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Acoustic recognition of predators by mantled howler monkeys (*Alouatta palliata*): A playback experiment with naïve and experienced subjects

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Abstract

Objectives: When the production of antipredator behaviors is costly, prey is expected to stop displaying such behaviors and lose the ability to recognize extirpated predators. However, the loss or maintenance of predator recognition abilities is conditional on the eco-evolutionary context of prey. Here, we examined the behavioral responses of naïve and experienced mantled howler monkeys (*Alouatta palliata*) to simulated acoustic cues from natural predators.

Methods: We studied experienced individuals in the Uxpanapa Valley and naïve individuals in Los Tuxtlas (Veracruz, México). Jaguars (*Panthera onca*) and harpy eagles (*Harpia harpyja*), the main predators of howler monkeys, are extant in the Uxpanapa Valley but have been extirpated in Los Tuxtlas for approximately 70 and 45 years, respectively. We exposed six naïve and six experienced groups to playbacks of acoustic stimuli from the two predators and a non-predator control species (plain chachalacas, *Ortalis vetula*), and recorded the latency, frequency, and duration of antipredation behaviors ($n = 127$ trials).

Results: In contrast with experienced mantled howler monkeys, naïve subjects did not respond to trials from harpy eagles. However, response patterns were generally similar between naïve and experienced individuals when exposed to jaguar stimuli.

Discussion: Our findings suggest that naïve mantled howler monkeys do not recognize harpy eagle calls, but they respond to jaguar calls in a manner consistent with experienced individuals. These results illustrate how different mechanisms for the recognition of extirpated predators operate within a single species according to evolutionary and ecological experience.

KEYWORDS
antipredator behavior, harpy eagles, jaguars, relaxed selection

1 | INTRODUCTION

Predation imposes strong selective pressures on prey populations, favoring the evolution of antipredation traits that enhance survival and reproductive success (Caro, 2005). These traits, however, entail costs due to various trade-offs that prey face in allocating limited resources to antipredator defenses or other fitness-enhancing traits: investment in antipredation defenses may detract resources from growth, reproduction, immune function, or competitive ability (Brown, 1988, 1999; Brown & Kotler, 2004; Houston et al., 1993;

Jolly & Phillips, 2021; Schwanz et al., 2011, 2012). Currently, predator populations face impacts from human intervention, from disturbance to management practices (e.g., Berger et al., 2001; McClure et al., 2018; Ripple et al., 2014), leading to swift alterations in prey's ecological context. Understanding how prey cope with these changes is crucial for comprehending the broader ecological implications of human intervention in predator–prey dynamics.

The ecological (i.e., contemporary) and evolutionary (i.e., historical) experience of prey with their predators allows predicting how they respond to cues from extinct predators (Hettena et al., 2014). Whereas prey would always benefit from recognizing cues from extant predators, they may either retain or lose that ability following the extirpation of their predators (Carthey & Blumstein, 2018). Retention is more likely when prey and predators share a long coevolutionary history (the "ghosts of predators past" hypothesis: Peckarsky & Penton, 1988) and when prey still have ecological experience with other predators (i.e., the "multipredator hypothesis": Blumstein, 2006; Blumstein et al., 2009; see also Byers, 1997; Coss, 1999), as it is unlikely that antipredation traits evolve and persist independently for each predator type (Coss, 1999; Curio, 1973; Sih et al., 2023). In contrast, the loss of cue discrimination ability after predator extirpation is expected when traits allowing for discrimination and antipredator responses are costly to prey (i.e., the "relaxed selection" hypothesis: Lathi et al., 2009). Even in the absence of costly antipredation traits, the lack of learning opportunities should lead to the loss of predator recognition abilities (Berger et al., 2001). Differences between these scenarios are well illustrated by macropod responses to predator loss: when isolated from all predators, individuals do not display antipredator behaviors but, when at least some predators remain, a suite of behaviors are presented (Blumstein et al., 2004; Blumstein & Daniel, 2005).

