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Anthropogenic Noise Influences the Activity of Mantled Howler Monkeys

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ABSTRACT

Animals exhibit varying degrees of behavioral tolerance to anthropogenic noise. However, our understanding of how different species tolerate noise, and the specific behavioral consequences of noise exposure remains limited. We hypothesized that mantled howler monkeys (*Alouatta palliata*) show differential tolerance (i.e., likelihood to change their behavior) to different noise traits. We observed 18 adult subjects from two groups at Los Tuxtlas, Mexico, for 606 focal samples, recording 1488 noise events. Assessed noise traits were the number of noise occurrences, sound pressure level (SPL, measured with a sound meter), noise duration, and proximity to noise. The number of noises and SPL significantly increased the probability of activity change. Behavioral transition analysis revealed non-random patterns, with noise mostly disrupting rest-to-feed sequences while increasing move-to-feed transitions. The number of noises had the most consistent effects across behaviors, altering the activity budget for feeding, resting, locomotion, and vigilance. As the number of noises increased, feeding time rose from 9% to 14%, locomotion from 7% to 14%, and vigilance more than tripled from 2% to 7%, while resting declined from 80% to 63%. Increased noise duration resulted in decreased feeding (from 12% to 4%) but increased locomotion (from 7% to 15%). Thus, mantled howler monkeys exhibit a complex, trait-specific tolerance pattern to noise, showing greater sensitivity to the number of noises and noise intensity while potentially developing higher tolerance to duration and distance. These findings highlight the importance of implementing noise mitigation strategies in areas where wildlife interfaces with humans.

RESUMEN

Los animales tienen grados variables de tolerancia conductual al ruido antropogénico. Sin embargo, nuestro conocimiento sobre cómo diferentes especies toleran el ruido y cuáles son las consecuencias conductuales específicas de la exposición al ruido sigue siendo limitado. Planteamos la hipótesis de que los monos aulladores de manto (*Alouatta palliata*) muestran una tolerancia diferencial (es decir, distinta probabilidad de cambiar su conducta) frente a diferentes atributos del ruido. Observamos 18 adultos de dos grupos en Los Tuxtlas, México, durante 606 muestras focales, registrando 1488 eventos de ruido. Las características del ruido evaluadas fueron el número de ocurrencias de ruido, el nivel de presión sonora (SPL, medido con un sonómetro), la duración del ruido y la proximidad al ruido. El número de ruidos y el SPL aumentaron significativamente la probabilidad de cambio de actividad. El análisis de transiciones conductuales reveló patrones no aleatorios, con el ruido interrumpiendo principalmente las secuencias de descanso a alimentación e incrementando las transiciones de desplazamiento a alimentación. El número de ruidos mostró los efectos más consistentes entre conductas, alterando la distribución del tiempo dedicado a alimentación, descanso, locomoción y vigilancia. A medida que aumentó el número de ruidos, el tiempo de alimentación subió del 9% al 14%, la locomoción del 7% al 14% y la vigilancia más que se triplicó del 2% al 7%, mientras que el descanso disminuyó del 80% al 63%. Un incremento en la duración del ruido se asoció con una reducción de la alimentación (del 12% al 4%) pero con un aumento de la locomoción (del 7% al 15%). Así, los monos aulladores de manto exhiben un patrón complejo de tolerancia específica a rasgos del ruido, mostrando mayor sensibilidad al número de ruidos y a la intensidad del ruido, mientras que potencialmente desarrollan una mayor tolerancia a la duración y a la distancia. Estos hallazgos subrayan la importancia de implementar estrategias de mitigación del ruido en áreas donde la fauna silvestre interactúa con las personas.

1 | Introduction

Humans have profoundly altered natural environments worldwide through urbanization, agriculture, pollution, resource depletion, and climate change (Vitousek et al. 1997; Ellis et al. 2010; Foley et al. 2005; Butchart et al. 2010; Dirzo et al. 2014). Despite these significant disruptions, wildlife demonstrates remarkable coping abilities (Wong and Candolin 2015; Sih et al. 2011). These responses include behavioral and physiological adjustments, which together contribute to species' resilience amid rapid environmental change (Thibert-Plante and Hendry 2011; Halpern et al. 2008; Fuentes 2017). Within this context, understanding behavioral tolerance has become increasingly critical for explaining the persistence of species in human-altered landscapes (Bejder et al. 2009; Blumstein 2016; Čapkun-Huot et al. 2024). Tolerance may be defined as the degree of reaction to stimuli signaling potentially risky situations, and emerges through multiple pathways including genetic predisposition, epigenetic effects, and learning processes, each influencing the speed of acquisition, reversibility, specificity, and duration of responses to environmental stimuli (Čapkun-Huot et al. 2024). Investigating these tolerance mechanisms provides crucial insights into how species persist in human-modified environments and enables more effective conservation strategies that consider species-specific responses to anthropogenic change (Beale 2007; Čapkun-Huot et al. 2024). For instance, female Canada geese (*Branta canadensis*) become progressively less tolerant to human approaches as their eggs' hatching date approaches (Clermont et al. 2019), showing that tolerance varies with reproductive state, while urban-tolerant eastern chipmunks (*Tamias striatus*) improve body condition through anthropogenic food access but face increased vulnerability to other risks (Lyons et al. 2017). These variable tolerance responses may directly influence population viability, human-wildlife conflict intensity, and the effectiveness of conservation interventions, making mechanistic understanding of tolerance essential for predicting and managing wildlife responses to anthropogenic disturbances.

