & Swaddle, 2011; Shannon et al., 2016).

Primates, an Order that includes >500 taxa, is one of the world's most endangered taxonomic groups (Estrada et al., 2017), and has been the subject of extensive research during the last decades (Junker et al., 2017). Nevertheless, our knowledge of the effects of anthropogenic noise on wild primates is scant. There is evidence that, in the presence of noise, primates: (i) change their vocalizations by calling less frequently (black tufted-ear marmosets, *Callithrix penicillata*; black-fronted titi monkeys, *Callicebus nigrifrons*; mantled howler monkeys, *Alouatta palliata*), calling for longer (black tufted-ear marmosets) or shorter (black-fronted titi monkeys) periods, modifying the diel pattern of calling (black-fronted titi monkeys), or by changing the acoustic attributes of vocalizations (black tufted-ear marmosets) (Cañadas-Santiago et al., 2020; Duarte et al., 2018; Santos et al., 2017); (ii) modify their movement patterns, by reducing (Bolivian gray titi monkeys, *Plecturocebus donacophilus*) or increasing (mantled howler monkeys) time spent moving (Cañadas-Santiago et al., 2020; Hernani Lineros et al., 2020), and by avoiding noise (black tufted-ear marmosets: Duarte et al., 2011; pygmy marmosets, *Cebuella pygmaea*: Sheehan & Papworth, 2019); (iii) spend more time vigilant (mantled howler monkeys: Cañadas-Santiago et al., 2020; pygmy marmosets: Sheehan & Papworth, 2019); (iv) spend less time resting and feeding (pygmy marmosets: Sheehan & Papworth, 2019); and (v) increase physiological stress levels (mantled howler monkeys: Cañadas-Santiago et al., 2020; but see Hernani Lineros et al., 2020). Thus, all species examined to date respond to anthropogenic noise, although specific responses vary among taxa.

Here, we focus on mantled howler monkeys. Howler monkeys are arboreal quadrupeds and can be found in different tropical forest types, from tropical dry forests to evergreen forests (Crockett, 1998). Compared to other platyrrhines, howler monkeys are resilient to anthropogenic disturbance, as they may be found in areas where other primate species have become extinct (Bicknell & Peres, 2010; Gilbert, 2003). However, there is consistent evidence that howler monkey demography, behavior, and physiology is negatively impacted by anthropogenic disturbance (Arroyo-Rodríguez & Dias, 2010), thus raising the question of whether their resilience in the short-term may still entail long-term extinction (Bicca-Marques et al., 2020). Accordingly, 63% of howler monkey taxa assessed by the International Union for Conservation of Nature (IUCN) are in a threatened category and 84% have decreasing population trends (*N* = 19 taxa: IUCN, 2021). The study of the impact of anthropogenic disturbance on howler monkeys has mostly focused on correlating measures of habitat spatial patterns (e.g., forest fragment size: Arroyo-Rodríguez et al., 2013) and vegetation structure and composition (e.g., floristic diversity: Cristóbal-Azkarate et al., 2005) with a specific realm of response (e.g., behavior: Dias & Rangel-Negrín, 2015a; demography: Alcocer-Rodríguez et al., 2021; Cristóbal-Azkarate et al., 2017; Dias et al., 2015; stress physiology: Gómez-Espinosa et al., 2014; Rangel-Negrín et al., 2014). Howler monkeys modify their behavior and stress physiology in response to increased human presence, although it is unclear whether such changes are linked to human presence per se, anthropogenic noise, or some other stimuli (Aguilar-Melo et al., 2013; Behie et al., 2010; de la Torre et al., 1999).

