Primates
https://doi.org/10.1007/s10329-025-01218-z

ORIGINAL ARTICLE

Spatial organization of mantled howler monkeys in relation to dog disturbance

Cathy G. Rubio Corona[1] · Ariadna Rangel Negrín[1] · Pedro A. D. Dias[1]

Received: 12 March 2025 / Accepted: 5 October 2025

Abstract
Predation risk fundamentally shapes primate social structure by influencing cooperation, competition, and spatial organization within groups. Although domestic dogs (*Canis lupus familiaris*) represent one of the world's most impactful invasive species affecting wildlife, their influence on primate social structure remains largely understudied. We examined how dog presence and barks influence interindividual proximity among group members in mantled howler monkeys (*Alouatta palliata*). We studied two habituated groups (10 and 8 adults, respectively) in Veracruz, Mexico, combining 242 h of observational data with experimental playbacks of dog barks at different intensities (40 and 80 dB). We calculated proximity indices from instantaneous sampling of interindividual proximity. Howler monkeys were closer immediately following exposure to dogs, partially supporting our hypothesis that interindividual proximity would change in response to dogs. Contrary to predictions, individuals were farther from each other as bark intensity increased and as proximity to dog stimuli decreased. During longer timeframes, individuals were closer when exposed to low-intensity barks compared to periods without dog stimuli. These findings demonstrate that dogs influence howler monkey spatial organization through context-dependent effects that vary with stimulus characteristics and temporal scale. Despite the short-term nature of this study, the consistency between observational and experimental results suggests these patterns are reliable. Therefore, these results contribute to our understanding of how invasive predators affect primate social structure and highlight the importance of managing free-ranging dogs in areas where they overlap with wildlife populations.

Keywords *Alouatta* · Barks · *Canis* · Invasive species · Proximity · Social structure

Introduction

The balance between the costs and benefits of sociality shapes interaction patterns and the resulting social relationships that define social structure across species and contexts (Alexander 1974; Krause and Ruxton 2002). Understanding the factors that influence social structure is crucial for comprehending animal ecology and evolution, particularly how ecological pressures like predation affect cooperative and competitive relationships within groups (Clutton-Brock 2009; Silk 2007). Predation risk can significantly influence social structure by altering dominance relationships, coalition formation, and patterns of reciprocity (Isbell 1994; Lima and Dill 1990; Trivers 1971). Animals typically respond to predatory threats by adjusting their interaction networks, often forming tighter social bonds that enhance information transfer and establish clearer roles in collective defense (Couzin and Krause 2003; Kelley et al. 2011).

Domestic dogs (*Canis lupus familiaris*) are the third most impactful invasive species, after cats (*Felis catus*) and rats (*Rattus* spp.), regarding their effects on wildlife (Doherty et al. 2017). With a global population exceeding one billion, dogs are the most abundant carnivores on Earth (Gompper 2014) and can severely impact native fauna when not properly managed. Dogs affect wildlife through multiple mechanisms, including direct predation, competition, disease transmission, and disturbance (Hughes and Macdonald 2013). As predators, dogs have contributed to the extinction or endangerment of numerous species worldwide, particularly small to medium-sized mammals, ground-nesting birds, and reptiles (Doherty et al. 2017). Wildlife often fails to habituate to dogs, resulting in

✉ Pedro A. D. Dias
pedroaddias@gmail.com

[1] Primate Behavioral Ecology Lab, Instituto de Neuroetología, Universidad Veracruzana, Xalapa, Mexico

persistent behavioral alterations even when the threat of predation is minimal (Weston and Stankowich 2014).