Predation is a strong selective pressure for primates and has shaped many aspects of their anatomy, physiology, behavior, and ecology (e.g., Engh et al., 2006; Semple et al., 2002; Shultz & Dunbar, 2006; Terborgh, 1990; van Schaik, 1983). Most primates live in tropical forests and other wooded habitats (Galán-Acedo et al., 2019), where low visibility and good sound propagation compared with open habitats make acoustic signals an important communication channel (Waser & Waser, 1977). A few studies suggest that both innate predispositions and learning seem to be involved in the ability of primates to recognize acoustic cues from predators they have no ecological experience with. First, individuals born in captivity, without predation experience, but who regularly listen to predator calls display antipredation behaviors when exposed to predator playbacks (Geoffroy's marmosets, *Callithrix geoffroyi*: Searcy & Caine, 2003), suggesting that exposure to cues from predators may be involved in the expression of innate recognition mechanisms. Second, individuals without experience with predators (i.e., that have not been predated nor exposed to predator cues) do not discriminate between calls from predators and non-predators (captive cotton-top tamarins, *Saguinus oedipus*: Friant et al., 2008; wild pig-tailed langurs, *Simias concolor*: Yorzinski & Ziegler, 2007), suggesting that learning is critical for recognition. Whereas the first example supports the multipredator hypothesis and the possibility that predator recognition is "hardwired" (Byers, 1997; Coss, 1999), the second aligns with the expected results of relaxed selection and highlights that the lack of exposure to predator stimuli (i.e., learning) precludes the expression of antipredation responses. Although scant, this evidence suggests interspecific variation in the ability to retain predator cue recognition, as observed in other animal groups (Hettena et al., 2014), although methodological differences among studies could also contribute to such variation.

Jaguars (*Panthera onca*) and harpy eagles (*Harpia harpyja*) are major predators of howler monkeys (genus *Alouatta*: Cristóbal-Azkarate et al., 2015). These arboreal platyrrhine primates are resilient to habitat disturbance (Arroyo-Rodríguez & Dias, 2010) and persist in areas where other animals, including their major predators, are extirpated (Rangel-Negrín et al., 2014). Therefore, howler monkeys are good models for exploring the impact of predator loss on prey recognition abilities. Previous research indicates that mantled howler monkeys (*A. palliata*) without contact with harpy eagles for 10–20 generations do not display behavioral responses to playbacks of calls from this predator, suggesting that they do not recognize predators with which they have no contact (i.e., ecological experience; Gil-da-Costa et al., 2003). Compared with similar-sized primates, howler monkeys have high-energy expenditure (Pontzer et al., 2014) and follow an ecological strategy of energy expenditure minimization (Milton, 1980; Strier, 1992). Under a relaxed selection scenario, these energetic constraints could favor the loss of costly behavioral responses to stimuli without ecological relevance. After 1 year of exposure to reintroduced harpy eagles, during which these raptors hunted them, mantled howler monkeys displayed behavioral responses toward harpy playbacks suggesting recognition of the acoustic cues produced by these predators (e.g., vigilance: Gil-da-Costa et al., 2003). These results indicate that evolutionary experience is insufficient to retain cue discrimination (even for a short period), but that ecological experience with predators rapidly elicits adaptive responses in this species.

In this study, we aimed to confirm previous evidence that mantled howler monkeys do not recognize their predators after living without them for several generations. We hypothesized that, if antipredator behavior is subjected to relaxed selection, then, in contrast with experienced individuals, naïve mantled howler monkeys should not discriminate between cues from predators and non-predators. Accordingly, their responses to simulated predator calls should be slower, less frequent, and shorter.

2 | METHODS

2.1 | Ethical note

Our research protocols were approved by the Secretaría de Medio Ambiente y Recursos Naturales (permits SGPA/DGVS/04015/21 and SPARN/DGVS/00278/22) and complied with the legal requirements of the Mexican law. The research also adhered to the American Society of Primatologists Principles for the Ethical Treatment of Nonhuman Primates.

