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Dog barks influence the physiological stress and behavior of a wild primate

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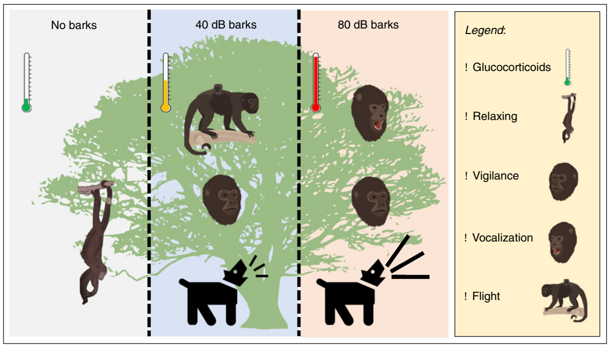
HIGHLIGHTS

- The effects of dog disturbance on primates have seldom been assessed.
- We used playback experiments to examine the impact of barks on mantled howler monkey physiology and behavior.
- Physiological stress increased with dog bark intensity and behavioral responses were variable.
- Dog barks disturb mantled howler monkeys, both physiologically and behaviorally.

GRAPHICAL ABSTRACT



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ABSTRACT

Non-lethal impacts of dogs on primates have seldom been assessed. We used an experimental approach to determine if mantled howler monkeys (*Alouatta palliata*) perceive dog barks as an aversive stimulus and thus display physiological and behavioral responses toward simulated barks. For one year (1754 h of observations) we studied 16 adult males belonging to five groups in Los Tuxtlas (Mexico), and recorded the occurrence of naturally occurring dog barks, their sound pressure level (SPL), and the behavioral responses of howler monkeys to barks. We then exposed males to bark playbacks at two SPL treatments, 40 and 80 dB in a total of 50 experiments. We assayed glucocorticoid metabolite concentrations in fecal samples (fGCM) as a marker of the physiological stress response of males. We also recorded the duration of vigilance, vocalizations, and flight in relation to playbacks. Naturally occurring barks were frequent and usually elicited behavioral responses by males. fGCM concentrations increased after bark playbacks and with stimuli intensity. Time spent vigilant increased following playbacks independently of stimuli intensity but both vocalizations and flight were linked to stimuli intensity: vocalizations were the longest after barks played-back at 80 dB, but males spent more time fleeing in response to 40 dB bark playbacks. These results provide evidence that dog barks are pervasive in the habitat of mantled howler monkeys living at Los Tuxtlas and disturb males, both physiologically and behaviorally. Although the potential costs of physiological and behavioral responses could not be determined, there is sufficient evidence to assume that they do have negative impacts on individuals. Therefore, our study provides avenues for future research on dog-wildlife interactions and valuable information for the design of conservation actions aimed at mitigating the impact of dogs on mantled howler monkeys.

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1. Introduction

Following domestication ca. 40,000 years ago (Bergström et al., 2020; Freedman et al., 2014; Perri et al., 2021), dogs (*Canis lupus familiaris*) dispersed widely throughout the globe and the current world population of domestic dogs is probably over 1 billion (Gompper, 2014). They are the most abundant carnivores, and maintain close association with humans (Miller et al., 2014; Serpell, 2017), which does not mean that all dogs live equally: some dogs are permanently under human care and rely on humans for food and shelter; others roam freely, and may either supplement the diet provided by humans with resources they find independently or rely exclusively on their own foraging abilities (Hughes and Macdonald, 2013; Vanak and Gompper, 2009). Whereas the impact of the former in the environment may be restricted to specific contexts (e.g., walks: Weston and Stankowich, 2014), dogs that roam freely affect wildlife in a variety of ways and represent a threat to the persistence of several species (Doherty et al., 2017; Young et al., 2011).

Dogs affect wildlife through predation, competition, disease transmission, and hybridization (Doherty et al., 2017; Hughes and Macdonald, 2013). Disturbance caused by dogs is a more subtle type of impact, but it has nonetheless several effects on wildlife. In this context, disturbance pertains to the responses of wildlife to aversive stimuli (Weston and Stankowich, 2014). It is unlikely that wildlife habituates (i.e., decrease their responses due to repeated stimulation: Hinde, 1970) to dogs because (i) individuals that experienced attacks are expected to maintain responses to dogs through time, as predation is a strong selective pressure (Krebs and Davies, 1997); (ii) individuals that have not experienced dog attacks may still recognize them as potential predators through various mechanisms (Carthey and Blumstein, 2018); and (iii) independently of predation risk, dogs may be perceived as an aversive stimulus due to their conspicuous (e.g., barking) and unpredictable behavior (e.g., frequent changes in the direction and speed of movement; Glover et al., 2011; Miller et al., 2001). Wildlife is thus expected to respond physiologically and/or behaviorally to dogs, and those responses may entail costs, such as increased energy expenditure, loss of reproductive opportunities, or increased physiological stress (e.g., Gingold et al., 2009; Græsli et al., 2020; Lenth et al., 2008; Lima, 1998; MacArthur et al., 1982). Understanding the non-lethal impacts of dogs is therefore important for the conservation and management of wildlife.

Glucocorticoids (GCs) are the main modulators of physiological stress responses in vertebrates and are involved in coping with ongoing and future challenges (i.e., have reactive and predictive functions; Sapolsky et al., 2000). During stress, GC actions result in the increase of circulating glucose, contributing to the depletion of present and, when the effect of a stressor is prolonged, future energy stores (Sapolsky et al., 2000). Therefore, GCs are good indicators of the physiological consequences of stress, and its measurement provides insights into the selective forces acting on animal populations that face energetic and psychosocial challenges. In primates, there is consistent evidence of GC modulation in response to both natural (e.g., social rank, predation: Beehner and Bergman, 2017) and anthropogenic challenges (e.g., habitat loss, hunting: Kaisin et al., 2021). There is no information, however, on the influence of dogs in the physiological stress response of primates.

Howler monkeys (genus *Alouatta*) are platyrrhine primates with a wide distribution in the Americas. Domestic dogs affect howler monkeys living in disturbed habitat. First, when their habitat does not provide sufficient resources (i.e., food, mates, space), howler monkeys may descend to the ground to reach new areas. During these movements they may be attacked by dogs (e.g., Candelero-Rueda and Pozo-Montuy, 2010; Chaves et al., 2022; Corrêa et al., 2018; Lopes et al., 2022; Raño et al., 2016). Second, when howler monkeys use power lines to cross roads and open areas between forest patches they risk being electrocuted. Following electrocution individuals drop to the ground where they can be attacked by dogs (Corrêa et al., 2018). Dog attacks result in the injury or death of individuals indicating that, similarly to what happens with vertebrates in general (Doherty et al., 2017) and other primate species (Anderson, 1986), predation is the major impact of dogs on howler monkeys. There are no studies, however, of non-predation impacts of dogs on howler monkeys, which is surprising given the pervasive presence of dogs in tropical forests (e.g., Lessa et al., 2016; Massara et al., 2018). For instance, we do not know whether howler monkeys perceive dogs as a disturbance when they have not experienced dog attacks (e.g., in areas where they do not travel on the ground, and thus the risk of dog attacks is low). Given the consistent evidence that dogs disturb wildlife and that such disturbance imposes several costs, it is important to understand if howler monkeys display similar physiological and behavioral responses to dogs.