The impacts of dogs on wild primates are of particular concern yet remain understudied. At least 40 species of non-human primates are known to interact with domestic and feral dogs, with encounters ranging from casual to predatory (Anderson 1986). Dogs have been documented preying on various primate species in regions where human settlements overlap with primate habitats (e.g., Galetti and Sazima 2006; Nautiyal et al. 2024; Oliveira et al. 2008), and serve as hunting companions for capturing primates (Fa and Brown 2009; Fuentes 2006). Beyond direct predation, dogs influence primate behavior through disturbance, potentially disrupting daily movement patterns, activity budgets, and social interactions (Bidner 2014; Nautiyal et al. 2024; Ruhiyat 1991; Willems and Hill 2009). Despite these observations, systematic studies on how dogs affect primate social structure remain scarce. Most research has focused on individual behavioral responses like vigilance, alarm calls, and flight rather than dyadic and group-level effects. This knowledge gap is significant because alterations in social structure can affect reproductive success, resource acquisition, and ultimately survival (Chancellor and Isbell 2009; Fedigan et al. 2008; Schülke et al. 2010; Silk et al. 2003). Therefore, research examining how dogs influence primate social structure is needed for both theoretical understanding and conservation planning.

Howler monkeys (genus *Alouatta*) are arboreal platyrrhines that are preyed upon by several species (Cristóbal-Azkarate et al. 2015). Their antipredation behavior includes vigilance, alarm calling, and predator mobbing (Miranda et al. 2005, 2006; Treves et al. 2001), and is contingent on predation mode (i.e., aerial or terrestrial: Sánchez-Vidal et al. 2024). There is no direct evidence that predation influences the social structure of howler monkeys, but observation of individuals moving to take cover in response to potential predators (Ferrari 2009) suggest that interindividual proximity may be affected by it. Although mantled howler monkeys are strictly arboreal in continuous forests, habitat fragmentation increasingly forces terrestrial movements (Arroyo-Rodríguez and Dias 2010), where they can be attacked by dogs (e.g., Chaves et al. 2022; Corrêa et al. 2018; Lopes et al. 2022). Recently it has been reported that mantled howler monkeys (*A. palliata*) respond both physiologically and behaviorally to dog barks, with increased glucocorticoid hormone concentrations, vigilance, vocalizations, and flight responses depending on bark intensity (Rangel-Negrín et al. 2023). However, how these responses translate to changes in their social structure remains unexplored. Howler monkeys have relatively low rates of social interaction but complex spatial relationships that reveal social structure (Corewyn and Kelaita 2014; Dias and Rodríguez-Luna 2005; Dias et al. 2010; Wang and Milton 2003). Therefore, examining interindividual proximity patterns may provide valuable insights into how dog disturbance affects social structure in howler monkeys.

The present study aimed to determine how domestic dogs influence interindividual proximity in mantled howler monkeys. We hypothesized that if howler monkeys perceived dogs as aversive stimuli, their spatial organization would change in response to dogs. Based on theoretical and empirical evidence suggesting that predation risk decreases with increasing proximity among group members (e.g., Hamilton 1971; Hill and Dunbar 1998), we predicted that individuals would be closer (1) following exposure to dogs (sight and hearing), (2) with increased dog bark intensity, and (3) with increasing dog proximity. To test these predictions, we conducted both observational monitoring of natural dog encounters and experimental playbacks of dog barks at different intensities, measuring how interindividual proximity among group members changed in response to these stimuli at short (immediate 15 min response) and long (1 h focal sample) timeframes.

Methods

Study site and subjects

We conducted this study at La Flor de Catemaco, a private property dedicated to ornamental plant cultivation, primarily ferns, palms, and *Monstera* sp. The site is located on the shores of Lake Catemaco in Veracruz, Mexico (18.440149 N, -95.046752 W). The 165-hectare property includes a 100-hectare fragment of preserved high evergreen forest. The climate is warm-humid with year-round rainfall, with average temperatures ranging from 20 to 26 °C and annual precipitation between 1900 and 4600 mm. The region has experienced significant anthropogenic disturbance over the past 60 years, resulting in a mosaic landscape of original and secondary forests, agricultural fields, and human settlements (Von Thaden et al. 2020).

