


RESEARCH PAPER

Howling on the edge: Mantled howler monkey (*Alouatta palliata*) howling behaviour and anthropogenic edge effects in a fragmented tropical rainforest in Costa Rica

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Abstract

The function of long calling is a subject of interest across animal behaviour study, particularly within primatology. Many primate species have male-specific long-distance calls, including platyrrhines like the folivorous howler monkey (*Alouatta* spp.). Howler monkeys may howl to defend resources such as feeding trees or areas of rich vegetation from other monkey groups. This study tests the ecological resource defence hypothesis for howling behaviour in the mantled howler monkey (*Alouatta palliata*) and investigates how anthropogenic forest fragmentation may influence howling behaviour. More specifically, this study examines how howling bout rate, duration, precursors and tree species richness, DBH, and canopy cover vary in 100 m anthropogenic edge and interior forest zones at La Suerte Biological Research Station (LSBRS), a fragmented tropical rainforest in Costa Rica. Results show that tree species richness and canopy cover are higher in forest interior at this site, suggesting that monkeys should howl at greater rates in the interior to defend access to these higher-quality vegetation resources. Overall, our results supported the ecological resource defence hypothesis. The main howl precursor was howling from neighbouring groups. Although howling rate did not differ between forest zones, howling bouts from forest interior were longer, had a greater number of howls per bout and were preceded by different precursors than howls from anthropogenic edge zones, including more howls from neighbouring groups. Our findings provide some of the first evidence for behavioural edge effects in primate vocal communication behaviour.

KEYWORDS

Alouatta, ecological resource defence hypothesis, forest fragmentation, long call, loud call, roar

1 | INTRODUCTION

In group-living animals, social relationships are mediated by a variety of vocal signals. While many vocalizations are used by both sexes, some are sex-specific and used only by mature males (Bradbury &

Vehrencamp, 1998; Snowdon, 2004). A distinctive and ubiquitous type of male-specific vocalization is the loud call or long call, named for the long distance (≥ 1 km for some species) that these vocalizations carry (Delgado, 2006; Wich & Nunn, 2002). Many animals produce long calls, ranging from insects to amphibians to mammals (e.g.,

deer, Clutton-Brock & Albon, 1979; insects and anuran amphibians, reviewed in Prestwich, 1994; primates, reviewed in Wich & Nunn, 2002). Long calls are complex in form, repetitive and contagious, in that hearing a call prompts other males to counter-call in response (Gautier & Gautier, 1977; reviewed in Delgado, 2006). Long calls are also energetically expensive and may honestly advertise male quality (Bradbury & Vehrencamp, 1998; Prestwich, 1994; Zahavi, 1975), with males who call at higher rates or for longer durations demonstrating superior body condition (e.g., red deer [*Cervus elaphus*], McComb, 1991; chacma baboon [*Papio ursinus*], Kitchen, Seyfarth, Fischer, & Cheney, 2003) or genetic quality (e.g., anurans, Gerhardt, 1994; Welch, Semlitsch, & Gerhardt, 1998). Long calls are most commonly found in animal species that live in forested areas, where long-range visual communication is not always possible, suggesting that the long call is a signal adapted to carry through foliage, rather than through open space (de Vore, 1979; Waser & Brown, 1986; Wich & Nunn, 2002).