Anthropogenic noise, defined as sound produced by human activities that alters the natural acoustic environment, represents a particularly widespread and often overlooked form of environmental pollution (Barber et al. 2010; Shannon et al. 2016). This sensory pollutant originates from diverse sources including vehicular traffic, industrial operations, construction, recreational activities, and domestic animals (Kunc and Schmidt 2019). Unlike natural ambient sounds, anthropogenic noise is typically louder, more frequent, more persistent, and less predictable than natural acoustic stimuli (Popper and Hastings 2009; Blickley and Patricelli 2010). The impacts of anthropogenic noise on wildlife are numerous and often detrimental, affecting communication, physiology, reproduction, and spatial distribution (Francis and Barber 2013). Behaviorally, many species demonstrate significant changes in response to noise, including altered vocalization patterns, disrupted feeding behaviors, increased vigilance, and modified movement patterns (Shannon et al. 2016; Kunc and Schmidt 2019). For instance, birds in urban environments often increase the frequency of their calls to overcome traffic noise (Slabbekoorn and Den Boer-Visser 2006; Luther and Derryberry 2012), while marine mammals show disrupted communication (e.g., reduced calling rates or complete cessation of vocalizations) and elevated stress hormones in response to shipping noise (Weilgart 2007; Rolland et al. 2012). Evidence regarding tolerance development to noise is mixed; some species demonstrate habituation over time, gradually reducing their response to repeated noise exposure, while others show sensitization, with responses intensifying with continued exposure (Bejder et al. 2006; Blumstein 2016). This variability in tolerance appears to depend on noise traits (intensity, occurrence, predictability), species traits (sensory capabilities, behavioral plasticity), ecological factors (habitat quality, alternative resources; Bejder et al. 2009; Francis et al. 2009), and socio-ecological factors (e.g., distance to neighboring groups: Sobroza et al. 2024).

Research on noise impacts in wild primates remains notably scarce compared to studies on birds and marine mammals, despite growing evidence of significant behavioral responses. These responses include increased vigilance, decreased feeding time, increased locomotion, spatial avoidance of noise sources, and changes in communication modalities (e.g., Birke 2002; Brumm et al. 2004; Egnor and Hauser 2006; Duarte et al. 2011; Santos et al. 2017; Sheehan and Papworth 2019; Hernani Lineros et al. 2020; Sobroza et al. 2024). For instance, titi monkeys (*Callicebus nigrifrons*) residing near mining activities show reduced vocalization activity and altered patterns of daily movements, suggesting that anthropogenic noise disrupts normal daily activity (Duarte et al. 2011). Similarly, pygmy marmosets (*Cebuella pygmaea*) exposed to human speech reduced feeding and resting, reflecting a direct behavioral impact linked to tourism-generated noise (Sheehan and Papworth 2019). Urban black-tufted marmosets (*Callithrix penicillata*) also avoid noisy areas, even when food availability is high in noisy areas, indicating that noise directly influences habitat use and foraging decisions (Duarte et al. 2011). These examples demonstrate that adjustments to activity budgets (i.e., the balance of time allocated to activities crucial for survival and reproduction) represent a critical component in primates' strategies for coping with anthropogenic noise. As sensitive indicators of environmental challenges (Dunbar et al. 2009), changes in activity budgets may provide insights into the ecological impacts of human disturbances and are thereby important for informing more effective wildlife management and mitigation strategies (Laiolo 2010).

Howler monkeys (*Alouatta* spp.) are arboreal platyrrhines with a folivore-frugivore diet and an energy-conserving activity budget. They typically allocate 57%–80% of their daily time to resting, 13%–24% to feeding, and minimal time to social interaction and traveling, rarely moving more than 700 m daily (Di Fiore and Campbell 2007). Mantled howler monkeys (*A. palliata*) inhabit forests from southern Mexico to Ecuador and demonstrate considerable behavioral flexibility in response to habitat disturbance (e.g., Cristóbal-Azkarate and Arroyo-Rodríguez 2007; Dunn et al. 2009; Dias and Rangel-Negrín 2015). Recent studies have begun to document the behavioral responses of mantled howler monkey populations in Mexico (*A. p. mexicana*) to anthropogenic noise. Specifically, individuals reduce vocal activity, increase mobility, and dedicate more time to vigilance when anthropogenic noise occurs nearby (Cañadas-Santiago et al. 2020; Gómez-Espinosa et al. 2022; Dias et al. 2023a). Moreover, the probability of vocalization and vigilance increases with noise intensity (Cañadas-Santiago et al. 2020; Gómez-Espinosa et al. 2022). However, comprehensive understanding of how noise traits influence mantled howler monkey activity budgets remains limited, despite the importance of such knowledge to the design of effective conservation and management strategies for this Endangered primate (Dias et al. 2023a; Rangel-Negrín et al. 2023).

We aimed to examine how anthropogenic noise influences the behavior of mantled howler monkeys. The multidimensional framework to study tolerance proposed by Čapkun-Huot et al. (2024) comprises several components: speed of acquisition, specificity, reversibility, and duration. As longitudinal data would be required to examine speed of acquisition, reversibility, and duration of tolerance, we focused on the specificity component, which pertains to whether tolerance is general or stimulus-specific. Accordingly, we hypothesized that the tolerance of mantled howler monkeys to anthropogenic noise depends on noise traits, such that individuals would show trait-specific responses to noise, with potentially greater behavioral responses to some noise traits than others. We predicted that individuals would change their ongoing activity when exposed to noise, with the likelihood of behavioral change increasing with increasing numbers of noise occurrences, intensity, and duration, and decreasing with distance from the noise source (prediction 1). Furthermore, we predicted that noise exposure would alter the activity budgets of individuals, with increased numbers of noise occurrences, intensity, and duration of noise, and decreased distances from noise sources, associated with reduced time allocated to resting, feeding, and socialization, and increased time dedicated to locomotion, vigilance, and vocalization (prediction 2).