We have previously determined that human presence, and particularly noise, has stronger effects on the behavior and physiological stress of individuals than changes in habitat spatial patterns (e.g., land-cover changes; Cañadas-Santiago et al., 2020). However, we could not assess whether different noise types elicited different behavioral responses and if, in addition to the amount of exposure to noise, the acoustic properties of noise affected their behavior. In the present study, we had two aims: (i) to describe the types, rates, and sound pressure level (i.e., the pressure of sound waves within a certain frequency range in the air relative to a reference pressure) of anthropogenic noises that occur in the habitat of mantled howler monkey groups; (ii) to determine if behavioral responses to anthropogenic noise by male mantled howler monkeys are influenced by noise type and rate, and noise sound pressure level. Concerning the latter, we stated two hypotheses based on previous evidence on the effects of anthropogenic noise on wildlife (Francis & Barber, 2013; Kight & Swaddle, 2011; Shannon et al., 2016). First, the likelihood of observing a behavioral response to anthropogenic noise depends on the type and sound pressure level of noise. We predicted that responses should vary among noise types and should be more likely at increasing sound pressure level. Second, we hypothesized that the displaying of each behavioral response type would be modulated by the rate and sound pressure level of anthropogenic noises. We predicted that behavioral responses should be more likely toward noises that occur more frequently and those with increasing sound pressure level. Given that previous exposure may affect behavioral responses to noise (Bejder et al., 2009; Ellison et al., 2012; Harding et al., 2018; LaZerte et al., 2016; Radford et al., 2016) we also explored behavioral variation among groups.

2 | MATERIALS AND METHODS

2.1 | Ethics statement

Research protocols were approved by the Secretaria de Medio Ambiente y Recursos Naturales (permit SGPA/DGVS/13528/19) and adhered 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. After July 2020, we followed the recommendations of Lappan et al. (2020) to reduce the risk of zoonoses between human and nonhuman primates.

2.2 | Study sites and subjects

We conducted the study in the Los Tuxtlas Biosphere Reserve, Veracruz (Mexico). During the past 60 years, the original tropical evergreen rainforest of the region has been disturbed by human activities, resulting in a mosaic of forest fragments scattered in a matrix of anthropogenic land covers (Von Thaden et al., 2020). We focused on four forest fragments where mantled howler monkeys have been studied for up to 20 years and in which noise associated with humans is recurrent (Table 1). All groups are habituated to the presence of researchers.

We identified the study subjects by the natural markings in their fur and a variety of other physical traits, including scars, broken fingers, and facial features. Given that the reproductive state affects the behavior of female mantled howler monkeys (e.g., females are more active at lactation onset than at other states: Rangel-Negrín et al., 2021), in this study we concentrated on the 16 adult males residing in the five study groups.

2.3 | Noise sampling

We conducted fieldwork from January to December 2020 (240 fieldwork days). During this time, we visited each group for a mean (±SD) of 4 (±2) days per month. Each day we followed groups for seven consecutive hours (7:00–8:00 to 15:00–16:00, depending on the time of the year). We attempted to record all instances of anthropogenic noise during each fieldwork day by noting the type of noise and measuring sound pressure level with a digital sound meter (TN-ST106, Tenmars, Taiwan; measuring range = 30–130 dB; sampling frequency = 20.8 µS (48 kHz); frequency band = 10 Hz–16 kHz). We recorded sound pressure level at ground level, whereas mantled howler monkeys are arboreal and, in the study area, live in dense tropical forests. Thus, the sound pressure level measures that we report here do not correspond to the sound that reaches howler monkeys in the canopy due to variation in attenuation effects (e.g., absorption, refraction, scattering: Larsen & Radford, 2018). This implies that our measurements only allow indirect inference of the potential direct impacts of the sound pressure level of anthropogenic noise on mantled howler monkeys (e.g., hearing impairment risk).

Following Hernani Lineros et al. (2020), we classified noise as: aerial traffic (aircrafts); human voice (normal conversation, laugh, loudspeaker, scream); recreation (firecracker, music, radio); tools/machinery (chainsaw, hammer, ladder, lawnmower, machete, sprinkler); traffic (boat, jet ski, horn, siren, vehicle); and unknown (when we could not identify the source of noise). We calculated rates of anthropogenic noise by dividing the number of recorded noises by sampling effort (in hours).

2.4 | Behavioral sampling

Following the occurrence of an anthropogenic noise, we recorded the behavioral response of the first male that performed any of the following behaviors: flight (moving away in the opposite direction of

TABLE 1 Attributes of subjects, groups, and habitats studied at Los Tuxtlas, Mexico.