2.2 | Study sites and subjects

We conducted the study in two different areas of southern Mexico. The first was the Los Tuxtlas Biosphere Reserve (Veracruz state). Deforestation in this area began in the mid-1950s and resulted in severe loss of tropical rainforests and defaunation (Dias & Rangel-Negrín, 2022). The main predators of mantled howler monkeys have been extirpated in the area for several decades: the last report of a jaguar dates from 1955 (Hall & Dalquest, 1963), and the last recorded observation of a harpy eagle was in 1978 (Pérez-Higareda, 1979). The second area was the Uxpanapa Valley, a tract of evergreen tropical forest that is part of the Selva Zoque, some 150 km south of Los Tuxtlas. Deforestation in this area has also been historically high (Hernández et al., 2013), although at a lower intensity than in Los Tuxtlas (70% vs. 83% of deforestation: Galán-Acedo et al., 2021). Jaguars are still present in Uxpanapa (Solórzano-García et al., 2017; Vivas-Lindo et al., 2020) and, although the last formal report of harpy eagle sightings dates from 1994 (Peterson et al., 2003; Vargas et al., 2006), there are recent accounts of their potential presence in the area (Monroy-Ojeda, 2022; A. Monroy-Ojeda, personal communication). Therefore, whereas mantled howler monkeys living at Los Tuxtlas have not had contact with these predators for approximately 70 (jaguars) and 45 (harpy eagles) years (naïve hereafter), those at Uxpanapa Valley are likely currently exposed to predation from them (experienced hereafter). Regarding the presence of other howler monkey predators in the study sites, at Los Tuxtlas pumas (*Puma concolor*) have also been extirpated and ocelots (*Leopardus pardalis*) are very rare (Coates-Estrada & Estrada, 1986; Ríos-Solís et al., 2021), whereas both species are extant at Uxpanapa (Cristóbal-Azkarate et al., 2014). Black hawk-eagles (*Spizaetus tyrannus*) are present at both sites (Ortega-Álvarez et al., 2018).

We selected six groups in each area (Table 1) and classified each subject according to age and sex (Balcells & Veà Baró, 2009). When more than one group inhabited a forest fragment, we used physical traits (e.g., body size, patches of blond hair in the fingers and tail) to recognize some individuals and thus reliably identify study groups.

2.3 | Acoustic stimuli

Playback stimuli consisted of sounds produced by a terrestrial predator model (jaguar growls) and an aerial predator model (harpy eagle shrieks). Jaguar growls and harpy eagle shrieks are stimuli that elicit antipredator behaviors in different species of primates (Adams & Kitchen, 2020; Friant et al., 2008; Gil-da-Costa et al., 2003). As a control model, we used vocalizations of plain chachalacas (*Ortalis vetula*), a bird species that is present in both study areas and is not a predator of mantled howler monkeys. We retrieved uncompressed audio files from Animal Sound Archive (Museum für Naturkunde Berlin) and Xeno-Canto and edited them on Adobe Audition CC (Version 6, Adobe Systems, Mountain View, CA, USA) to remove background noise. Edited audio files (WAV; 705 kbps) consisted of two vocalization bouts, each lasting approximately 15 s, with a 20-s silence between them (Adams & Kitchen, 2020). Each audio file included 5 min of silence before the first vocalization bout to allow us to move away from the speaker, position close to the group, and determine the location of subjects before the beginning of the trial. To avoid pseudoreplication, we prepared six different audio files per stimulus so that each group was exposed only once to a specific audio. We randomly selected audio files among all stimuli and presented them to groups without repetition.

2.4 | Experimental protocol

We conducted playback experiments from July 2022 to April 2023. On each experimental day we first located study groups and then

TABLE 1 Mantled howler monkey groups studied in two areas in southern Mexico.

Area/group	Males	Females	Immatures	Unknown	Group size	Location
Los Tuxtlas						
Group 1	3	4	2	1	10	18°36′08″N, 95°04′07″O
Group 2	4	6	2	1	13	18°38′40″N, 95°05′30″O
Group 3	4	4	3	2	13	18°38′26″N, 95°05′28″O
Group 4	4	4	2	1	11	18°26′22″N, 95°03′00″O
Group 5	4	3	1	2	10	18°26′42″N, 95°03′05″O
Group 6	6	2	1	2	11	18°37′08″N, 95°04′52″O
Uxpanapa						
Group 7	3	6	2	1	12	17°19′20″N, 94°31′49″O
Group 8	3	3	2	2	10	17°19′17″N, 94°33′01″O
Group 9	2	3	3	1	9	17°20′57″N, 94°26′58″O
Group 10	2	4	4	1	11	17°20′29″N, 94°28′02″O
Group 11	3	3	3	1	10	17°20′45″N, 94°27′04″O
Group 12	2	2	1	1	6	17°20′48″N, 94°27′32″O

followed them until subjects rested or fed. We began trials when (i) most adults (>50%) were resting or feeding without moving in the canopy, (ii) at least two adult individuals could be clearly observed, and (iii) no vocalizations had been emitted by the focal group or other neighboring groups during the previous 15 min. We broadcasted audios with a smartphone (Huawei P60 Pro), a 2-Channel Bridgeable 500 W amplifier (Pioneer, GM-A3702), and a speaker (Bose 151 SE). The speaker was powered by a sealed rechargeable 12 V/7 battery (Powersonic PS-1270 F). During the jaguar trials we placed the speaker on the ground, while for the harpy eagle trials, we raised it ca. Six meters above ground level using a folding pole stick. We alternated the height of the speaker for control trials because plain chachalacas use both ground and above-ground forest levels.