We studied two groups of mantled howler monkeys that have been monitored systematically since 2012 (Dias et al. 2023a). The first group ("Group 1") consisted of four adult males and six adult females (none of which had any associated immature during the study), whereas the second group ("Group 2") comprised four adult males, four adult females, three juveniles, and one infant. For this study, we focused exclusively on adult individuals, who were identified through distinctive physical characteristics such as scars and markings on hands and feet. All study subjects were habituated to human presence.

Sampling of mantled howler monkey behavior

We conducted observational sampling from July to September 2023, recording data for an average of 6 hours per day, 4 days per week, weather permitting. Using focal animal sampling (Altmann 1974), one observer and a field assistant collected data during 1-h samples using binoculars. Every 10 min, we recorded the proximity between the focal animal and all other group members using instantaneous sampling. We categorized interindividual proximity as: contact (X1), < 1 m (X2), 1–5 m (X3), and > 5 m (X4), following previously established methods for studying howler monkey interindividual proximity (Wang and Milton 2003; Dias and Rodríguez-Luna 2005). If the focal animal was out of sight for more than two consecutive instantaneous samples or for a total of three instantaneous samples during the focal period, we canceled the focal sample. Similarly, if distance measurements could not be obtained for at least 25% of adult group members, we canceled the focal sample. These criteria ensured both representativeness and comparability of interindividual proximity recordings across focal samples. During the observational phase, we completed 250 focal samples and 1694 instantaneous records during 55 fieldwork days.

Sampling of dog presence and barks

Simultaneously with recording interindividual proximity, we sampled all occurrences of dog presence or barking in the area where the primates were located. Each time we heard or saw a dog, one observer recorded a waypoint on a GPS (Garmin Etrex 10) at the center of the howler monkey group (i.e., the geometric midpoint between the positions of all visible adult group members) and then ran to the place where dog stimuli were detected and recorded a second location while another kept observing the monkeys. The straight-line distance between the two waypoints was calculated with the "Measure Distance" function of the GPS. We measured the intensity of dog barks using the sound pressure level (SPL) with a sound meter (TN-ST106, Tenmars, Taiwan) that was continuously recording SPL. SPL is the most used indicator to assess acoustic wave intensity, correlating with perceived volume and is measured in decibels (dB; Long 2014). We measured SPL at the group's location rather than standardizing measurements to a fixed distance from the sound source. As sound pressure decreases with distance, our SPL measurements represent the actual acoustic stimulus intensity experienced by the monkeys, which is the biologically relevant parameter. A dog barking loudly at 50 m may produce the same SPL at the howler monkeys' location as a dog barking softly at 10 m, and both would represent equivalent acoustic stimuli from the howler monkeys' perspective.

Nine dogs that were regularly found in the area were recognized. Of these, four belonged to the company manager (a Belgian Shepherd, a German Shepherd, a Chihuahua and a small-sized unidentified breed); two medium-sized female creole dogs belonging to the workers; a medium-sized black dog that came to the area to obtain food (but which the workers said was not theirs); and two medium-sized creole dogs whose presence was infrequent. All but the Chihuahua roamed the ranch freely.

Experimental assessment of the impact of dog barks on interindividual proximity

For the experimental phase, we obtained dog bark recordings from YouTube (free of copyright) and edited them using Audacity software. Each audio file was configured with one minute of initial silence (allowing the observers to position themselves for recording), followed by three rounds of 22 s bark sequences alternated with 10 s silence periods. The final audio files were 2:30 min in duration. We created five different audio files to avoid pseudoreplication and habituation (Fischer et al. 2013). All recordings featured barks from a single medium-sized dog.