2 | Methods

2.1 | Study Site and Subjects

We conducted the study at Los Tuxtlas, located in southeastern Veracruz State, Mexico. The region is highly heterogeneous with elevations ranging from sea level to 1780 m. The habitat is characterized by tropical rainforest with evergreen vegetation, a warm-humid climate with mean annual temperatures of 24°C–26°C, and mean annual precipitation of 3000–4000 mm. The area experiences two main seasons: a dry period from March to May and a rainy season from June to February. Fruit availability is highest at the beginning of the rainy season (April–June) and from August to October, while young leaves are available year-round with peak availability from March to June.

The specific study site was La Flor de Catemaco, a ranch located at km 9.5 of the Catemaco–Coyame highway (18°26′43″N, 95°02′49″W). This ranch primarily produces ornamental plants, particularly *Chamaedorea elegans* palm, resulting in understory vegetation dominated by this species. Because these palms require canopy cover, the ranch has maintained all tall trees that were originally part of the forest, creating a canopy of 100 ha with native vegetation. The site features paths facilitating access and movement throughout the area. Workers perform manual vegetation clearing and transport materials in vehicles, generating anthropogenic noise.

We have monitored mantled howler monkeys inhabiting La Flor de Catemaco since 2002 (Dias et al. 2023b). During the study period, the population consisted of 56 howler monkeys distributed across six groups and two solitary adult males. We focused on two groups: Group 1 comprised of four adult males, six adult females, and four immatures; and Group 2 consisting of four adult males, four adult females, and five immatures. Individuals were identified based on distinctive physical characteristics including scars and color patterns on limbs and tails.

2.2 | Sampling of Mantled Howler Monkey Behavior

We observed the 18 adult subjects (8 adult males and 10 adult females) from June 14, 2023, to March 3, 2024 (8 months), totaling 110 days of field observations. Observations were conducted from 06:30 to 16:30, with a minimum of 5 days per week, depending on weather conditions and group location. We used the focal-animal sampling method with continuous recording during 1-h periods, during which we noted the duration of the activities (Table 1). To increase temporal independence between records, we avoided conducting consecutive focal samples on the same individual by rotating observations so that an individual was only recorded again after all other individuals in the group had been sampled. We collected a total of 606 complete focal samples (i.e., with a duration of 1-h), averaging 33.66 ± 3.23 h of observation per individual.

2.3 | Sampling of Anthropogenic Noise

The sampling of noise was conducted simultaneously with focal-animal sampling by a second observer. We continuously recorded: (1) the ambient sound pressure level; and (2) all anthropogenic noises that occurred during behavioral sampling, such as motorcycles, trucks, voices, and others. For each noise event, we documented the time of occurrence, the duration, the number of occurrences, and its source (Table 2). We considered noise events independently if they were separated by > 5 s. To determine the distance from the noise source to the mantled howler monkey group, one observer recorded a waypoint on a GPS (Garmin Etrex 10) at the center of the group and then moved quickly to the origin of the noise and recorded a second location. The straight-line distance between the two waypoints was calculated with the "Measure Distance" function of the GPS. Given that the GPS that we used may have a horizontal measurement error of 5 to 10 m, for further analysis we converted continuous measurements to six distance categories: 5–9 m, 10–14 m, 15–19 m, 20–29 m, 30–39 m, and > 40 m.

We used the sound pressure level (SPL), representing the pressure exerted by sound waves in the air relative to a reference pressure, as the indicator of noise intensity. We measured continuous SPL using a Tenmars (Taiwan) sound level meter with automatic data logging capability at 1-s intervals, stored on internal memory. The measurement range was 30–130 dB, sampling frequency was 48 kHz (20.8 μs), and frequency response range was10 Hz–16 kHz. The device computed A-weighted equivalent continuous sound levels (LAeq) by applying an A-weighting filter and integrating the squared sound pressure over time, in accordance with standard practices. Prior to each field session, the sound level meter was calibrated using a Class 1 acoustic calibrator producing a reference tone of 94 dB at 1 kHz, in accordance with the manufacturer's guidelines. We also recorded whether a change in the focal individual's activity occurred, noting both the initial activity and the activity to which the individual changed. A total of 1488 anthropogenic noise events were identified, at a rate of 2.5 noises per hour of observation.

TABLE 1 | Mantled howler monkey activities recorded in this study.

Activity	Definition
Feed	Inspect food, bring food to mouth, chew and swallow, move while feeding within a food patch[b]
Rest	Sleep or static without interaction[b]
Locomotion	Movement to a new area or tree[b]
Socialize	Social interactions[a]
Vigilance	Head up, eyes open and attention not focused on another activity[b]
Vocalize	Vocalizations[c]

[a] Dias and Rangel (2015).
[b] Cano-Huertes et al. (2017).
[c] Cañadas-Santiago et al. (2020).

TABLE 2 | Noise types and number of noise occurrences recorded in the habitat of mantled howler monkeys.