Our aim was to investigate the disturbance responses of the Endangered Mexican mantled howler monkeys (*A. palliata mexicana*) to dogs. Specifically, we followed an experimental approach to examine the hypothesis that mantled howler monkeys perceive dog barks as an aversive stimulus and thus display physiological (physiological stress) and behavioral (flight, vigilance, and vocalizations) responses toward simulated dog barks. We tested three predictions of this hypothesis. First, if mantled howler monkeys perceive dogs as an aversive stimulus, they should display both behavioral and physiological responses to barks, independently of stimuli intensity. Second, alternatively, mantled howler monkeys may perceive dog barks as an aversive stimulus, but respond according to bark intensity, such that behavioral and physiological responses are only elicited by stronger stimuli (i.e., louder barks). Third, given that previous experience may determine how individuals react to stimuli, the physiology and behavior of mantled howler monkeys in response to barks should vary among groups.

2. Materials and methods

2.1. Ethics statement

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

2.2. Study sites and subjects

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

2.3. Naturally occurring dog barks and howler monkey behavior (non-experimental)

From January to December 2020 (240 fieldwork days) we visited each group for a mean (±SD) of 4 (±2) days per month and a mean of 7.3 (±4) consecutive hours (7:00–8:00 to 14:00–15:00, depending on the time of the year). We used focal animal sampling and 10 min continuous recordings (Altmann, 1974) to study the following behaviors: approach (movements ≤ 45° from the direction of a stimulus: Van Belle and Estrada, 2020), flight (movements ≥ 135° from the direction of a stimulus: Van Belle and Estrada, 2020), socialize (affiliation, agonism: Dias and Rangel-Negrín, 2015a), vigilance (visual exploration of the environment directed beyond the reach of the animal's arm:

Treves, 2000), vocalize (barks and roars: da Cunha et al., 2015). We observed the study groups for a total of 1754 h (Table 2).

We recorded all instances of dog barking. Specifically, we measured the sound pressure level (SPL) and the duration of dog barks. We measured SLP continuously with a sound meter TN-ST106, Tenmars, Taiwan; measuring range = 30–130 dB; sampling frequency = 20.8μS (48 kHz); frequency band = 10 Hz–16 kHz) and noted SLP at the onset of dog barks. We also recorded the behavioral response of the first male that displayed any of the behaviors described above following a dog bark. If males did not display any of these behaviors after 10 min, we recorded the event as a "no-response".

2.4. Dog bark playbacks

We opportunistically recorded the spontaneous barks of mongrel dogs that resided in the study area. All dogs were males and had small to medium size (ca. 45–55 cm of height). We recorded barks at 2 m from each dog using a Marantz PMD 660 recorder and a Sennheiser MKE-600 microphone. We used Audacity (Audacity Team, 2021) to isolate barks from background noise and to prepare audio playbacks. Each audio had a 10 min duration and consisted of 5 min of silence followed by five to eight bark bouts of 30 to 45 s with 5 to 10 s silence intervals between them. The initial silence allowed us to move away from the speaker and position ourselves closer to the group to sample the behavioral responses of males to playbacks. To avoid pseudoreplication, we prepared different exemplars of each playback, which we randomly used as playback stimuli in the experiments.

We used a KSR speaker (KSA-6915, 13,000 W PMPO, 250 W RMS) to broadcast the barks. Prior to the playback experiments, we determined the distance between the speaker and the study subjects and the speaker volume that would be required for the bark sounds to reach mantled howler monkeys at two SPL treatments (40 and 80 dB, which were the minimum and maximum SPL of naturally occurring dog barks; see Results section). In a similar environment to those where we would conduct the experiments, we placed the speaker at ground level and recorded SLP at increasing distances (assessed with a measuring tape) from the speaker while regulating the speaker's volume so that barks sounded natural.

2.5. Experimental protocol

We exposed the five study groups to dog bark playbacks from June to December 2021. We located groups on the early morning and started the experiments after the focal group had its first feeding bout of the day and all adult individuals were resting (i.e., sleep or static without interaction) for 10 min. The mean ± SD starting time of the experiments was 9:47 ± 2:32 h. Once the speaker's volume and distance from the group were set, we began the playback experiments. At the onset of dog barks, we performed a 10 min behavioral sampling that consisted of two parts: (i) we scanned all group males for the occurrence of the following behaviors: vigilance, vocalizations, and flight. These were the most frequent behavioral responses of males to dog barks during the non-experimental stage of the study (see *Naturally occurring dog barks* section of Results); (ii) when a male displayed any of the target behaviors (i.e., vigilance, vocalizations, and flight), besides noting his identity, we recorded the duration of the behavior.

After the end of the playback experiments, we followed groups for the rest of the day. If before, during, or after the experiments we observed any of the following, which are stimuli with the potential to affect mantled howler monkey behavior and physiology, we discarded the experiment and rescheduled it: aggression (Dias et al., 2017; n = 2 experiments); noise produced by aerial traffic, human voice (not produced by researchers), and tools/machinery (e.g., chainsaw, lawnmower: Gómez-Espinosa et al., 2022; n = 5 experiments); mating (Dias et al., 2022; n = 1 experiment). Given the aim of this study, we also discarded experiments if dogs were seen near mantled howler monkeys or if we recorded dog barks before, during, or after the experiments (n = 3 experiments). Each group was exposed five times to each SLP treatment, 40 and 80 dB, resulting in 10 experiments per group and a total of 50 experiments.

2.6. Fecal sample collection and hormonal assays

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

We collected fecal samples from the forest floor immediately after deposition when we could unambiguously match them to male identity. We deposited samples in polyethylene bags labeled with the identity of each individual and stored them in a cooler with ice packs while in the field and in a freezer at −20 °C once back at the field station. We collected 216 fecal samples during the non-experimental stage of the study (mean ± SD = 43.2 ± 4.8 samples per group, 13.5 ± 2.4 samples per male) and 172 samples during the experimental stage (mean ± SD = 34.4 ± 6.4 samples per group, 10.8 ± 0.8 samples per male; Supporting information Table S1).