The audio files were played through a Motorola E6s cellular phone connected via Bluetooth to a Redlemon BTS-06 speaker. Prior to field experiments, we determined the appropriate volume settings and distances (determined with a laser rangefinder Huepar HLR1000 pro) to achieve the desired sound pressure levels for two treatments: low intensity (40 dB) and high intensity (80 dB), following Rangel-Negrín et al. (2023). The low intensity (40 dB) was achieved at half volume at 17 m distance, while the high intensity (80 dB) required full volume at the same 17 m distance.

Between September and November 2023, we conducted a total of 32 playbacks, eight playbacks per treatment per group, with a mean ± SD of 4.9 ± 2.5 days between consecutive playbacks. Groups were located in the early morning, and playbacks began when all adult individuals were resting and no other significant disturbances occurred at least 1 h prior to experiment onset (e.g., intense anthropogenic noise: Dias et al. 2023b, Gómez-Espinosa et al. 2022; intergroup encounters: Maya-Lastra et al. 2024). During experiments, we positioned the speaker at 17 m (determined with the rangefinder) from the trunk of the tree where the majority (> 50%) of howler monkeys were resting and concealed it with leaf litter and natural materials. The playbacks were randomly selected from among the five prepared audio files. We selected the first individual to display a behavioral response to playbacks as a focal subject and conducted a 1 h follow with instantaneous recordings of their proximity to other group members as described above, accumulating a total of 32 focal samples, corresponding to 32 sampling hours and 224 instantaneous records.

Data organization and analysis

To analyze interindividual proximity among group members, we calculated a proximity index for each instantaneous record to create a continuous variable that captured the overall spatial cohesion of the group, following established methods for howler monkeys (Dias and Rodríguez-Luna 2005). In this index, observation frequencies of individuals in each proximity category were multiplied by a weighting factor that decreased with increasing distance. The sum of these values was divided by the number of individuals per group (excluding the focal animal) to make indices comparable between the two groups:

$$\mathrm{Ip} = [(X1 \times 1) + (X2 \times 0.5) + (X3 \times 0.25) + (X4 \times 0.125)] / (n-1)$$

Where Ip is the proximity index, X1-4 are the number of individuals in each interindividual proximity category, and n is the number of individuals per group (modified from González-Hernández et al. 2014).

We used observational data to assess the influence of exposure to dogs (i.e., presence/absence of dog stimuli, either acoustic or visual), bark intensity, and dog proximity on mantled howler monkey interindividual proximity. We calculated the variation between consecutive proximity indices (Δ proximity) associated with exposure to dog stimuli ($n = 41$) as the difference between the instantaneous recording preceding and that following dog presence or bark. This derived variable should reflect changes in interindividual proximity at a short timeframe (i.e. within 15 min) and produced negative values when proximity increased (i.e., individuals were closer) following stimulus exposure, zero values when proximity remained unchanged, and positive values when proximity decreased (i.e., individuals were farther) after stimulus exposure. To analyze the effect of dog exposure, we compared proximity changes during dog encounters with control periods. We selected control periods from our observational data using the following criteria: (1) same focal individuals as those observed during dog encounters, (2) matched time of day (± 1 h), and (3) confirmed absence of any dog stimuli for at least 30 min before and during the recording period. We then calculated Δ proximity from those control observations. We analyzed the influence of dog exposure (fixed categorical predictor, yes/no) on Δ proximity with a linear mixed-effects model (LMM) with subject identity added as a random factor. To analyze the influence of bark intensity and distance to dog stimuli we ran two LMMs, in which Δ proximity was the response variable, SPL of barks (in dB) and distance between dog stimuli (visual or acoustic) and the focal subject (in m) were fixed predictors in each model, and focal animal identity was a random factor.