	Group				
Attribute	Balzapote	Borrego	La Flor G1	La Flor G2	Montepío
Location	18°36′45″ N 95°04′04″ W	18°38′24″ N 95°05′21″ W	18°26′19″ N 95°03′07″ W	18°26′02″ N 95°03′04″ W	18°37′10″ N 95°05′02″ W
Number of studied males	3	4	3	3	3
Group size	18	39	8	16	32
Fragment size (ha)	10	63.8	100	100	106.2
Distance to nearest human settlement (m)	200	140	730	1200	1435
Distance to the nearest road (m)	450	0	0	0	0
Main human activities	Fishing, cattle grazing, mining	Fishing, cattle grazing	Ornamental plant production	Ornamental plant production	Cattle grazing

the sound); socialize (social interactions as defined by Dias & Rangel-Negrín, 2015b); approach (moving toward the noise, which could also include vocalizations and branch shaking/breaking); vigilance (visual exploration of the environment directed beyond the reach of the animal's arm: Treves, 2000); vocalization (mainly barks and roars: da Cunha et al., 2015). If males did not display any of these behaviors after 5 min, we recorded the event as a "no-response." We observed the study groups for a total of 1753 h (Balzapote = 252 h; Borrego = 182 h; Flor G1 = 559 h; Flor G2 = 536 h; Montepío = 224 h).

2.5 | Data analysis

To determine if the characteristics of noise determined the likelihood of mantled howler monkeys displaying a behavioral response, we ran a generalized linear model. We used a binomial error structure (and logit link function) for a binary response variable (i.e., behavioral response yes/no) and used the type of noise, noise pressure level, and group identity as predictors. We ran the model without interactions between predictors because interactions resulted in variance inflation factors >4 for several terms. We ran post hoc Tukey's contrasts to determine which levels of noise type and group identity differed significantly.

To determine the most common behavioral responses of male mantled howler monkeys to the different types of anthropogenic noise, we used χ^2 goodness-of-fit tests. In these tests, we compared observed frequencies with expected frequencies calculated on the premise that each behavioral type should have a similar likelihood to be displayed. We calculated Pearson's residuals to best illustrate the contribution of each behavioral type to the overall test results.

To determine if the likelihood of displaying each behavior (i.e., approach, flight, socialize, vigilance, vocalizations) was linked to anthropogenic noise attributes, we used binomial generalized linear models. In these models, the response was a two-vector variable composed of the daily number of noises that elicited the behavior under analysis and the number of noises that did not elicit it. Predictors were the number of anthropogenic noises recorded per day, mean noise sound pressure level per day, group identity, and the interactions between group identity and the other predictors. We also added the number of observation hours per day as an offset variable to account for interday variation in sampling effort. Multicollinearity among predictors in these models was now (i.e., variance inflation factor < 3). We used Tukey's contrasts as post hoc tests in these models. We could only model vigilance and vocalizations because other behavioral responses (flight, socialize, and approach) occurred at low frequencies and did not allow for statistical analysis. All statistical analyses were performed in R (R Core Team, 2022).

3 | RESULTS

3.1 | Characterization of anthropogenic noise

We recorded a total of 1746 anthropogenic noise events (Table 2). The most frequent type of noise was traffic, which accounted for more than half of all recorded noises, whereas the source of a few noises could not be identified and the noise with the lowest number of recordings was aerial traffic. When observation effort is accounted for, overall, traffic was still the most common noise type, although in the habitat of two groups human voice was the most frequent type of anthropogenic noise. The area inhabited by Borrego was the noisiest, with a noise rate that almost doubled that of the second noisiest area (Balzapote), followed by those inhabited by Flor G1, Montepío, and Flor G2.

We recorded the sound pressure level of 671 anthropogenic noises. Aerial traffic and recreation noises had on average the highest sound pressure level, although in general sound pressure level was not highly variable among anthropogenic noise types (Table 3). On average, aerial traffic had the highest sound pressure level for three groups (Borrego, Flor G1, and Flor G2), whereas recreation noise had the highest sound pressure level for another two groups (Balzapote and Montepío). Sound pressure level was higher in the areas inhabited by Balzapote and Borrego than elsewhere.

TABLE 2 The absolute number (and rates, per hour, within parenthesis) of anthropogenic noises recorded in the habitat of five mantled howler monkey groups studied between January and December 2020, at Los Tuxtlas, Mexico.