One observer installed the equipment ca. thirty meters from the closest subject. This distance varied according to the availability of vegetation that ensured that the speaker was out of the group's visual range and that provided proper support for the folding stick when needed. Another observer stayed with the group to ensure none of the study subjects approached the area where the equipment was being prepared.

All tracks were played in a randomized order for each study group among the three stimuli (i.e. control, harpy, and jaguar tracks). We played each track once to each study group to avoid pseudoreplication. We conducted one trial per experimental day in naïve groups but, we did two trials on four experimental days with experienced groups. In all cases, we decided to run a second trial because on the first individuals did not display any behavioral response to the control stimulus. The interval between these consecutive experiments was approximately 3 h, allowing the subjects to engage in other activities, such as foraging or traveling, before starting the second trial. On two occasions, two different naïve groups had vocal activity a few seconds before the playbacks began (one due to a helicopter flying above, and the other because subjects responded to a calling neighbor) and we could not stop the playbacks before they were audible. On both cases we stoped the playbacks, rescheduled the trials, and those specific tracks were not used again in those groups. We aimed at exposing each group four times to each treatment (i.e., control, harpy, and jaguar) but we could not conduct all trials in the predation-exposed groups due to difficulties in reaching groups in mountainous areas. Thus, we conducted 72 trials with the naïve subjects (24 trials per treatment) and 55 with experienced subjects (17 control, 19 harpy, and 19 jaguar trials). The mean time elapsed between consecutive trials in each group was 8.5 days for naïve groups and 8.9 days for experienced groups.

2.5 | Behavioral data collection

We used focal animal sampling and 30-min continuous recording (Altmann, 1974) to observe the first adult who displayed the following behaviors: vigilance, vocalization, approach, and avoidance. We recorded vigilance as the frequency of head movements associated with the visual exploration of the environment toward the area where the speaker was placed. We recorded vocalizations by measuring the duration of loud calling bouts. A loud calling bout is defined as the emission of vocalizations, mainly roars and barks, in different combinations by one or several individuals that can range from a few seconds to 60 min with short (<1 min) silence pauses (da Cunha et al., 2015). We measured the duration of approaches, defined as locomotion toward the speaker, and avoidance, that is locomotion away from the speaker. We also recorded the time elapsed between the beginning of the playbacks and the first displayed anti-predator behavior (i.e., latency). When none of the subjects displayed antipredator behavior, observation sessions were interrupted after 10 min.

2.6 | Data organization and analysis

We used mixed models to examine if variation in antipredator behaviors (i.e., latency to first behavior, frequency of vigilance, and duration of all behaviors) was influenced by exposure to predators (Table S1). Fixed factors in all models were experience, with two levels, naïve/experienced; treatment, with two levels, either control/harpy or control/jaguar playbacks; and the interaction between these variables. We added group identity as a random factor to all models to account for the repeated sampling of groups. We fitted latency and frequency models with negative binomial distribution error and log-link function to control for overdispersion in data and duration models with a Gaussian distribution error. Q–Q plots of observed versus expected model residuals and Kolmogorov–Smirnov tests indicated normality. We assessed the effect size of each model with marginal pseudo-coefficients of determination. Given that we were specifically interested in variation in antipredator behavior associated with exposure to treatment depending on experience, the results section is focused on the description of the interaction term. We used Tukey contrasts as post hoc tests when the interaction term was significant.

Comparisons of complete models (i.e., including fixed and random predictors) with a null model with group identity as the sole predictor using likelihood ratio tests yielded significant results ($p < 0.001$ for the six comparisons), indicating that the random factor accounted for a small proportion of the variance in antipredation behaviors. We also did not find evidence that factors related to study design (trial number, time between trials, distance from speaker to subjects) and demography (group size, number of immatures per group) influenced the results (Table S2).