We combined observational and experimental data to assess the effect of dog bark intensity on interindividual distances on a long timeframe (i.e. 1 h focal animal samples). Specifically, we compared the mean proximity indices per focal sample of the first individuals that responded to each playback experiment (e.g., looked in the direction of the speaker, vocalized) with focal samples of those same individuals collected during the observational period when no dog stimuli were present. We randomly selected focal samples from the observational data although accounting for the following criteria: (1) focal samples were matched by time of day (± 1 h), (2) no dog stimuli occurred for at least 30 min before and the focal sample. This approach allowed for a more rigorous assessment of behavioral responses specifically attributable to the experimental stimuli rather than to time-dependent variables. We then compared mean proximity indices among dog bark intensity conditions (fixed predictor; no dog barks/40 dB/80 dB barks, $n = 66$) with a LMM with focal animal identity added as a random factor. We used Tukey contrasts as post-hoc tests in this model.

We evaluated model fit through visual inspection of Q-Q plots and verified residual normality with Shapiro–Wilk tests, which in all cases indicated no significant violation of statistical assumptions. We calculated pseudo-determination coefficients (R^2) for each model as effect size measures. 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 ($P < 0.001$ for all tests; i.e., fixed factors were more influential). All analyses were conducted in R statistical software 4.4.3 (R Core Team 2025).

Results

After exposure to dog stimuli during the observational sampling, mantled howler monkeys came closer to other group members in a short timeframe (i.e., 15 min; $\chi^2_{2,82} = 7.6$, $P = 0.006$, $R^2 = 0.21$; Fig. 1a; Fig. S1). In

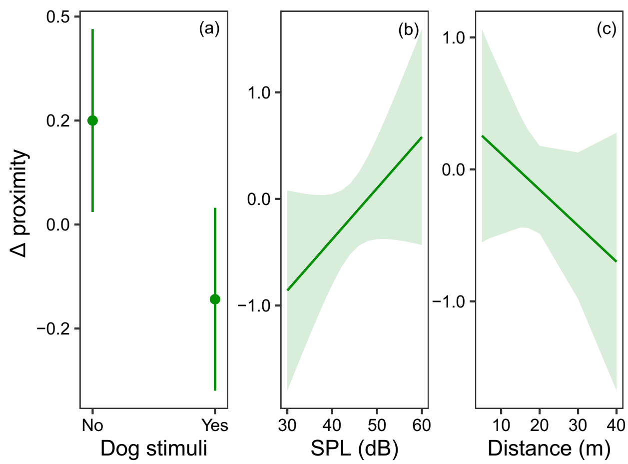

Fig. 1 Mixed-effects model results of the influence of naturally occurring dogs on the variation in interindividual proximity in mantled howler monkeys. In **a**, dots are the predicted estimates and lines are their 95% confidence intervals. In **b** and **c**, solid lines are the predicted estimates, and shaded areas are their 95% confidence intervals

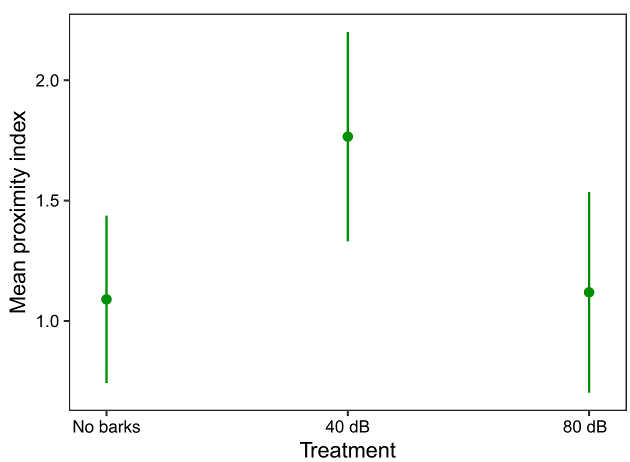

Fig. 2 Mixed-effects model results of the influence of sound pressure level (in dB) of experimental dog barks on the variation in interindividual proximity. Dots are the predicted estimates, and lines are their 95% confidence intervals

contrast, individuals were farther from each other as bark intensity increased ($\chi^2_{41}=4.3$, $P=0.039$, $R^2=0.46$; Fig. 1b) and as proximity to dog stimuli decreased ($\chi^2_{41}=4.1$, $P=0.043$, $R^2=0.34$; Fig. 1c).