Noise type	Site					
	Balzapote	Borrego	Flor G1	Flor G2	Montepío	Total
Traffic	87 (0.35)	264 (**1.45**)	401 (**0.72**)	202 (**0.38**)	7 (0.03)	961 (0.55)
Human voice	154 (**0.61**)	73 (0.40)	86 (0.15)	66 (0.12)	108 (0.48)	487 (0.28)
Recreation	60 (0.24)	52 (0.29)	4 (0.01)	3 (0.01)	13 (0.06)	132 (0.08)
Tool/machinery	19 (0.08)	0 (0.00)	77 (0.14)	35 (0.07)	1 (<0.01)	132 (0.08)
Aerial traffic	3 (0.01)	3 (0.02)	2 (0.00)	4 (0.01)	12 (0.05)	24 (0.01)
Unknown	0 (0.00)	0 (0.00)	7 (0.01)	3 (0.01)	0 (0.00)	10 (0.01)
Total	323 (1.28)	392 (2.15)	577 (1.03)	313 (0.58)	141 (0.63)	1746 (1.0)

Note: The noise type with the highest rate for each group is in bold.

TABLE 3 Mean ± SD sound pressure level (in dB) of anthropogenic noises (sound pressure level in dB) recorded in the habitat of five mantled howler monkey groups studied between January and December, 2020, at Los Tuxtlas, Mexico (*N* = 671 noises).

Noise type	Site Balzapote	Borrego	Flor G1	Flor G2	Montepío	Total
Aerial traffic	n.m.	47.5 ± 3.5	45.0 ± 6.1	41.0 ± 5.2	32.4 ± 1.8	41.5 ± 4.3
Recreation	46.3 ± **5.4**	42.2 ± 2.5	33.3 ± 3.1	38.0 ± 4.7	32.7 ± 1.3	38.5 ± 3.2
Human voice	44.0 ± 3.4	42.5 ± 2.4	29.1 ± 4.3	34.3 ± 4.2	31.5 ± 2.0	36.3 ± 4.3
Tool/machinery	42.1 ± 3.8	42.0 ± 4.9	32.7 ± 3.2	33.3 ± 3.0	31.0 ± 1.7	36.2 ± 5.6
Traffic	46.2 ± 0.9	n.r.	38.1 ± 5.5	33.0 ± 4.2	n.m.	35.8 ± 5.0
Total	44.6 ± 3.5	43.5 ± 3.2	33.7 ± 4.3	35.9 ± 4.3	31.9 ± 1.8	37.9 ± 4.5

Note: Highest mean sound pressure for each group is in bold.

Abbreviations: n.m., not measured (i.e., we could not obtain a sound pressure level measure for this sound); n.r., not recorded (i.e., this sound type was not recorded at the site).

3.2 | Behavioral responses to noise

A majority (61%, 1062 of 1746 recordings) of anthropogenic noises did not elicit a behavioral response by males. However, noise type ($\chi^2_{4,\ 671} = 55.6$, $p < 0.001$), group identity ($\chi^2_{4,\ 671} = 53.7$, $p < 0.001$), and sound pressure level ($\chi^2_{1,\ 671} = 165.1$, $p < 0.001$), influenced the likelihood of behavioral responses ($R^2 = 0.45$; Table 4). In particular, males responded more: (1) to aerial traffic than to all other sound types (post hoc tests $p < 0.001$; Figure 1a); (2) to human voice, recreation, and tools/machinery than to traffic (post hoc tests $p < 0.001$; Figure 1a); (3) in Flor G1, Flor G2, and Montepío than in Balzapote (post hoc tests $p < 0.001$; Figure 1b); (4) in Flor G1 and Flor G2 than in Borrego (post hoc tests $p < 0.001$); and 5) to noise with high sound pressure level (Figure 2).

The most frequent behavioral response of howler monkeys to noise was vocalization (56%), followed by vigilance (38%), socialization (3%), flight (2%), and approach (1%). Vigilance was the most frequent behavior displayed toward recreation, whereas vocalizations were frequently produced in response to aerial traffic, tools/machinery, and traffic (Table 5). Human voice mostly elicited vigilance and vocalizations.