Noise type	Description	Number of occurrences
Vehicle (terrestrial)	Car, motorcycle, truck, tractor, trailer, ambulance	997
Aircraft	Airplane, helicopter	159
Tools/machinery	Chainsaw, hammer, ladder, lawnmower, machete, motor, sprinkler	159
Human	Handclap, sneeze, music, voice	78
Other	Horn, detonation, firecracker, nonidentified noise	53
Motorboat	Motorboats	38

2.4 | Data Organization and Analysis

To evaluate the first prediction (i.e., about behavioral changes), we first determined the probability of behavioral change in the absence of anthropogenic noise. We conducted a survival analysis using the Kaplan–Meier estimator to determine the latency between a control point and a behavioral change. We used the start time of each focal sample as the control point and calculated latencies between this moment and the first behavioral change. If anthropogenic noise was recorded before the first behavioral change, that focal sample was excluded from the analysis. The median latency to the first behavioral change was 8.5 min, with a 95% confidence interval of 7.4 to 10.1 min ($n = 261$ observations; Figure 1). Based on this analysis, we adopted a conservative value of 7.4 min as the threshold for considering a behavioral change to be associated with a noise event.

We then identified all noise events in the database and verified whether a change in the focal animal's activity occurred within 7.4 min of each event's onset. Activity changes occurring within 7.4 min were classified as responses to noise, while those occurring after 7.4 min were classified as non-responses. We conducted two generalized linear mixed models (GLMMs), the first with a negative binomial distribution and logit link function, and the second with a binomial distribution and logit link function to test prediction 1. For the first model, the dependent variable was the number of behavioral changes in 1-h focal samples (i.e., number of occasions in which a behavioral change was recorded

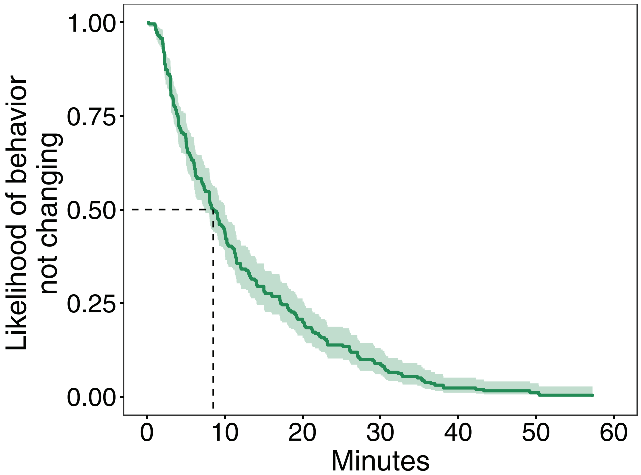

FIGURE 1 | Kaplan–Meier survival curve on the likelihood that mantled howler monkeys change their activity in the absence of anthropogenic noise. The dashed lines indicate that at 8.5 min of observation time there is a 50% likelihood that an activity change.

within 7.4 min of a noise), the fixed predictor was the number of noise occurrences per focal sample, and the random predictor was focal individual identity to account for repeated measures. In the second model we organized data per anthropogenic noise event, and the dependent variable was the occurrence of a behavioral response within 7.4 min of a noise (i.e., yes/no). The fixed predictors were the duration (in seconds), distance (categorical variable with six levels), and SPL (in dB) of each noise, and the random predictor was focal individual identity. The first model should capture additive responses to multiple disturbances on a long timeframe (i.e., 1 h) allowing for the assessment of the number of noise events on behavior, whereas the second model examines immediate (i.e., within 7.4 min of noise occurrence) behavioral responses to individual noise events, allowing us to assess the direct effects of specific noise traits (duration, distance, and SPL) on behavior.

To further understand behavioral responses of mantled howler monkeys to noise at this temporal scale (i.e., shortly after noise), we constructed a 6 × 6 contingency table of initial and final activity when noise resulted in an activity change ($n = 585$ events). We then used a chi-square test of independence to determine whether change patterns differed from random expectations. Expected frequencies were calculated under the null hypothesis that the probability of transitioning to any given activity was independent of the initial behavior. We calculated standardized residuals for each change to identify specific patterns that deviated significantly from expected frequencies. Standardized residuals greater than 2.0 or less than −2.0 (corresponding approximately to $p < 0.05$) indicated transitions that occurred significantly more or less frequently than expected by chance.

To evaluate predictions about changes in activity budgets (prediction 2), we used GLMMs with binomial distribution and logit link function where the dependent variables were time dedicated to each activity (feeding, resting, locomotion, socialization, vigilance, and vocalization) per focal sample. In each model, the dependent variable consisted of two vectors representing time dedicated to the activity per focal sample and time not dedicated to that activity. The fixed predictors were the number of noise occurrences, their duration, distance, and SPL, and focal individual identity was the random predictor. Socialization and vocalizations were recorded in only 33 and 97 of the total 606 focal samples, respectively, and had very low duration (mean ± SD duration: socialization 0.2 ± 1.4 min, vocalizations 0.4 ± 1.2 min) and could not be modeled as other activities. Therefore, we modeled them as occurrences (i.e., occurred/did not occur) per focal sample with binomial GLMMs using the same fixed, random, and control variables used in other models.