We freeze-dried (FreeZone 18, Labconco, Kansas City, MO) all fecal samples within a maximum of 6 months after collection. We extracted fGCM from dried samples following a modification of the method by Wasser et al. (2000). Briefly, we mixed 0.6 g of homogenized, lyophilized, and pulverized feces for 20 h in 4.0-ml analytical-grade methanol. We centrifuged extracts (460 g for 30 min) and recovered the supernatant. After complete evaporation of the solvent in a water bath at 60 °C for 20 h, we reconstituted pellets with 3-ml albumin buffer which we used for fGCM assays.

We determined fGCM concentrations with a chemiluminescent immunoassay using a commercial kit (Cortisol, Immulite, Siemens, Los Angeles, CA, USA; sensitivity = 5.5 nmol/L; calibration range = 28–1380 nmol/L) and an automated immunoassay system (Immulite 1000 analyzer, Siemens, Munich, Germany). The antibody in this kit is highly specific to cortisol, showing low (8.6 %) cross-reactivity with corticosterone and we have previously validated its use to assess fGCM variation in mantled howler monkeys (Cañadas-Santiago et al., 2020). Pooled fecal extracts, when added to the standard curve points, exhibited a similar slope (R^2 = 0.95, n = 8, P < 0.001), and serial dilutions of a fecal pool yielded results that were parallel to the kit's standards (t = 0.9, n = 4, P = 0.402). Intra-assay variation (coefficient of variation) averaged 12.1 % (n = 4 samples) and inter-assay variation was 13.7 % (n = 4 samples). We report fGCM values as ng/g (dry feces).

2.7. Data organization and analysis

We used descriptive statistics to investigate the patterns of naturally occurring dog barks in terms of occurrence, rates (i.e., frequency per unit of time), and SPL, and Spearman correlations to assess association among these measures. We also used descriptive statistics to explore the behavioral responses of males to naturally occurring dog barks.

We defined baseline conditions for mantled howler monkeys as days in which we did not see dogs in the vicinity of the study groups and did not hear dog barks. We used these baseline days as matched controls (MC) to assess the effects of experimental dog barks on the behavior and fGCM of males. For the statistical analysis of male behavior, in our baseline dataset we randomly selected as MC focal animal samples from the first male that responded to each experimental playback (i.e., 50 focal animal samples in baseline days matched with observations of the same males in the 50 playback experiments). For the statistical analysis of male fGCM, we selected as

MC fecal samples that we collected from all males the day after a baseline day ($n = 216$ samples).

We used linear mixed models to test our predictions. First, we built a model in which mean fGCM concentrations per male per treatment ($n = 48$) were the response variable, treatment (i.e., MC, 40 dB playbacks, 80 dB playbacks) and group identity ($n = 5$) were fixed predictors, and male identity ($N = 16$) was a random factor to account for the repeated measuring of males. Second, we ran three models with the same fixed and random predictors and the duration of vigilance, vocalizations, and flight per treatment as the response variables in each model. We log transformed fGCM and durations to improve model fit and we checked that the assumptions of normally distributed and homogeneous residuals were fulfilled by visually inspecting Q–Q plots and residuals plotted against fitted values (Supporting information Fig. S1). Model residuals did not deviate significantly from normality (all Kolmogorov–Smirnov tests $P > 0.05$).

We compared complete models (i.e., with fixed and random predictors) with a null model including only the random factor with likelihood ratio tests to determine whether the random factor accounted for a larger proportion of variation in response variables than the fixed factors (Pinheiro and Bates, 2000). In all cases we found significant differences ($P < 0.001$ in all tests, i.e., fixed factors were more influential in the response variables than the random factor). We calculated marginal pseudo-coefficients of determination for each model to assess the deviance in response variables explained by each model (i.e., goodness-of-fit). We performed all statistical analyses in R (R Core Team, 2022).

3. Results

3.1. Naturally occurring dog barks

We recorded dog barks in almost half of the sampling days and dog barks occurred at a rate of one bark per 3.7 observation hours (Table 1). The SPL of dog barks varied between 39 and 79.8 dB, with a mean of 43.2 dB. Variation among groups in the occurrence, rate, and SPL of barks was notable in some cases (e.g., bark rate in Balzapote was eight times larger than in La Flor de Catemaco), and these variables were positively correlated (occurrence & rate: $r_s = 0.98$, $n = 5$, $P = 0.005$; occurrence & SPL: $r_s = 0.90$, $n = 5$, $P = 0.083$; rate & SPL: $r_s = 0.87$, $n = 5$, $P = 0.054$).

A majority (75 %, $n = 355$ barks) of dog barks elicited a behavioral response by mantled howler monkey males. The most frequent type of behavior was vigilance (43 % of responses), followed by vocalization (35 %), flight (20 %), threat (2 %), and socialization (1 %).

3.2. Responses to bark playbacks

The fGCM concentrations of mantled howler monkeys were lower in days without dog barks (i.e., matched controls, MC) than when they were exposed to barks played back at 40 dB and 80 dB ($\chi^2_2 = 75.5$, $P < 0.001$; $P < 0.01$ for all post-hoc pairwise comparisons; Fig. 1a) but were not affect by group identity ($\chi^2_4 = 3.3$, $P = 0.509$). Males spent more time: (i) vigilant ($\chi^2_2 = 27.5$, $P < 0.001$) following dog barks than in MC without barks ($P < 0.001$ for all post-hoc pairwise comparisons; Fig. 1b); (ii) vocalizing ($\chi^2_2 = 20.1$, $P < 0.001$) in response to 80 dB barks than to both 40 dB barks and MC ($P < 0.001$ for all post-hoc pairwise comparisons; Fig. 1c); and (iii) fleeing ($\chi^2_2 = 16.7$, $P < 0.001$) after 40 dB barks than after both 80 dB barks and MC ($P < 0.001$ for all post-hoc pairwise comparisons; Fig. 1d).

Table 2
The occurrence, rate, and sound pressure level (SPL) of dog barks recorded in the habitat of five mantled howler monkey groups at Los Tuxtlas (Mexico).

Group	Occurrence [a]	Rate [b]	SPL (dB) [c]
Balzapote	49 (33)	0.28 (252)	46.0 (4.7)
Borrego	64 (36)	0.78 (182)	44.9 (1.3)
La Flor G1	44 (68)	0.09 (559)	42.6 (6.7)
La Flor G2	29 (83)	0.09 (536)	42.2 (5.1)
Montepío	45 (20)	0.19 (225)	43.6 (1.9)
Total	43 (240)	0.27 (1754)	44.3 (4.1)

[a] Percentage of days with bark recordings (total number of sampling days indicated in parenthesis).

[b] Frequency of bark recordings divided by the number of sampling hours (indicated in parenthesis).

[c] Mean SPL of dog barks (SD indicated in parenthesis).