Across the day, the likelihood of responding to noise with vigilance was influenced by sound pressure level ($\chi^2_{1,\ 239} = 76$, $p < 0.001$) and number of noises recorded ($\chi^2_{1,\ 239} = 5$, $p = 0.019$), as well as by the interactions between each of these predictors and group identity (sound pressure level: $\chi^2_{4,\ 239} = 16$, $p = 0.002$; number of noises: $\chi^2_{4,\ 239} = 37$, $p < 0.001$; $R^2 = 0.60$; Table 4). Specifically, vigilance was positively related to sound pressure level ($\beta = 0.17$), negatively related to the number of noises recorded ($\beta = -0.35$), the slope of the relationship between vigilance and sound pressure level was different between groups Balzapote and Flor G2 (post hoc test $p = 0.001$; Figure 3a), and that of the relationship between vigilance and number of noises recorded was different between Balzapote and both Flor G1 and Montepío (post hoc tests $p < 0.001$; Figure 3b). Vocalization responses were related to sound pressure level ($\chi^2_{1,\ 239} = 21$, $p < 0.001$), the interaction between sound pressure level and group identity ($\chi^2_{4,\ 239} = 27$, $p < 0.001$), and the interaction between the number of noises recorded and group identity ($\chi^2_{4,\ 239} = 28$, $p < 0.001$; $R^2 = 0.60$), but not to the number of noises recorded alone ($\chi^2_{1,\ 239} = 0.4$, $p = 0.839$). Howler monkeys were more likely to vocalize following high sound pressure level noises ($\beta = 0.01$), the slope of this relationship was steeper in Montepío than in other habitat (post hoc tests $p < 0.05$; Figure 3c), and the relationship between vocalization responses and the number of noises recorded was different between Montepío (negative) and Balzapote, Flor G1, and Flor G2 (no relationship) groups (post hoc tests $p < 0.01$; Figure 3d).

4 | DISCUSSION

In this study, we described anthropogenic noise occurring in the areas inhabited by five mantled howler monkey groups and the behavioral responses of males toward it. Anthropogenic noise was common, diverse, and varied among groups in terms of frequency of occurrence, type, and sound pressure level. Males did not display behavioral responses toward most anthropogenic noise, but as predicted, were more likely to respond to certain noise types and toward noise with high sound pressure levels. Additionally, group identity was an influential factor in the likelihood of displaying behavioral responses to noise. The most common behavioral responses to noise were vocalization and vigilance. Males vocalized in response to noise with high sound pressure level, although this relationship depended on group identity. Similarly, the effect of the daily number of noises recorded on vocalizations varied among groups. Males were more likely to display vigilance toward high sound pressure levels and infrequent noise but, again, these relationships varied among groups. Thus, this study demonstrates that anthropogenic noise is pervasive in the habitat of mantled howler monkeys living at Los Tuxtlas and influences the behavior of males.

The high number of noises recorded in this study indicates that anthropogenic noise represents a salient component of the soundscape of the Los Tuxtlas region. Some noise types, such as road traffic and human voice, were particularly frequent, probably due to the proximity of roads and human settlements to the areas inhabited by

TABLE 4 GLM results of models exploring the likelihood of displaying a behavioral response, vigilance, and vocalizations following anthropogenic noise by mantled howler monkeys studied between January and December 2020, at Los Tuxtlas, Mexico.

Model/term	Estimate	SE	*z*	*p* Value	95% CI Lower	95% CI Upper
Occurrence of a behavioral response						
Type[a]						
Aerial traffic	−2.08	0.42	−4.936	<0.001	−2.940	−1.282
Recreation	−1.16	0.50	−2.299	0.022	−2.165	−0.185
Tools/machinery	−0.78	0.58	−1.341	0.18	−1.931	0.360
Traffic	−2.88	0.45	−6.454	<0.001	−3.795	−2.042
Sound pressure level	0.21	0.02	10.034	<0.001	0.171	0.253
Group[b]						
Borrego	−0.79	0.46	−1.690	0.091	−1.730	0.102
Flor G1	2.04	0.41	4.946	<0.001	1.254	2.878
Flor G2	2.64	0.48	5.529	<0.001	1.727	3.599
Montepío	1.91	0.42	4.543	<0.001	1.089	2.737
Vigilance						
Number of noises	−0.35	0.07	−4.936	<0.001	−0.504	−0.223
Sound pressure level	0.17	0.02	7.907	<0.001	0.132	0.219
Number of noises x group						
Borrego	0.11	0.19	0.573	0.567	−0.289	0.482
Flor G1	0.36	0.07	4.804	<0.001	0.223	0.518
Flor G2	0.26	0.16	1.681	0.093	−0.051	0.569
Montepío	0.40	0.09	4.541	<0.001	0.234	0.583
Sound pressure level × group						
Borrego	−0.02	0.02	−0.988	0.323	−0.074	0.025
Flor G1	−0.06	0.01	−3.861	<0.001	−0.088	−0.029
Flor G2	−0.05	0.02	−2.217	0.027	−0.089	−0.005
Montepío	−0.04	0.02	−1.877	0.060	−0.073	0.001
Vocalizations						
Number of noises	0.02	0.05	0.285	0.776	−0.093	0.122
Sound pressure level	0.07	0.02	3.411	<0.001	0.028	0.107
Number of noises × group						
Borrego	0.13	0.55	0.243	0.808	−0.996	1.373
Flor G1	0.00	0.06	−0.041	0.967	−0.116	0.113
Flor G2	−0.01	0.13	−0.078	0.938	−0.273	0.244
Montepío	−1.13	0.34	−3.371	<0.001	−1.932	−0.584
Sound pressure level × group						
Borrego	−0.06	0.08	−0.761	0.447	−0.269	0.062
Flor G1	0.03	0.02	1.882	0.060	−0.001	0.060
Flor G2	0.05	0.02	2.568	0.010	0.013	0.092
Montepío	0.16	0.04	4.092	<0.001	0.092	0.253