All models included sex and time of day (i.e., hour at focal sample onset) as control variables, as these factors can influence howler monkey activity (e.g., Bicca-Marques and Calegaro-Marques 1998; Estrada et al. 1999). We standardized noise attributes by centering and scaling (subtracting the mean and dividing by the standard deviation) to facilitate comparison of effect sizes across different measurement scales. Model assumptions were verified through residual analyses (linearity, dispersion, outliers, and uniformity). Variance inflation factor (VIF) was used to diagnose multicollinearity of fixed predictors. Distance from noise and noise SPL were collinear in activity budget models (VIF > 10), so we only retained the latter. We evaluated the contribution of random factors relative to fixed factors by comparing complete models with null models using likelihood ratio tests (LRT). Pseudo-determination coefficients were calculated to determine the goodness of fit for each model. All analyses were performed in R 4.4.5 (R Core Team 2025).

3 | Results

3.1 | First Prediction: Activity Changes

As the number of noise occurrences per animal-focal sample increased, the probability of mantled howler monkeys modifying their activity also increased ($\chi^2_{1,606} = 93.6$, $p < 0.001$; Table 3, Figure 2a). Similarly, as sound pressure level (SPL) increased the likelihood of activity change also increased ($\chi^2_{3,1488} = 12.8$, $p < 0.001$; Figure 2b). Neither noise duration ($\chi^2_{3,1488} = 0.3$, $p = 0.586$) nor distance from the noise source ($\chi^2_{5,1488} = 4.33$, $p = 0.5.3$) showed significant relationships with activity changes.

We found highly non-random activity change patterns following the occurrence of noise ($\chi^2 = 375.7$, df = 25, $p < 0.001$). Eight changes occurred significantly more frequently than expected by chance, while three occurred significantly less frequently (Table S1). The most common transitions were vigilance to rest and move to feed and the most underrepresented transition was rest to feed (Figure 3).

3.2 | Second Prediction: Activity Budget Changes

In the absence of noise, mantled howler monkeys allocated 47.1% (SD = 14.6) of their time to resting, followed by feeding (6.8%, SD = 10.8), locomotion (4.4%, SD = 7.4), vigilance (1.2%), vocalization (0.3%), and socializing (0.2%; Figure S1). Under noise conditions, resting decreased to 45.9% (SD = 14.3) and feeding decreased slightly to 6.4% (SD = 9.7). Conversely, locomotion increased to 5.5% (SD = 8.3), vigilance increased to 1.6%, and vocalization increased to 0.4%. Socializing remained unchanged at 0.2%.

The number of noise occurrences demonstrated the most consistent effects across behaviors, significantly altering the activity budget for feeding, resting, locomotion, and vigilance (Table 3). Noise duration significantly impacted feeding (negatively) and locomotion (positively), while noise SPL did not significantly influence any of the observed behaviors. The socialization and vocalization models showed no significant relationships with any of the anthropogenic noise predictors.

The models for feeding, resting, and vigilance differed significantly from null models, indicating substantial effects of noise on these behavioral patterns (LRT $p < 0.001$). Feeding was affected by the number of noise occurrences and duration (Table 4). As the number of noise occurrences increased, howler monkeys spent more time feeding, with an approximate increase from 9% to 14% of their time budget across the observed occurrence range (Figure 4a). Conversely, increased noise duration had the opposite effect, with feeding time declining sharply from 12% to 4% as duration increased across the observed range

TABLE 3 | Mixed-effects models of the influence of the attributes of anthropogenic noise on the likelihood that mantled howler monkeys changed their activity.

Model/predictor	R^2m (R^2c)[a]	Estimate	SE	z	p
Model 1 (number of behavioral changes per focal sample)[b]	0.38 (0.39)				
Number of noise occurrences		0.54	0.06	9.7	< 0.001
Sex		0.21	0.21	1.0	0.310
Time of the day		0.02	0.04	0.5	0.603
Model 2 (occurrence of behavioral change per noise event)	0.02 (0.03)				
Noise duration		0.02	0.05	0.4	0.681
Noise distance[c]	First	0.22	0.23	1.0	0.336
	Second	−0.25	0.39	−0.6	0.528
	Third	−0.07	0.16	−0.5	0.641
	Fourth	−0.23	0.38	−0.6	0.551
	Fifth	−0.36	0.30	−1.2	0.234
Noise SPL		−0.20	0.06	−3.4	0.001
Sex		0.03	0.15	0.2	0.863
Time of the day		−0.11	0.05	−2.0	0.048

[a] The first value is the conditional coefficient of determination, corresponding to the proportion of variance explained by the fixed factors, while the second (in parenthesis) is the marginal coefficient of determination, corresponding to the proportion of variance explained by both the fixed and the random factors.

[b] Both models were significantly different from null models including control and random factors (LRT test $p < 0.05$).

[c] Comparisons against the "Sixth" category.

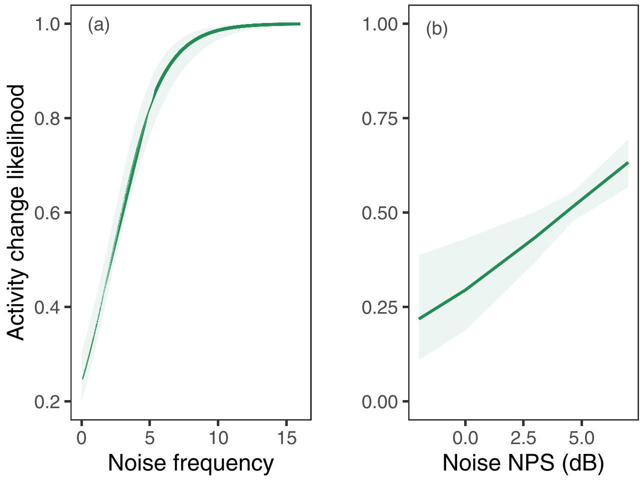

FIGURE 2 | Changes in mantled howler monkey activity as a function of the number of noise occurrences (a) and SPL (sound pressure level; b). Green lines represent the predicted values from mixed-effects models, and the shaded areas represent 95% confidence intervals.