4. Discussion

We described the attributes of naturally occurring dog barks in the habitat of five mantled howler monkey groups and used playback experiments to assess the influence of barks on the physiological stress and behavior of males. Dog barks were frequent, recorded in all studied habitats, and often elicited behavioral responses by males. Males showed physiological stress responses to dog barks, proxied here via fecal glucocorticoid metabolite concentrations (fGCM), which increased with stimuli intensity. Regarding the behavioral responses to simulated barks, males spent more time vigilant following barks than when no barks were recorded, independently of stimuli intensity. In contrast, both vocalization and flight responses were linked to stimuli intensity, such that vocalizations were longest in response to simulated barks at 80 dB, but males spent more time fleeing in response to 40 dB barks. The physiological and behavioral responses of males to dog barks were not influenced by group identity. These results provide evidence that dog barks are pervasive in the habitat of mantled howler monkeys living at Los Tuxtlas and disturb males.

We recorded dog barks in the habitat of all study groups although their attributes were variable. It is possible that such variation is linked to the spatial configuration of study sites. For instance, Borrego is a 64-ha fragment that stands 140 m from a village, and we recorded a dog bark each 1.3 h of observations there, whereas Montepío is 106 ha, 1435 m from the nearest settlement, and we recorded a bark at that site every 5.3 h. As the propagation of dog barks (like that of any other sound) decreases with distance, presence of barriers, ground effects, and air absorption (Wahlberg and Larsen, 2017), barks produced by dogs that were in settlements closer to the smaller forest fragments had higher SPL and were thus more likely to be recorded (Balzapote and Borrego). Additionally, as

Table 1
Attributes of the groups and habitats of mantled howler monkeys studied at Los Tuxtlas, Mexico.

Attribute	Group				
	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
Number of groups per fragment	1	4	3	3	2
Fragment size (ha)	10	63.8	100	100	106.2
Distance to nearest human settlement (m)	200	140	730	1200	1435
Distance to 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

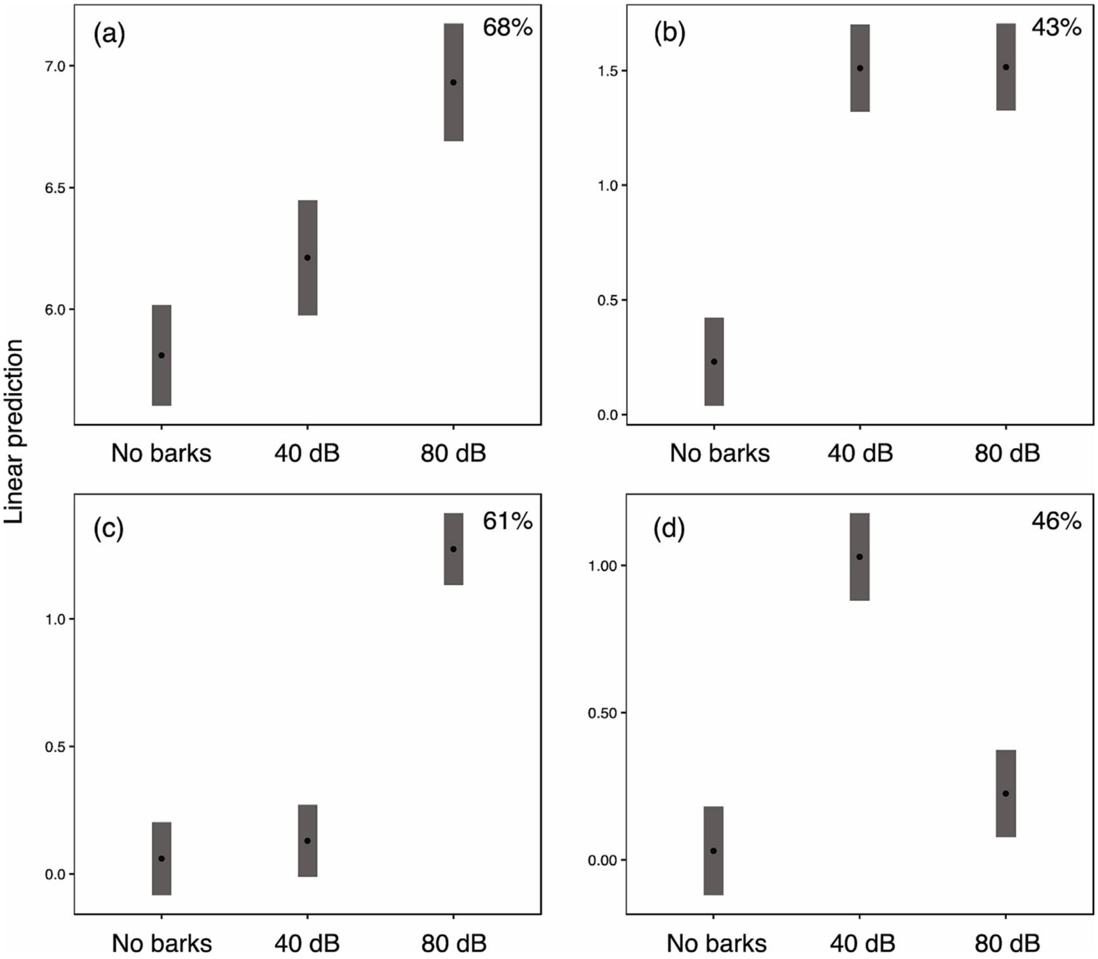

Fig. 1. Estimates (black dots) and 95 % confidence intervals (gray rectangles) of mixed effects models on the influence of dog barks on the physiological stress and behavior of male mantled howler monkeys: a) fecal glucocorticoid metabolites; b) duration of vigilance; c) duration of vocalizations; d) duration of flight. Marginal pseudo-coefficients of determination of each model (i.e., goodness-of-fit) are also shown (%).

dogs that roam through natural landscapes usually arrive from urban areas (Pérez et al., 2018; Villatoro et al., 2016), the closer a forest fragment is to a settlement the higher the likelihood that it is visited by dogs. Small sample size and large variation in sampling effort among groups are however confounding factors that call for caution in interpreting these results. For instance, the rate of dog barks decreased with increasing sampling effort, thus limiting a reliable assessment of the influence of previous experience (or frequency of exposure) on male behavior. Future research based on a landscape-scale approach (Fahrig, 2005) may be important to understand the patterns of dog presence in the habitat of mantled howler monkeys and provide valuable information for the management of both canids and primates.