Abbreviation: GLM, generalized linear model.

[a]Comparisons against the human voice category.

[b]Comparisons against the group Balzapote.

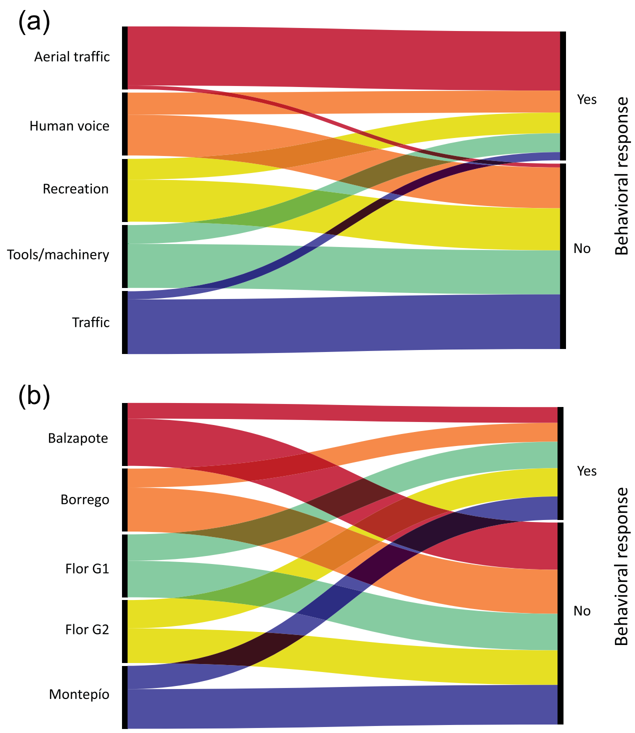

FIGURE 1 The proportion of anthropogenic noises that elicited a behavioral response by mantled howler monkey males studied in Los Tuxtlas between January and December 2020: (a) responses according to noise type and (b) responses according to group identity.

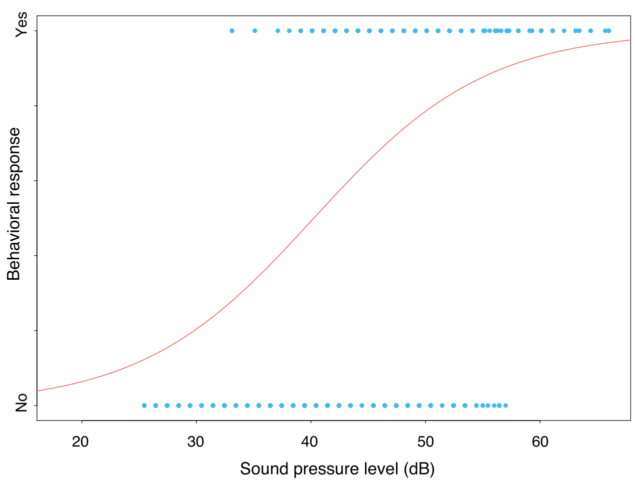

FIGURE 2 The likelihood of displaying a behavioral response toward anthropogenic noises according to sound pressure level (dB) in mantled howler monkey males studied in Los Tuxtlas between January and December 2020.

mantled howler monkeys studied here (i.e., <2000 m). Other noise types were rather infrequent, although some had high sound pressure level. Such was the case with recreation sounds and aerial traffic. Indeed, the latter had the highest mean sound pressure level but the lowest rate for three groups. The significant influence of variation in sound pressure level on male behavior suggests that our measures, although performed at ground level, are biologically meaningful for mantled howler monkey.