(Figure 4b). Mantled howler monkeys reduced their resting time from approximately 80% to 63% of their activity budget as the number of noise occurrences increased (Figure 4c). As the number of noise occurrences increased, locomotion time rose from approximately 7% to 14% across the observed range (Figure 4d). Similarly, increased noise duration was associated with increased locomotion, from about 7% to 15% across the observed duration range (Figure 4e). Vigilance showed the strongest proportional response to the number of noise occurrences. As the number of noise occurrences increased across the observed range, vigilance behavior more than tripled, rising from approximately 2% to 7% of the activity budget (Figure 4f).

4 | Discussion

Anthropogenic noise is a widespread and often overlooked form of environmental pollution that significantly impacts wildlife across taxa (Barber et al. 2010; Shannon et al. 2016). Our study demonstrates that anthropogenic noise is associated with behavioral changes in mantled howler monkeys, with responses varying according to specific noise traits. This pattern supports our hypothesis that tolerance development is a complex, trait-specific process rather than an absolute phenomenon. We found that the number of noise occurrences and noise intensity significantly increased the likelihood of activity changes, while both the number of noise occurrences and duration altered activity budgets, with different effects on different activities. Mantled howler monkeys appeared more sensitive to some noise traits (number of noise occurrences and intensity) than others (duration and distance), suggesting that tolerance development occurs along multiple dimensions as outlined in the framework by Čapkun-Huot et al. (2024). Understanding these responses is critical for conservation management, as even species with considerable behavioral flexibility experience disruptions from noise pollution that could affect long-term fitness through altered time and energy allocation.

Our first prediction that individuals would alter their ongoing activity when exposed to noise was strongly supported, with the

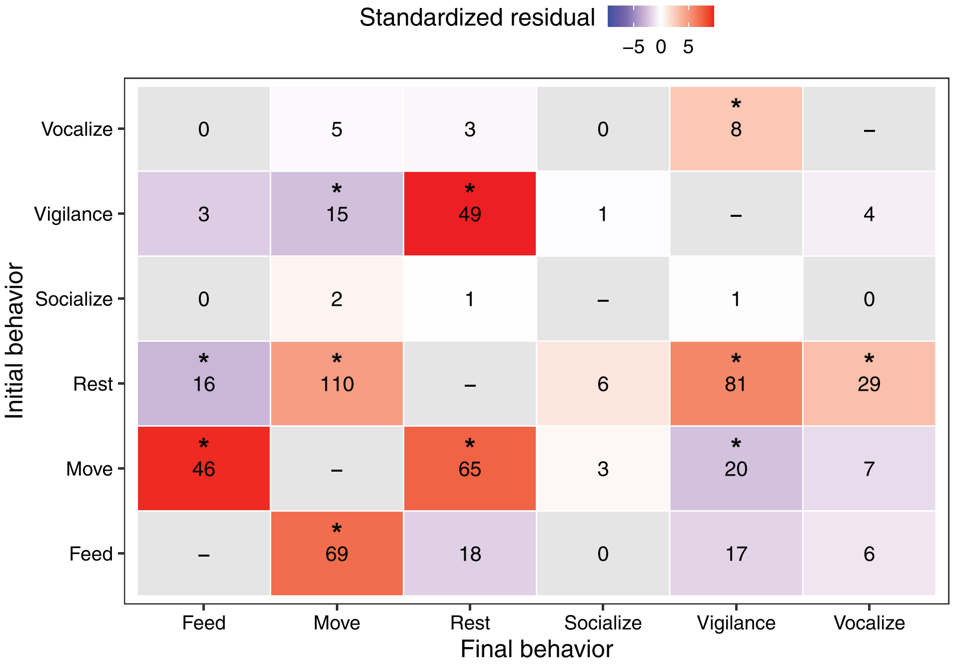

FIGURE 3 | Heatmap of activity changes showing standardized residuals from chi-square analysis. Numbers indicate observed transition frequencies. Colors represent deviation from expected: Red indicates overrepresented transitions, blue indicates underrepresented transitions. Asterisks (*) mark transitions with standardized residuals $|z| > 2.0$.

likelihood of behavioral change increasing significantly with the number of noise occurrences and intensity (SPL). This response pattern is consistent with previous studies documenting behavioral changes in wildlife exposed to anthropogenic noise (Kunc and Schmidt 2019) and in primates specifically (e.g., Duarte et al. 2011; Sheehan and Papworth 2019; Hernani Lineros et al. 2020). While the number of noise occurrences and noise intensity strongly predicted behavioral changes, duration and distance did not show significant effects, suggesting that howler monkeys are particularly sensitive to noise loudness rather than its persistence or proximity (Blumstein 2016). This differential response reveals a nuanced pattern of trait-specific tolerance development, where monkeys may have more rapidly developed tolerance to certain aspects of noise (duration and distance) while maintaining sensitivity to intensity (Bejder et al. 2009; Čapkun-Huot et al. 2024). The importance of noise intensity is consistent with previous work showing that high-intensity sounds can elicit physiological stress responses in primates (Westlund et al. 2012), including howler monkeys (Cañadas-Santiago et al. 2020; Gómez-Espinosa et al. 2022; Dias et al. 2023a). This selective sensitivity suggests that howler monkeys engage in complex evaluation of noise stimuli rather than simple habituation, reflecting the specificity component of the tolerance framework, in which responses may be stimulus-specific rather than generalized across perturbation characteristics (Čapkun-Huot et al. 2024).