3 | RESULTS

Most trials elicited a behavioral response by mantled howler monkeys (73%, $n = 127$ playback experiments). When a response was recorded, males ($n = 60$) were more frequently first responders than females ($n = 33$). The behavior that more commonly was first displayed was vigilance (69% of playbacks), followed by nonresponses

TABLE 2 Mixed model results of the effects of experience and playback treatment on the behavioral responses of mantled howler monkeys ($n = 127$ trials).

Model/predictor	R^{2}[a]	χ^2	p
Harpy Eagle			
Latency	0.18		
Experience		8.5	0.004
Treatment		0.1	0.762
Experience × treatment		0.4	0.516
Frequency	0.43		
Experience		1.5	0.218
Treatment		10.2	0.001
Experience × treatment		14.9	<0.001
Duration	0.18		
Experience		6.1	0.014
Treatment		3.2	0.074
Experience × treatment		6.8	0.009
Jaguar			
Latency	0.62		
Experience		0.3	0.566
Treatment		124.2	<0.001
Experience × treatment		21.9	<0.001
Frequency	0.82		
Experience		1.1	0.284
Treatment		182.6	<0.001
Experience × treatment		21.3	<0.001
Duration	0.61		
Experience		2.2	0.137
Treatment		133.8	<0.001
Experience × treatment		23.6	<0.001

[a] Marginal pseudo-coefficients of determination (i.e., variance explained by fixed factors).

(26%), and vocalizations (5%). Approach and avoidance (locomotion) were never observed as a first response. Latency to first behavioral response did not vary between control and harpy eagle trials in both naïve and experienced subjects, although overall naïve subjects responded quicker (Table 2, Figure 1; Table S3). The frequency and duration of behaviors increased significantly among experienced subjects following harpy eagle stimuli compared with control trials whereas no such change occurred among naïve subjects. Longer behavioral responses were recorded for naïve than for experienced subjects, independent of treatment type.

Regarding jaguar stimuli, naïve and experienced subjects showed similar response patterns for the three behavioral measures: quicker, more frequent, and longer responses in jaguar than in control trials. Within treatments, there were differences related to experience in the frequency of behaviors in both control (higher in naïve) and jaguar (higher in experienced) trials, as well as in the duration of behaviors in control trials (higher in naïve).

4 | DISCUSSION

In this study, we assumed that temporal matching between stimulus presentation and the behavior of mantled howler monkeys allows for exploring predation recognition ability in this species. We examined the behavioral responses of naïve and experienced mantled howler monkeys toward simulated acoustic cues from predators to determine if predator recognition is subjected to relaxed selection. We found mixed support for our hypothesis. As predicted, in contrast with experienced mantled howler monkeys, naïve subjects did not recognize harpy eagle stimuli. However, response patterns were generally similar between naïve and experienced individuals when exposed to jaguar stimuli. Therefore, relaxed selection does not universally explain the ability to recognize cues from extinct predators in this species. We sampled the first individuals who displayed behavioral responses to playbacks. As we did not know who they were (we did not identify study subjects systematically), we could not assess inter and intraindividual behavioral variation and this could potentially lead to pseudoreplication issues in our statistical models. Therefore, our results should be interpreted with caution.

Our results concur with previous evidence that mantled howler monkeys lose the ability to recognize acoustic cues from extinct harpy eagles (Gil-da-Costa et al., 2003), and provide support for the relaxed selection hypothesis on the loss of predator cue discrimination abilities (Lathi et al., 2009). There are no estimations of howler monkey predation rates by harpy eagles, but platyrrhines are an important food resource for this raptor (27% of food biomass), second only to sloths (50% of food biomass: three-toed sloths, *Bradypus tridactylus*, and two-toed sloths, *Choloepus didactylus*: Miranda, 2015). Given that sloths do not distribute in Mexico, primate predation by harpy eagles may have been historically high in southern Mexico. In the absence of such strong selective pressure, the loss of the ability to recognize harpy eagle cues may be related to genetic or developmental processes (Lathi et al., 2009). As it is unlikely that genetic changes favoring the loss of predator cue detection could occur in such a short period (45 years), lack of learning opportunities for predator cue recognition (Berger et al., 2001) is a more parsimonious explanation for naïve mantled howler monkey behavior toward harpy eagle stimuli. Similar results have been observed in other primates (Friant et al., 2008; Yorzinski & Ziegler, 2007) and mammals (Blumstein et al., 2002, 2004; Blumstein & Daniel, 2005; Waaleboer et al., 2024).