TABLE 5 Frequencies of behavioral responses of mantled howler monkeys to anthropogenic noises and goodness-of-fit test results.

	Noise				
Behavior	Aerial traffic	Human voice	Recreation	Tools/ machinery	Traffic
Flight	0 (−2.1)	1 (−6.7)	2 (−3.2)	0 (−4.4)	0 (−7.2)
Socialize	0 (−2.1)	18 (−4.2)	0 (−3.7)	0 (−4.4)	3 (−6.7)
Approach	0 (−2.1)	4 (−6.2)	1 (−3.4)	0 (−4.4)	1 (−7.0)
Vigilance	7 (1.1)	106 (8.7)	37 (6.2)	25 (1.4)	59 (1.1)
Vocalize	16 (5.3)	**104 (8.4)**	29 (4.1)	70 (11.7)	193 (19.8)
χ^2	43.3	247.5	91.5	195.8	539.7
p	<0.001	<0.001	<0.001	<0.001	<0.001

Note: Numbers within parenthesis are Pearson residuals, which indicate the amount and direction of the difference between the observed and expected values. Behaviors contributing the largest proportion of nonrandomness in χ^2 tests are in bold.

The most common noise, traffic, resulted in less behavioral responses than some comparatively infrequent noises, such as recreation and tools/machinery. Mantled howler monkeys may become tolerant toward these frequent noises due to repeated exposure which, in the long term, could lead to habituation (Bejder et al., 2009; Rankin et al., 2009). Still, it is possible that traffic represents a mild stimulus to mantled howler monkeys given that it had the lowest mean sound pressure level. Alternatively, perhaps traffic sound pressure level was low because mantled howler monkeys avoid roads, as observed in other studies (e.g., Duarte et al., 2011; Gagnon et al., 2007; Jaeger et al., 2005; Reijnen et al., 1995; Supporting informationVideo S1). Irrespective of noise type, behavioral responses were more frequent toward high sound pressure noises, indicating that the addition of intense anthropogenic noise to the environment affects mantled howler monkeys. This result converges with previous evidence that intense noise, even if intermittent (e.g., aerial traffic), is perceived as a threat by wildlife (Francis & Barber, 2013).

The likelihood of mantled howler monkeys behaving in response to anthropogenic noise varied among groups. The small sample of groups studied here hinders a quantitative analysis of the potential causes for such variation, but it is interesting to note that the group with the highest rate of anthropogenic noise was the one that responded less to noise (Borrego). This result could further support the possibility that frequent exposure to anthropogenic noise leads to tolerance in this species (Brown et al., 2012; Conomy et al., 1998; Harding et al., 2018; Weisenberger et al., 1996). However, there was also a significant difference between the two groups from La Flor (one of which had the lowest noise rate) and the group with the second-highest rate (Balzapote), with the former responding less to noise than the latter. This contrast is suggestive of sensitization, a