The analysis of activity transitions provided further insight into the functional significance of noise-induced behavioral changes. The highly non-random transition patterns reveal specific behavioral pathways through which mantled howler monkeys respond to anthropogenic noise. The most overrepresented transitions (vigilance to rest and movement leading to feeding) suggest an adaptive response pattern where brief vigilance bouts allow animals to assess threats before resuming essential activities. Conversely, the significant underrepresentation of rest-to-feed transitions indicates that noise disrupts the natural progression from resting to feeding (Milton 1980), potentially explaining the paradoxical increase in feeding time with higher noise frequency observed in the activity budget analysis (see below). This pattern suggests that feeding bouts initiated after noise-induced movement (move-to-feed transitions were 2.94 times more frequent than expected) may represent compensatory feeding behavior (Dunbar et al. 2009), where individuals attempt to recover energy expenditure from increased movement and vigilance. These altered activity sequences warrant further investigation, as deviations from natural activity patterns in mantled howler monkeys have been associated with increased energetic costs and reduced foraging success in disturbed habitats (Dunn et al. 2009, 2010).

Our second prediction regarding changes in activity budgets was partially supported. The number of noise occurrences showed the most consistent effects, significantly altering time allocation to feeding (increased), resting (decreased), locomotion (increased), and vigilance (increased). Noise duration significantly decreased feeding time and increased locomotion, suggesting that longer noise events induce more substantial behavioral adjustments. Notably, while noise intensity (SPL) significantly affected immediate activity changes, it did not significantly affect longer-term activity budgets, suggesting a distinction between immediate responses and sustained adjustments in time allocation. Neither socialization nor vocalization showed significant relationships with any of the noise traits, suggesting that these social behaviors may be maintained despite noise disturbance, perhaps due to their essential role in group cohesion. The analysis of activity changes helps explain these seemingly contradictory patterns: while noise duration decreased overall feeding time, the increased

TABLE 4 | Mixed-effects models on the influence of the attributes of anthropogenic noise on the activity budgets of mantled howler monkeys.

Model/predictor	R^2m (R^2c)[a]	Estimate	SE	z	p
Feed[b]	0.36 (0.68)				
Number of noise occurrences		0.08	0.02	4.2	< 0.001
Noise duration		−0.20	0.03	−7.6	< 0.001
Noise SPL		0.03	0.02	1.7	0.097
Sex		0.20	0.16	1.2	0.224
Time of the day		0.20	0.02	9.8	< 0.001
Rest	0.14 (0.49)				
Number of noise occurrences		−0.14	0.01	−9.5	< 0.001
Noise duration		0.00	0.01	0.0	0.974
Noise SPL		0.00	0.02	0.1	0.951
Sex		−0.11	0.11	−1.0	0.294
Time of the day		−0.10	0.02	−6.9	< 0.001
Locomotion	0.15 (0.75)				
Number of noise occurrences		0.12	0.02	6.0	< 0.001
Noise duration		0.13	0.02	7.3	< 0.001
Noise SPL		−0.02	0.02	−0.8	0.425
Sex		−0.07	0.18	−0.4	0.708
Time of the day		0.04	0.02	1.6	0.104
Socialization	0.03 (0.03)				
Number of noise occurrences		0.00	0.21	0.0	0.997
Noise duration		−0.10	0.25	−0.4	0.692
Noise SPL		−0.23	0.26	−0.9	0.372
Sex		−0.07	0.43	−0.2	0.875
Time of the day		−0.24	0.22	−1.1	0.293
Vigilance	0.37 (0.72)				
Number of noise occurrences		0.21	0.03	6.4	< 0.001
Noise duration		−0.01	0.04	−0.2	0.806
Noise SPL		−0.07	0.04	−1.6	0.108
Sex		−0.06	0.15	−0.4	0.693
Time of the day		−0.11	0.04	−2.7	0.006
Vocalize	0.35 (0.35)				
Number of noise occurrences		0.19	0.14	1.4	0.176
Noise duration		0.21	0.13	1.6	0.109
Noise SPL		0.19	0.13	1.4	0.151
Sex		2.59	0.36	7.2	< 0.001
Time of the day		0.01	0.14	0.0	0.970

[a] The first value is the conditional coefficient of determination, corresponding to the proportion of variance explained by the fixed factors, while the second (in parentheses) is the marginal coefficient of determination, corresponding to the proportion of variance explained by both the fixed and the random factors.

[b] Feed, rest, and vigilance models were significantly different from null models including control and random factors (LRT test $p < 0.05$) whereas no such difference existed in locomotion, socialization, and vocalization models.