The hypothalamo-pituitary-adrenocortical axis allows organisms to cope with unpredictable and/or uncontrollable stimulus through the release of glucocorticoid hormones (Sapolsky et al., 2000). Variation in the fGCM concentrations of mantled howler monkey males indicates that they respond physiologically to dog barks, which converges with evidence that wildlife does not habituate to the presence of dogs (Weston and Stankowich, 2014). This is further supported by two lines of evidence: fGCM concentrations and the behavior of males did not vary among groups despite dramatic differences in exposure rate (e.g., one bark per 1.3 vs. 11 h) and habitat attributes (e.g., Berger-Tal and Saltz, 2019; Kaisin et al., 2021), thus rejecting the third prediction; but previous experience and frequency of exposure do predict the behavioral responses of males to other acoustic stimuli (anthropogenic noise), such that individuals with high rates of exposure have waned responses (Gómez-Espinosa et al., 2022). Therefore, the strategies used by mantled howler monkeys to cope with dog barks differ from those elicited by other challenges. Note that there are several accounts of interactions between dogs and primates (e.g., Anderson, 1986; Nautiyal et al., 2023; Ordóñez-Gómez et al., 2016; Pihlström et al., 2021; Rimbach et al., 2013; Scheun et al., 2015; Waters et al., 2017), but this is the first evidence of a physiological response toward dogs in a primate species.

As proposed in the second prediction, mantled howler monkeys increased their fGCM concentrations with increasing SLP, suggesting that their physiological responses are associated with risk assessment (Blanchard and Blanchard, 1988). Specifically, it is possible that males perceive barks played back at 80 dB as a riskier stimulus and thus show stronger physiological responses compared to 40 dB barks, because former are interpreted as a more imminent threat (i.e., shorter distances to dogs) than the latter. In contrast, we found mixed results for the behavioral responses of males to varying intensity of dog bark stimuli that support either the first (vigilance) or the second prediction (vocalization and flight). Vigilance is a critical component of the behavioral strategies of many organisms, as it allows for monitoring predators and competitors and thus has high adaptive value (Beauchamp, 2015; Quenette, 1990; Treves, 2000). Given that it is the first step in the process of predation avoidance (Tyrrell and Fernández-Juricic, 2015), vigilance is a common behavior in the repertoire of prey (Treves, 2000), as observed in this study during the non-experimental stage, when it was the most frequent behavioral response of males to dog barks, and in studies with other primates (Anderson, 1986). This explains why the duration of vigilance did not vary between dog bark experimental treatments. Vocalizations and flight, in turn, are two possible outcomes of the processes of risk detection and assessment that follow vigilance. The allocation of more time to fleeing following 40 dB bark playbacks but more time to vocalizations after 80 dB barks indicates that males modulate their behavior according to stimuli attributes, SPL in this case. Specifically, mantled howler monkeys may try to evade dogs by fleeing when they perceive them as more distant but vocalize when encounters are imminent. In this context, vocalizations following dog barks may be functionally similar to alarm calls produced in response to natural predators (Camargo and Ferrari, 2007; Gil-da-Costa et al., 2003; McKinney, 2009).

This pattern of behavioral response to dog barks disagrees with optimality theory, according to which prey should not flee until the potential costs of staying in their position (e.g., being attacked) exceed the costs of escaping (e.g., increased energy expenditure; Ydenberg and Dill, 1986). Such disagreement may be explained by several features of the physiology and behavior of howler monkeys. Howler monkeys move cautiously and slowly through the canopy (Bezanson, 2006), and falls from trees are not uncommon, particularly among immatures (Glander, 1975; Jones, 1994). If a quick escape increases the risk of falling from trees and of a consequent attack by dogs, it may thus be costlier to wait until dogs are closer (i.e., higher SPL) than to flee as soon as the aversive stimulus is detected. Additionally, the production of vocalizations >90 dB accompanied by vigorous behavioral displays is expected to be energetically costly (Kitchen, 2004; Whitehead, 1989), especially for mantled howler monkeys, who have diets that include significant amounts of foods that are hard to digest and poor in readily available energy (Dias and Rangel-Negrín, 2015b). In this sense, the higher fGCM responses toward barks played back at 80 dB could reflect psychological stress evoked by an aversive stimulus and energetic stress associated with the demands of vocalizing. Parsing psychological and energetic impacts of dogs on mantled howler monkey physiology may be achieved by future research through the assessment of additional biomarkers (e.g., thyroid hormone, urinary C-peptide: Dias et al., 2017, 2022).

We could not determine if the physiological and behavioral responses of males to dog barks are costly. There is, however, abundant evidence that the recurrent activation of the physiological stress response and the displaying of the behaviors that were assessed here have associated costs. For instance, stress physiology may be critical for the survival of individuals facing unpredictable challenges, such that those with chronic activation of the stress response face higher mortality risk (Romero and Wikelski, 2010). Additionally, given that time and energy devoted to cope with unpredictable challenges tradeoff against other critical components of individual budgets, such as reproduction, foraging, or socialization (e.g., Græsli et al., 2020; Le Grand et al., 2019; Tisdale and Fernández-Juricic, 2009), the behavioral responses toward dogs impose opportunity costs (e.g., stop foraging to flee). Therefore, from a conservation and management perspective, it is prudent to assume that mantled howler monkeys are negatively impacted by dogs and design actions directed at preventing those impacts (Miller et al., 2014; Parsons et al., 2016; Smith et al., 2019; WHO/WSPA, 1990; Williams et al., 2009). Such actions are increasingly important given a recent increase in deforestation in the Los Tuxtlas Biosphere Reserve (Von Thaden et al., 2020). The resulting encroachment of howler monkeys in forest fragments will probably increase their vulnerability to disturbance and attacks by dogs as, for instance, they are more likely to move through the ground when living in smaller and isolated forest fragments (Arroyo-Rodríguez and Dias, 2010).

In conclusion, dog barks are recurrent in the habitat of mantled howler monkeys living at Los Tuxtlas and elicit both physiological and behavioral responses in males, according to bark intensity. Although the potential costs of these responses could not be determined, there is sufficient evidence to assume that they do have negative impacts on individuals. Therefore, our study provides avenues for future research on dog-wildlife interactions and valuable information for the design of conservation actions aimed at mitigating the impact of dogs on mantled howler monkeys.

CRediT authorship contribution statement

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).

Eugenia Eréndira 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).

David Roberto Chavira Ramírez: investigation (equal); methodology (equal); resources (equal); supervision (equal); validation(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).

Data availability

Data will be made available on request.

Declaration of competing interest

We declare no conflicts of interest.

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Appendix A. Supplementary data

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References

Altmann, J., 1974. Observational study of behavior: sampling methods. Behaviour 49, 227–266. https://doi.org/10.1163/15685 3974X00534.

Anderson, J.R., 1986. Encounters between domestic dogs and free-ranging non-human primates. Appl. Anim. Behav. Sci. 15, 71–86. https://doi.org/10.1016/0168-1591(86)90024-9.

Arroyo-Rodríguez, V., Dias, P.A.D., 2010. Effects of habitat fragmentation and disturbance on howler monkeys: a review. Am. J. Primatol. 72, 1–16. https://doi.org/10.1002/ajp.20753.