Contrary to our prediction, naïve mantled howler monkeys displayed consistent behavioral responses to jaguar trials that were, in general, similar to those of experienced individuals. It is possible that jaguar predation represented a stronger selective pressure for mantled howler monkeys than harpy eagles, or that they shared a longer period of coevolution, a condition that favors the maintenance of predator recognition abilities according to the "ghosts of predators past" hypothesis (Peckarsky & Penton, 1988). A heightened response toward jaguars could also indicate that predation of howler monkeys and other platyrrhines by terrestrial predators is more common and the diversity of predator species is higher than for aerial predators (e.g., Chinchilla, 1997; Cristóbal-Azkarate et al., 2015; Mourthé &

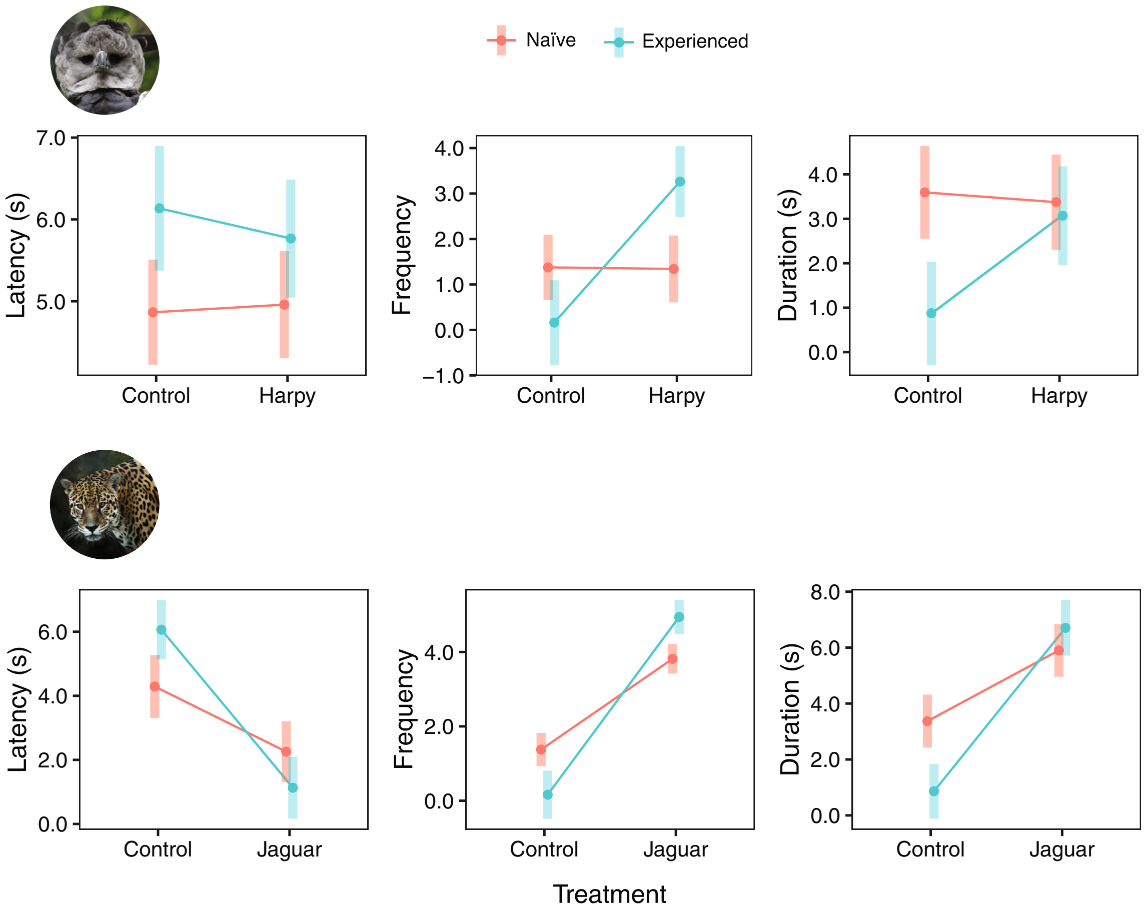

FIGURE 1 Linear (and generalized) mixed model results on the influence of the interaction between experience in exposure to predators and treatment (control, harpy eagle, and jaguar calls) on the behavioral responses of mantled howler monkeys to acoustic stimuli: Latency to first response (left panels); frequency of vigilance (middle panels); and duration of responses (right panels). Dots are the predicted estimate values by the models and rectangles are their 95% confidence intervals. $N = 127$ trials.