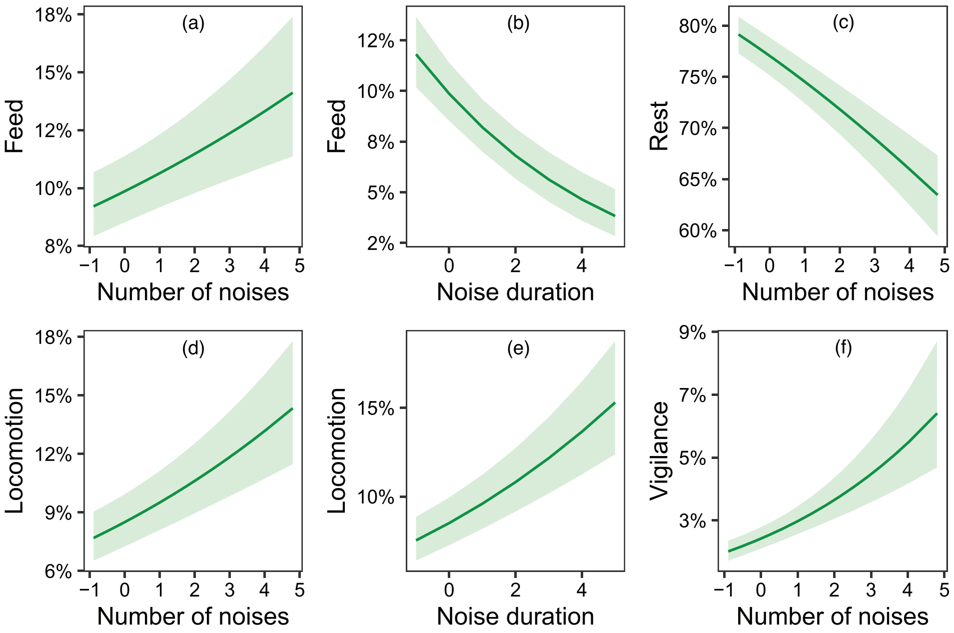

FIGURE 4 | Effects of anthropogenic noise on the activity budgets of mantled howler monkeys. Panels show the relationship between noise traits and the percentage of time spent on different behaviors: (a, b) feeding behavior in relation to the number of noise occurrences and duration, respectively; (c) resting behavior in relation to the number of noise occurrences; (d, e) locomotion behavior in relation to the number of noise occurrences and duration, respectively; and (f) vigilance behavior in relation to the number of noise occurrences. Green lines represent the predicted values from mixed-effects models, and the shaded areas represent 95% confidence intervals. *y*-axis scales differ among panels.

move-to-feed transitions following noise events suggest that individuals engage in opportunistic feeding after displacement, potentially as a stress-coping mechanism or to compensate for energetic costs of increased movement (Dunn et al. 2013; Dias et al. 2017). The reduction in resting time is particularly noteworthy, as howler monkeys typically devote 57%–80% of their daily activity to resting, a strategy thought to conserve energy given their folivorous-frugivorous diet (Di Fiore and Campbell 2007). These changes in activity budgets represent significant adjustments in time and energy allocation, which may influence individual well-being and ultimately affect fitness (Dunbar et al. 2009).

This study has several implications for primate conservation and management. The documented changes in activity indicate that even species with considerable behavioral flexibility, such as mantled howler monkeys, experience perturbations from noise pollution (Sih 2013; Wong and Candolin 2015). These effects may be more pronounced in species with less behavioral plasticity or those already facing other anthropogenic pressures. From a management perspective, our findings highlight the importance of noise mitigation strategies in protected areas, particularly in edge habitats where wildlife interfaces with human activities (Francis et al. 2009). Buffer zones with noise mitigation measures could significantly benefit primate populations inhabiting human-modified landscapes (Blickley and Patricelli 2010). In addition, temporal restrictions on high-noise activities during important feeding periods could help mitigate impacts, as our results show that feeding behavior is significantly affected by noise duration. Conservation strategies should consider differential responses to different noise traits, with a particular focus on reducing noise occurrence and intensity to minimize behavioral disruption (Berger-Tal et al. 2011). Future research should implement longitudinal analyses to assess whether the behavioral patterns we observed persist over extended timeframes. Such studies would strengthen causal inferences by determining if noise-induced behavioral changes represent temporary adjustments or lasting modifications to activity patterns with potential fitness consequences. Long-term monitoring would also reveal whether tolerance to specific noise traits continues to develop over time, potentially leading to habituation, or alternatively, whether prolonged exposure results in sensitization and more pronounced responses. These insights would significantly enhance our understanding of the ultimate impacts of anthropogenic noise on primate populations and improve the evidence base for conservation interventions.

In conclusion, this study demonstrates that anthropogenic noise affects the activity of mantled howler monkeys. We show that tolerance development in this species is not an all-or-nothing phenomenon, but rather a complex, trait-specific process that aligns with the multidimensional tolerance framework proposed by Čapkun-Huot et al. (2024). This trait-specific sensitivity provides important insights into how primates may develop selective tolerance to certain aspects of anthropogenic disturbance while remaining responsive to others. While behavioral flexibility may enable short-term coping with noise disturbance, the resulting changes in time allocation may have longer-term consequences for individual fitness and population viability.

Author Contributions

A.R.N. and P.A.D.D. originally formulated the idea; S.P.L.L., P.A.D.D., and A.R.N. developed methodology; S.P.L.L. conducted fieldwork; A.R.N. and P.A.D.D. provided project administration; S.P.L.L., P.A.D.D., and A.R.N. performed statistical analyses; all authors wrote the manuscript.

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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 openly available in figshare at https://figshare.com/, reference number https://doi.org/10.6084/m9.figshare.28628543.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Figure S1:** The activity budget of mantled howler monkeys (mean ± SD % of time) with and without anthropogenic noise. **Table S1:** Observed versus expected frequencies of activity changes following anthropogenic noise.