Audacity Team, 2021. Audacity Software 3.2. Audacity Team, Pittsburg.

Beauchamp, G., 2015. Animal Vigilance: Monitoring Predators And Competitors. Academic Press, San Diego, CA.

Beehner, J.C., Bergman, T.J., 2017. The next step for stress research in primates: to identify relationships between glucocorticoid secretion and fitness. Horm. Behav. 91, 68–83. https://doi.org/10.1016/j.yhbeh.2017.03.003.

Berger-Tal, O., Saltz, D., 2019. Invisible barriers: anthropogenic impacts on inter- and intra-specific interactions as drivers of landscape-independent fragmentation. Phil. Trans. R. Soc. B 374, 20180049. https://doi.org/10.1098/rstb.2018.0049.

Bergström, A., Frantz, L., Schmidt, R., Ersmark, E., Lebrasseur, O., et al., 2020. Origins and genetic legacy of prehistoric dogs. Science 370 (6516), 557–564. https://doi.org/10.1126/science.aba9572.

Bezanson, M.F., 2006. Leap, bridge, or ride? Ontogenetic influences on positional behavior in cebus and alouatta. In: Estrada, A., Garber, P.A., Pavelka, M.S.M., Luecke, L. (Eds.), New Perspectives in the Study of Mesoamerican Primates: Distribution, Ecology, Behavior, And Conservation. Springer Verlag, New York, pp. 333–348 https://doi.org/10.1007/0-387-25872-8_16.

Blanchard, D.C., Blanchard, R.J., 1988. Ethoexperimental approaches to the biology of emotion. Annu. Rev. Psychol. 39, 43–68. https://doi.org/10.1146/annurev.ps.39.020188.000355.

Camargo, C.C., Ferrari, S.F., 2007. Interactions between tayras (Eira barbara) and red-handed howlers (Alouatta belzebul) in eastern Amazonia. Primates 48, 147–150. https://doi.org/10.1007/s10329-006-0009-y.

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

Candelero-Rueda, R., Pozo-Montuy, G., 2010. Mortalidad de monos aulladores negros (Alouatta pigra) en paisajes altamente fragmentados de Balancán, Tabasco. In: Gamma, L., Pozo-Montuy, G., Contreras-Sánchez, W. (Eds.), Perspectivas en Primatología de México. Universidad Juárez Autónoma de Tabasco, Colección Rovirosa, México, pp. 65–76.

Carthey, A.J.R., Blumstein, D.T., 2018. Predicting predator recognition in a changing world. Trends Ecol. Evol. 33, 106–115. https://doi.org/10.1016/j.tree.2017.10.009.

Chaves, Ó.M., Souza Júnior, J.C., Buss, G., Hirano, Z.M.B., Jardim, M.M.A., Amaral, E.L.S., Godoy, J.C., Peruchi, A.R., Michel, T., Bicca-Marques, J.C., 2022. Wildlife is imperiled in peri-urban landscapes: threats to arboreal mammals. Sci. Total Environ. 821, 152883. https://doi.org/10.1016/j.scitotenv.2021.152883.

Corrêa, F.M., Chaves, Ó.M., Printes, R.C., Romanowski, H.P., 2018. Surviving in the urban–rural interface: feeding and ranging behavior of brown howlers (Alouatta guariba clamitans) in an urban fragment in southern Brazil. Am. J. Primatol. 80, e22865. https://doi.org/10.1002/ajp.22865.

da Cunha, R.G.T., de Oliveira, D.A.G., Holzmann, I., Kitchen, D.M., 2015. Production of loud and quiet calls in howler monkeys. In: Kowalewski, M., Garber, P.A., Cortés-Ortiz, L., Urbani, B., Youlatos, D. (Eds.), Howler Monkeys: Adaptive Radiation, Systematics, And Morphology. Springer, New York, pp. 337–368 https://doi.org/10.1007/978-1-4939-1957-4_13.

Dias, P.A.D., Rangel-Negrín, A., 2015a. An ethogram of the social behavior of adult Alouatta palliata mexicana and A. pigra. Retrieved December 5, 2022, from https://uv.mx/personal/pdias.

Dias, P.A.D., Rangel-Negrín, A., 2015b. Diets of howler monkeys. In: Kowalewski, M., Garber, P.A., Cortés-Ortiz, L., Urbani, B., Youlatos, D. (Eds.), Howler Monkeys: Behavior, Ecology, And Conservation. Springer, New York, pp. 21–56 https://doi.org/10.1007/978-1-4939-1960-4_2.

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

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

Doherty, T.S., Dickman, C.R., Glen, A.S., Newsome, T.M., Nimmo, D.G., Ritchie, E.G., Vanak, A.T., Wirsing, A.J., 2017. The global impacts of domestic dogs on threatened vertebrates. Biol. Conserv. 210, 56–59. https://doi.org/10.1016/j.biocon.2017.04.007.

Fahrig, L., 2005. When is a landscape perspective important? In: Wiens, J.A., Moss, M.R. (Eds.), Issues And Perspectives in Landscape Ecology. Cambridge University Press, Cambridge, UK, pp. 3–10 https://doi.org/10.1017/CBO9780511614415.002

Freedman, A.H., Gronau, I., Schweizer, R.M., Ortega-Del Vecchyo, D., Han, E., Silva, P.M., Galaverni, M., Fan, Z., Marx, P., Lorente-Galdos, B., et al., 2014. Genome sequencing highlights the dynamic early history of dogs. PLoS Genet. 10, e1004016. https://doi.org/10.1371/journal.pgen.1004016.

Gil-da-Costa, R., Palleroni, A., Hauser, M.D., Touchton, J., Kelley, J.P., 2003. Rapid acquisition of an alarm response by a neotropical primate to a newly introduced avian predator. Proc. R. Soc. Lond. B 270, 605–610. https://doi.org/10.1098/rspb.2002.2281.

Gingold, G., Yom-Tov, Y., Kronfeld-Schor, N., Geffen, E., 2009. Effect of guard dogs on behavior and reproduction of gazelles in cattle enclosures on the Golan Heights. Anim. Conserv. 12, 155–162. https://doi.org/10.1111/j.1469-1795.2009.00235.x.

Glander, K.E., 1975. Habitat And Resource Utilization: An Ecological View of Social Organization in Howling Monkeys. University of Chicago, Chicago Unpublished PhD Dissertation.

Glover, H.K., Weston, M.A., Maguire, G.S., Miller, K.K., Christie, B.A., 2011. Towards ecologically meaningful and socially acceptable buffers: response distances of shorebirds in Victoria, Australia, to human disturbance. Landsc. Urban Plan. 103, 326–334. https://doi.org/10.1016/j.landurbplan.2011.08.006.