Mean proximity indices per focal sample (i.e., long timeframe) varied significantly according to the intensity of experimental dog barks ($\chi^2_{3,66}=7.0$, $P=0.030$, $R^2=0.16$; Fig. 2). Specifically, individuals were significantly closer to each other when exposed to dog barks played at 40 dB compared to periods without dog stimuli (post-hoc test $P<0.05$).

Discussion

We investigated whether domestic dogs disturb mantled howler monkeys by examining how their presence and barks influence interindividual proximity among group members. We specifically evaluated whether interindividual proximity changed in response to dog presence, bark intensity, and proximity of the stimulus. Our analysis at different temporal scales revealed distinct patterns of spatial response. In the short-term analysis of consecutive recordings, we found that individuals came closer to each other immediately following exposure to dogs, supporting our first prediction. However, contrary to our second and third predictions, individuals moved farther from each other at higher bark intensities and with closer proximity to dog stimuli. In the long timeframe analysis, comparing one-hour focal samples, we found that individuals maintained closer proximity to each other when exposed to low-intensity barks compared to periods without dog stimuli. The contrasting results between short and long timeframes suggest that mantled howler monkeys employ flexible spatial strategies that vary with both the characteristics of the perceived threat and the temporal scale, likely reflecting adaptive mechanisms for balancing immediate predation risk against long-term energetic costs. Although we did not observe dog attacks during this study, and there are no documented dog attacks at La Flor de Catemaco, individuals still responded to dog stimuli, possibly due to generalized predator recognition mechanisms (Carthey and Blumstein 2018)) or because dogs represent inherently aversive stimuli through their conspicuous vocalizations and erratic movements (Glover et al. 2011; Miller et al. 2001).

The temporal variation in spatial responses to dog stimuli provides insight into the adaptive nature of antipredator behavior. In short timeframe comparisons, mantled howler monkeys showed increased interindividual proximity immediately following exposure to dogs. However, over longer periods, this effect was intensity-dependent, with only the lower-intensity barks resulting in increased proximity in one-hour samples. This pattern suggests that spatial adjustments are calibrated to both the presence and characteristics of potential threats, with differential responses that may reflect adaptive strategies to balance vigilance with energetic costs. Similar patterns of temporally variable responses have been documented in other species and reflect the need to minimize time spent in antipredator behaviors when threats are no longer imminent (Caro 2005; Hauser and Wrangham 1990; Lima and Dill 1990). Maintaining heightened vigilance and altered spacing patterns for extended periods would impose significant opportunity costs in terms of reduced feeding and social interaction time (Lima 1998; Underwood 1982).

Contrary to our predictions mantled howler monkeys tended to be farther from each other as bark intensity increased, and dog stimuli were closer. It has been previously reported that mantled howler monkeys vocalize more in response to louder dog barks but exhibit more flight behavior at lower bark intensities (Rangel-Negrín et al. 2023). This suggests a context-dependent response strategy where stronger stimuli trigger defensive displays (vigilance, vocalizations) that may require individuals to reposition themselves throughout the canopy, potentially decreasing interindividual proximity. Anecdotally, we observed that adult males typically responded first to bark playbacks and were more active than females in defense behaviors, often moving to position themselves between the perceived threat and the rest of the group. This interposition behavior, where males separate from the group to face a potential threat, has been documented in other primate species (Boesch 1991; Cowlishaw 1994; van Schaik and van Noordwijk 1989) and could account for the decreased interindividual proximity when threats were closer.