Barnett, 2014; Peetz et al., 1992). Stronger antipredator responses to terrestrial than to aerial predators has been observed in several primates. Rylands' bald-faced saki monkeys (*Pithecia rylandsi*), for instance, exhibit longer durations of antipredator behaviors when exposed to jaguar than to harpy eagle acoustic stimuli (Adams & Kitchen, 2020), and a greater number of red lemurs (*Eulemur fulvus rufus*) display escape behavior when exposed to fossa (*Cryptoprocta ferox*) playbacks than to Madagascar harrier-hawks (*Polyboroides radiatus*; Fichtel & Kappeler, 2002). Jaguars are terrestrial but prey on several arboreal mammals, and evidence of jaguar predation on howler monkeys is scarce but compelling: for instance, a jaguar preyed five howler monkeys from a six-member group over a 7-month period (Peetz et al., 1992).

Alternatively, it is possible that the contemporary presence of terrestrial predators favored the maintenance of antipredation responses toward jaguar cues (i.e., a multipredator recognition mechanism: Blumstein, 2006). On the one hand, ocelots are still present in Los Tuxtlas (A. Coyohua-Fuentes, personal observation) and, although considerably smaller (body length = 86.3 cm vs. 143 cm: Wilson & Mittermeier, 2009), have several common traits with jaguars, such as a spotted coat, stalking hunting strategy, and similar activity patterns (Herrera et al., 2018; Wilson & Mittermeier, 2009). On the other hand, dogs (*Canis lupus familiaris*) are an exotic predator that elicits both behavioral and physiological responses in howler monkeys (Rangel-Negrín et al., 2023). This possibility, however, is questioned by the fact that black hawk-eagles, which have been reported to prey on howler monkeys (Miranda et al., 2006), are also present in Los Tuxtlas (Ortega-Álvarez et al., 2018) and could thus function as an aerial predator template allowing for harpy eagle recognition in the same way that ocelots and dogs favor responses to extirpated jaguars. Future playback studies using stimuli from these other putative predators (there are no reports of howler monkey predation by ocelots, dogs, and black hawk-eagles in Los Tuxtlas) could provide clarification on the mechanisms underlying predator cue recognition in this species. Furthermore, as antipredator detection is conducted through different sensory channels and antipredator behaviors can also be elicited using visual models of predators (Hernández-Tienda et al., 2021; Meno et al., 2013; Pereira & Macedonia, 1991), we will also explore the role of sight in the maintenance of antipredator behaviors in mantled howler monkeys.

In sum, mantled howler monkeys have different behavioral responses toward simulated acoustic cues from two predator species that have been absent from their habitat for a similar period: they do not recognize harpy eagle calls but respond toward jaguar acoustic stimuli as experienced individuals do. For mantled howler monkeys living at Los Tuxtlas, relaxed selection and ghosts of predators past (or the multipredator hypothesis) seem to explain antipredator behavioral patterns. Therefore, our results illustrate how different mechanisms for the recognition of extinct predators operate within a single species according to its evolutionary and ecological experience.

AUTHOR CONTRIBUTIONS

Rafael Omar Sánchez Vidal: Conceptualization (equal); data curation (equal); formal analysis (equal); investigation (equal); methodology (equal); resources (equal); validation (equal); writing – original draft (equal). **Ariadna Rangel Negrín:** Conceptualization (equal); data curation (equal); formal analysis (equal); funding acquisition (equal); project administration (equal); resources (equal); supervision (equal); writing – original draft (equal). **Margarita Briseño Jaramillo:** Methodology (equal); supervision (equal); validation (equal); writing – original draft (equal). **J. Roberto Sosa López:** Methodology (equal); supervision (equal); validation (equal); writing – original draft (equal). **Pedro A. D. Dias:** Conceptualization (equal); data curation (equal); formal analysis (equal); funding acquisition (equal); methodology (equal); project administration (equal); resources (equal); supervision (equal); validation (equal); writing – original draft (equal).

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data analyzed in this study are available in the supporting information file.

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