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

Gómez-Espinosa, E., Dias, P.A.D., Rangel-Negrín, A., 2022. The influence of anthropogenic noise on the behavior of male mantled howler monkeys. Am. J. Primatol. 84, e23377. https://doi.org/10.1002/ajp.23377.

Gompper, M.E., 2014. The dog-human-wildlife interface: assessing the scope of the problem. In: Gompper, M.E. (Ed.), Free-ranging Dogs & Wildlife Conservation. Oxford University Press, Oxford, pp. 9–54 https://doi.org/10.1093/acprof:osobl/9780199663217.003.0001.

Græsli, A.R., Le Grand, L., Thiel, A., Fuchs, B., Devineau, O., Stenbacka, F., Neumann, W., Ericsson, G., Singh, N.I., Laske, T.G., Beumer, L.T., Arnemo, J.M., Evans, A.L., 2020. Physiological and behavioural responses of moose to hunting with dogs. Conserv. Physiol. 8, coaa122. https://doi.org/10.1093/conphys/coaa122.

Hinde, R.A., 1970. Animal Behaviour: A Synthesis of Ethology And Comparative Psychology. McGraw-Hill Book Company, New York.

Hughes, J., Macdonald, D.W., 2013. A review of the interactions between free-roaming domestic dogs and wildlife. Biol. Conserv. 157, 341–351. https://doi.org/10.1016/j.biocon.2012.07.005.

Jones, C., 1994. Injury and disease of the mantled howler monkey in fragmented habitats. Neotrop. Primates 2, 4–5.

Kaisin, O., Fuzessy, L., Poncin, P., Brotcorne, F., Culot, L., 2021. A meta-analysis of anthropogenic impacts on physiological stress in wild primates. Conserv. Biol. 35, 101–114. https://doi.org/10.1016/j.ygcen.2022.113985.

Kitchen, D.M., 2004. Alpha male black howler monkey responses to loud calls: effect of numeric odds, male companion behaviour and reproductive investment. Anim. Behav. 67, 125–139. https://doi.org/10.1016/j.anbehav.2003.03.007.

Krebs, J.R., Davies, N.B., 1997. Behavioural Ecology: An Evolutionary Approach. Fourth edition. Blackwell, Oxford, UK.

Le Grand, L., Thorsen, N.H., Fuchs, B., Evans, A.L., Laske, T.G., Arnemo, J.M., Sæbø, S., Støen, O.-G., 2019. Behavioral and physiological responses of Scandinavian brown bears (Ursus arctos) to dog hunts and human encounters. Front. Ecol. Evol. 7, 134. https://doi.org/10.3389/fevo.2019.00134.

Lenth, B.E., Knight, R.L., Brennan, M.E., 2008. The effects of dogs on wildlife communities. Nat. Areas J. 28, 218–227. https://doi.org/10.3375/0885-8608(2008)28[218,TEODOW]2.0.CO;2.

Lessa, I., Guimarães, T.C.S., Bergallo, H.G., Cunha, A., Vieira, E., 2016. Domestic dogs in protected areas: a threat to Brazilian mammals? Nat. Conserv. 14, 46–56. https://doi.org/10.1016/j.ncon.2016.05.001.

Lima, S.L., 1998. Nonlethal effects in the ecology of predator-prey interactions: what are the ecological effects of anti-predator decision-making? Bioscience 48, 25–34. https://doi.org/10.2307/1313225.

Lopes, S., Calegaro-Marques, C., Klain, V., Chaves, Ó.M., Bicca-Marques, J.C., 2022. Necropsies disclose a low helminth parasite diversity in periurban howler monkeys. Am. J. Primatol. 84, e23346. https://doi.org/10.1002/ajp.23346.

MacArthur, R.A., Geist, V., Johnston, R.H., 1982. Cardiac and behavioral responses of mountain sheep to human disturbance. J. Wildl. Manag. 46, 351–358. https://doi.org/10.2307/3808646.

Massara, R.L., Paschoal, A.M.D.O., Bailey, L.L., Doherty Jr., F.P., Hirsch, A., Chiarello, G.A., 2018. Factors influencing ocelot occupancy in Brazilian Atlantic Forest reserves. Biotropica 50, 125–134. https://doi.org/10.1111/btp.12481.

McKinney, T., 2009. Anthropogenic change and primate predation risk: crested caracaras (Caracara plancus) attempt predation on mantled howler monkeys (Alouatta palliata). Neotrop. Primates 16, 24–27.

Miller, S.G., Knight, R.L., Miller, C.K., 2001. Wildlife responses to pedestrians and dogs. Wildl. Soc. Bull. 29, 124–132.

Miller, K.K., Ritchie, E.G., Weston, M.A., 2014. The human dimensions of dog–wildlife interactions. In: Gompper, M.E. (Ed.), Free-ranging Dogs & Wildlife Conservation. Oxford University Press, Oxford, pp. 286–304 https://doi.org/10.1093/acprof:osobl/9780199663217.003.0012.

Nautiyal, H., Tanaka, H., Huffman, M.A., 2023. Anti-predator strategies of adult male Central Himalayan Langurs (Semnopithecus schistaceus) in response to domestic dogs in a human-dominated landscape. Primates https://doi.org/10.1007/s10329-023-01061-0.

Ordóñez-Gómez, J.D., Cristóbal-Azkarate, J., Arroyo-Rodríguez, V., Santillán-Doherty, A.M., Valdez, R.A., Romano, M.C., 2016. Proximal and distal predictors of the spider monkey's stress levels in fragmented landscapes. PLoS ONE 11, e0149671. https://doi.org/10.1371/journal.pone.0149671.

Parsons, A.W., Bland, C., Forrester, T., Baker-Whatton, M.C., Schuttler, S.G., McShea, W.J., Costello, R., Kays, R., 2016. The ecological impact of humans and dogs on wildlife in protected areas in eastern North America. Biol. Conserv. 203, 75–88. https://doi.org/10.1016/j.biocon.2016.09.001.

Pérez, G.E., Conte, A., Garde, E.J., Messori, S., Vanderstichel, R., Serpell, J., 2018. Movement and home range of owned free-roaming male dogs in Puerto Natales,Chile. Appl. Anim. Behav. Sci. 205, 74–82. https://doi.org/10.1016/j.applanim.2018.05.022.

Perri, A.R., Feuerborn, T.R., Frantz, L.A.F., Larson, G., Malhi, R.S., Meltzer, D.J., Witt, K.E., 2021. Dog domestication and the dual dispersal of people and dogs into the Americas. Proc. Natl. Acad. Sci. U. S. A. 118, e2010083118. https://doi.org/10.1073/pnas.201008311.