This pattern of intensity-dependent spatial responses parallels evidence from intergroup encounter effects, where proximity responses to conspecific threats also vary by context and species. Although some primates increase cohesion during intergroup encounters (e.g., chimpanzees, *Pan troglodytes*: Brooks et al. 2021; Samuni et al. 2017), others show no change (bonobos, *Pan paniscus*: Brooks et al. 2024) or even increased dispersion due to intragroup tension (tufted capuchin monkeys, *Cebus apella*: Polizzi di Sorrentino et al. 2012). These variable responses across threat types suggest that proximity adjustments reflect complex trade-offs between collective defense benefits and individual positioning needs. Although we could not analyze sex differences in spatial responses owing to small sample size, these observations suggest sex-specific roles in predator defense that warrant further investigation. Therefore, the differential responses to varying bark intensities and stimuli proximity may reflect a graded assessment system where lower-intensity stimuli signal moderate threat levels that are best managed through cohesion, while higher-intensity stimuli indicate immediate danger requiring individual repositioning for escape or defense (Beauchamp 2017; Frid and Dill 2002).

The relatively short duration of our study implies that these results should be taken with caution and may be deemed as preliminary. Yet, consistency between observational and experimental findings supports their reliability, and therefore the spatial responses of mantled howler monkeys observed in this study have implications for understanding the ecological consequences of dog–wildlife interactions. The energy expended in antipredator behaviors trades-off against other fitness-enhancing activities such as feeding, mating, and caring for offspring, and the cumulative costs of these behavioral adjustments could potentially affect individual fitness (Brown and Kotler 2004; Creel and Christianson 2008; Lima and Dill 1990), especially when considering the metabolic constraints underlying the physiological and ecological strategies of howler monkeys (Milton 1998). Moreover, changes in interindividual spacing patterns could alter social dynamics, affecting processes such as information transfer, disease transmission, and cooperative behaviors (Clutton-Brock et al. 1999; Strandburg-Peshkin et al. 2015). Given that domestic dogs are present throughout much of the range of howler monkeys and other platyrrhines, understanding these effects is crucial for developing effective conservation strategies.

In conclusion, domestic dogs and their barks influence the spatial organization of mantled howler monkeys, but in ways that are more complex than initially predicted. Our findings revealed context-dependent and temporally variable responses, with interindividual proximity increasing immediately after exposure to dogs but decreasing with higher bark intensities and closer proximity to dog stimuli. Over longer periods, low-intensity barks resulted in increased proximity. These results enhance our understanding of how invasive predators affect primate social structure and contribute to a growing body of research on dog–wildlife interactions. From a conservation perspective, our findings highlight the importance of managing free-ranging dogs in areas where they overlap with wildlife. Future studies should examine whether chronic exposure to dog disturbance leads to long-term changes in primate social structure and whether these changes accrue fitness consequences for individuals.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s10329-025-01218-z.

Acknowledgements We thank A. Coyohua-Fuentes and S. P. López-López for their support during fieldwork; Ing. J. L. Ponce Puente for allowing the work at La Flor de Catemaco S.A.; and A. Molina for administrative support. We thank L. Pacheco-Cobos and J. Jiménez-Huerta for valuable feedback on study design and two anonymous reviewers for constructive feedback on previous versions of the manuscript. The study was financed by Instituto de Neuro-etología (Universidad Veracruzana) and The Leakey Foundation. This research complied with the Guidelines for Field Primatology of the Primate Society of Japan. Research protocols were approved by the Secretariat of Environment and Natural Resources (SPARN/DGVS/00278/22) and conducted in accordance with NOM-059-SEMARNAT-2010. A. Rangel-Negrín and P.A.D. Dias thank Mariana and Fernando for their continued inspiration to understand primate behavior.

Author contributions ARN and PADD originally formulated the idea; CGCR and PADD developed methodology; CGCR conducted fieldwork; ARN and PADD provided project administration; CGCR and PADD performed statistical analyses; all authors wrote the manuscript.

Funding Instituto de Neuro-etología, Universidad Veracruzana, Leakey Foundation

Data availability The datasets used in this study are available from the corresponding author on reasonable request.

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