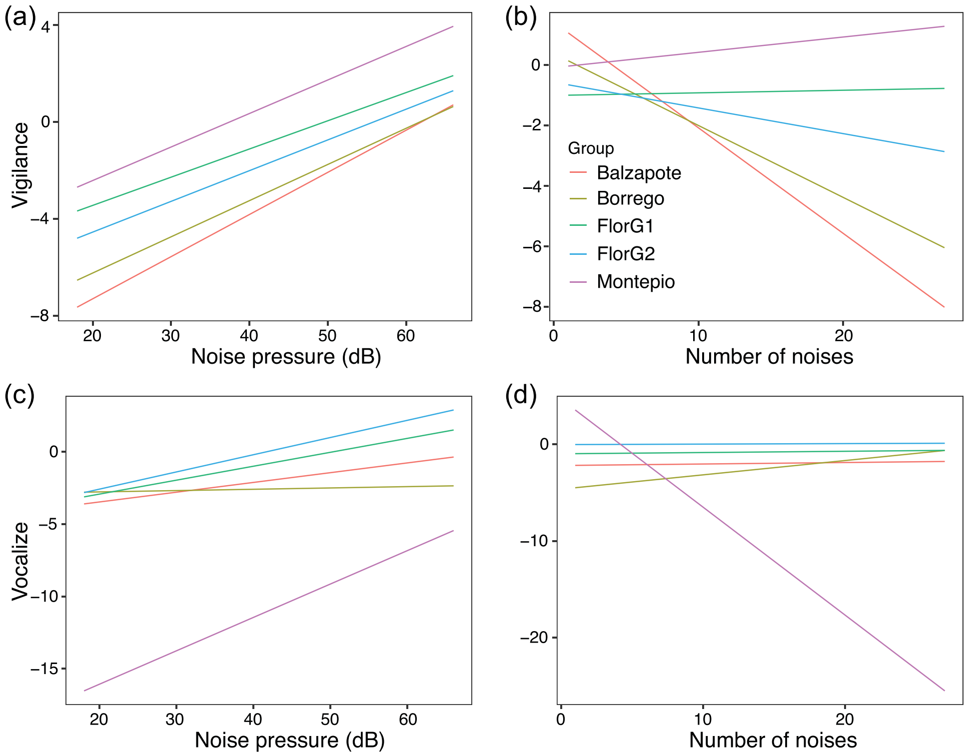

FIGURE 3 Variation (predicted estimates) in vigilance (a, b) and vocalization responses (c, d) to anthropogenic noise as a function of the interaction between group identity and both sound pressure level and the number of noises recorded in mantled howler monkey males studied in Los Tuxtlas between January and December 2020.

process whereby individuals have heightened responses to recurrent stimuli (Bejder et al., 2009). There are thus contrasting responses to anthropogenic noise that for now may best be interpreted as resulting from the influence of intrinsic (e.g., age, body condition, personality) and extrinsic factors (e.g., environmental context, repeated exposure, experience: Harding et al., 2019).

Vigilance and vocalizations accounted for a disproportionately high number of mantled howler monkey responses to anthropogenic noise. Flight, social interactions, and approaches, in contrast, were rarely recorded and associated with very specific events, such as seeking contact with another group member when a human voice was heard at close range. Rates of vigilance and vocalizations both increased with increasing sound pressure level, indicating that the acoustic properties of noise affect the behavior of mantled howler monkeys. By contrast, the rate of vigilance, but not the rate of vocalizations, was related to the number of anthropogenic noises recorded. Displaying vigilance and vocalizing in response to anthropogenic noise implies opportunity costs (i.e., abandoning current activity; Francis & Barber, 2013), but these behaviors may impose different energetic costs: vigilance consists of a visual examination of the environment that should not involve the mobilization of significant energy resources, whereas vocalizations are presumed to be energetically costly for howler monkeys (da Cunha et al., 2015). It is possible that following the assessment of a specific noise as nonthreatening, mantled howler monkeys react to it with relatively inexpensive vigilance instead of with vigorous vocalizations. Alternatively, and as previously suggested (Cañadas-Santiago et al., 2020), perhaps mantled howler monkeys try to remain unnoticed when noise is perceived as an immediate threat through both its intensity and rate, but produce conspicuous vocalizations when noise, although intense, is not assessed as eminently risky (Pater et al., 2009; Tablado & Jenni, 2015).

As in the case of the occurrence of behavioral responses, repeated contact and exposure seem to be important determinants of specific behavioral responses of mantled howler monkeys to noise. Two groups exposed to different noise rates and sound pressure levels had similar response profiles to noise, although one mostly responded with vigilance (Balzapote) and the other one with vocalizations (Montepío). A more precise understanding of the behaviors that are elicited by noise according to its attributes (type, intensity, rate) may be possible through field experimentation (e.g., playback experiments: Blickley & Patricelli, 2010), although our results provide suggestive evidence that anthropogenic noise influences the behavior of mantled howler monkeys at Los Tuxtlas.

AUTHOR CONTRIBUTIONS

Eugénia Erendira Gómez Espinosa: conceptualization (equal); data curation (equal); formal analysis (equal); investigation (equal); methodology (equal); validation (equal); visualization (equal); writing—original draft (equal); writing—review & editing (equal); Pedro 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 & editing (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 (lead); validation (equal); visualization (equal); writing—original draft (equal); writing—review and editing (lead).

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CONFLICTS OF INTEREST

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

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

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