Pihlström, H., Rosti, H., Lombo, B.M., Pillikka, P., 2021. Domestic dog predation on white-tailed small-eared galago (Otolemur garnettii lasiotis) in the Taita Hill,Kenya. Afr. Primates 15, 31–38.

Pinheiro, J., Bates, D., 2000. Mixed-effects Models in S And S-plus. Springer, New York.

Quenette, P.Y., 1990. Functions of vigilance behaviour in mammals: a review. Acta Oecol. 11, 801–818.

R Core Team, 2022. R: A Language And Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna.

Rangel-Negrín, A., Coyohua-Fuentes, A., de la Torre Herrera, A., Cano-Huertes, B., Reynoso-Cruz, E., Ceccarelli, E., et al., 2021. Female reproductive energetics in mantled howler monkeys (Alouatta palliata): a follow-up study. Am. J. Phys. Anthropol. 174, 396–406. https://doi.org/10.1002/ajpa.24222.

Raño, M., Kowalewski, M.M., Cerezo, A.M., Garber, P.A., 2016. Determinants of daily path length in black and gold howler monkeys (Alouatta caraya) in northeastern Argentina. Am. J. Primatol. 78, 825–837. https://doi.org/10.1002/ajp.22548.

Rimbach, R., Link, A., Heistermann, M., Gómez-Posada, C., Galvis, N., Heymann, E.W., 2013. Effects of logging, hunting, and forest fragment size on physiological stress levels of two sympatric ateline primates in Colombia. Conserv. Physiol. 1, cot031. https://doi.org/10.1093/conphys/cot031.

Romero, L.M., Wikelski, M., 2010. Stress physiology as a predictor of survival in Galapagos marine iguanas. Proc. R. Soc. Lond. B Biol. Sci. 277, 3157–3162. https://doi.org/10.1098/rspb.2010.0678.

Sapolsky, R.M., Romero, L.M., Munck, A.U., 2000. How do glucocorticoids influence stress responses? Integrating permissive, suppressive, stimulatory and preparative actions. Endocrinol. Rev. 21, 55–89. https://doi.org/10.1210/edrv.21.1.0389.

Scheun, J., Bennett, N.C., Ganswindt, A., Nowack, J., 2015. The hustle and bustle of city life: monitoring the effects of urbanisation in the African lesser bushbaby. Sci. Nat. 102, 57. https://doi.org/10.1007/s00114-015-1305-4.

Serpell, J., 2017. The Domestic Dog: Its Evolution, Behaviour And Interactions With People. Second edition. Cambridge University Press, UK.

Smith, L.M., Hartmann, S., Munteanu, A.M., Villa, P.D., Quinnell, R.J., Collins, L.M., 2019. The effectiveness of dog population management: a systematic review. Animals 9, 1020. https://doi.org/10.3390/ani9121020.

Tisdale, V., Fernández-Juricic, E., 2009. Vigilance and predator detection vary between avian species with different visual acuity and coverage. Behav. Ecol. 20, 936–945. https://doi.org/10.1093/beheco/arp080.

Treves, A., 2000. Theory and method in studies of vigilance and aggregation. Anim. Behav. 60, 711–722. https://doi.org/10.1006/anbe.2000.1528.

Tyrrell, L.P., Fernández-Juricic, E., 2015. Sensory systems and escape behavior. In: Cooper Jr., W.E., Blumstein, D.T. (Eds.), Escaping From Predators: An Integrative View of Escape Decisions. Cambridge University Press, Cambridge, pp. 322–342 https://doi.org/10.1017/CBO9781107447189.013.

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

Vanak, A.T., Gompper, M.E., 2009. Dogs Canis familiaris as carnivores: their role and function in intraguild competition. Mammal Rev. 39, 265–283. https://doi.org/10.1111/j.1365-2907.2009.00148.x.

Villatoro, F.J., Sepúlveda, M.A., Stowhas, P., Silva-Rodríguez, E.A., 2016. Urban dogs in rural areas: human-mediated movement defines dog populations in southern Chile. Prev. Vet. Med. 135, 59–66. https://doi.org/10.1016/j.prevetmed.2016.11.004.

Von Thaden, J.J., Laborde, J., Guevara, S., Mokondoko-Delgadillo, P., 2020. Dynamics of land use and land cover change in the Los Tuxtlas Biosphere Reserve (2006–2016). Rev. Mex. Biodivers. 91, e913190. https://doi.org/10.22201/ib.20078706e.2020.91.3190.

Wahlberg, M., Larsen, O.N., 2017. Propagation of sound. In: Brown, C.H., Riede, T. (Eds.), Comparative Bioacoustics: An Overview. Bentham Science, Oak Park, IL, pp. 61–120 https://doi.org/10.2174/97816810831791170101.

Wasser, S.K., Hunt, K.E., Brown, J.L., Cooper, K., Crockett, C.M., Bechert, U., Millspaugh, J.J., Larson, S., Monfort, S.L., 2000. A generalized fecal glucocorticoid assay for use in a diverse array of nondomestic mammalian and avian species. Gen. Comp. Endocrinol. 120, 260–275. https://doi.org/10.1006/gcen.2000.7557.

Waters, S., El Harrad, A., Chetuan, M., Bell, S., Setchell, J.M., 2017. Dogs disrupting wildlife: domestic dogs harass and kill Barbary macaques in Bouhachem forest,North Morocco. Afr. Primates 12, 55–58.

Weston, M.A., Stankowich, T., 2014. Dogs as agents of disturbance. In: Gompper, M.E. (Ed.), Free-ranging Dogs And Wildlife Conservation. Oxford University Press, UK, pp. 94–116 https://doi.org/10.1016/B978-1-4557-4462-6.00012-X.

Whitehead, J.M., 1989. The effect of the location of a simulated intruder on responses to long-distance vocalizations of mantled howling monkeys, Alouatta palliata. Behaviour 108, 73–103. https://doi.org/10.1163/156853989X00060.

WHO/WSPA, 1990. Guidelines for Dog Population Management. World Health Organisation, Geneva World Society for the Protection of Animals, London.

Williams, K.J., Weston, M.A., Henry, S., Maguire, G.S., 2009. Birds and beaches, dogs and leashes: dog owner's sense of obligation to leash dogs on beaches in Victoria,Australia. Hum. Dimens. Wildl. 14, 89–101. https://doi.org/10.1080/10871200802649799.

Ydenberg, R.C., Dill, L.M., 1986. The economics of fleeing from predators. Adv. Study Behav. 16, 229–249. https://doi.org/10.1016/S0065-3454(08)60192-8.

Young, J.K., Olson, K.A., Reading, R.P., Amgalanbaatar, S., Berger, J., 2011. Is wildlife going to the dogs? Impacts of feral and free-roaming dogs on wildlife populations. Bioscience 61, 125–132. https://doi.org/10.1525/bio.2011.61.2.7.