Across species, long calls are used primarily in contexts of mate defence, mate attraction and/or territorial defence (Delgado, 2006; reviewed in Kitchen, da Cunha, Holzmann, & de Oliveira, 2015). In non-human primates, three non-mutually exclusive hypotheses have been proposed as explanations for their adaptive function: the mate defence hypothesis, the mate attraction hypothesis and the ecological resource defence hypothesis (Delgado, 2006; Wich & Nunn, 2002). The mate defence hypothesis predicts that males in group-living species use long calls to communicate with males from other social groups to prevent these males from accessing resident females, and has found support from strepsirhines (e.g., ring-tailed lemur [*Lemur catta*], Bolt, 2013a), catarrhines (e.g., Thomas langur [*Presbytis thomasi*], Steenbeek, Assink, & Wich, 1999; chacma baboon, Kitchen, Cheney, & Seyfarth, 2004), platyrrhines (e.g., golden lion tamarin [*Leontopithecus rosalia*], Halloy & Kleiman, 1994) and apes (e.g., gibbon [*Hylobates* spp.], Cowlshaw, 1992). The mate attraction hypothesis predicts that long calls may attract females and entice them to copulate with calling males, and has found support from strepsirhines (e.g., gray mouse lemur [*Microcebus murinus*], Zimmermann & Lerch, 1993), catarrhines (e.g., Thomas langur [*P. thomasi*], Steenbeek et al., 1999) and apes (orangutan [*Pongo* spp.], Delgado, 2006; common chimpanzee [*Pan troglodytes*], Mitani & Nishida, 1993). Finally, the ecological resource defence hypothesis predicts that long calls are used to defend food and/or space resources, and while it has found support from species in diverse environments (e.g., catarrhines: mantled guereza [*Colobus guereza*], Harris, 2006), platyrrhines: ursine howler monkey [*Alouatta arcatoidea*], Sekulic, 1982, apes: gibbon [*Hylobates* spp.], Cowlshaw, 1996), it has rarely been evaluated in relation to anthropogenically altered forest landscapes. Anthropogenic activity is well known to impact vocalization in many animal species. Human-caused noise, for example, alters animal acoustic communication signals in both terrestrial and aquatic environments (e.g., insects, Lampe, Schmoll, Franzke, & Reinhold, 2012; Morley, Jones, & Radford, 2014; amphibians, Sun & Narins, 2005; Parris, Velik-Lord, & North, 2009; fish, Slabbekoorn et al., 2010; Radford, Kerridge, & Simpson, 2014; birds, Patricelli & Blickley, 2006; Nemeth & Brumm, 2010; Francis,

Ortega, & Cruz, 2011; cetaceans, Miller, Biassoni, Samuels, & Tyack, 2000; Nowacek, Thorne, Johnston, & Tyack, 2007; rodents, Rabin, Coss, & Owings, 2006). Anthropogenic noise causes animals to adjust the spectral properties of their vocal signals, likely in order to preserve communication efficiency (Luther & Magnotti, 2014). The vocalizations of non-human primates have changed in amplitude (i.e., call loudness) and duration (i.e., call length) in response to human-caused noise (macaque [*Macaca nemestrina* and *Macaca fascicularis*], Sinnott, Stebbins, & Moody, 1975; common marmoset [*Callithrix jacchus*], Brumm, Voss, Kollmer, & Todt, 2004; Roy, Miller, Gottsch, & Wang, 2011; cotton-top tamarin [*Saguinus oedipus*], Hotchkiss, Parks, & Weiss, 2015; gray mouse lemur, Schopf, Schmidt, & Zimmermann, 2016). The impact of other anthropogenic factors in natural environments—such as human-caused deforestation or proximity of vocalizers to anthropogenic forest edge—has not been studied in relation to primate vocalization characteristics.

With rampant deforestation occurring throughout tropical regions worldwide (Haddad et al., 2015), it is important to better understand how anthropogenic impact alters the natural behaviour of animals. Although forest edges occur naturally (e.g., when a forest borders a beach), anthropogenic deforestation greatly increases the proportion of forest edge relative to forest interior (Laurance, 1991). Forest edges represent transitional landscape zones, where differing amounts of sunlight, moisture and wind are present compared to the forest interior, impacting the vegetation and animals found there (Harris, 1988; Lovejoy et al., 1986). Edge effects especially impact indicator species like primates, and generally have a negative effect on biota, with both plant and animal biomass reduced in forest edge zones (Arroyo-Rodríguez & Mandujano, 2006; Estrada, Anzures, & Coates-Estrada, 1999). Edges also tend to have poorer-quality vegetation for animal species such as primates (Arroyo-Rodríguez & Mandujano, 2006; Estrada et al., 1999; Ross & Srivastava, 1994). In the present study, we considered tree species richness, tree diameter at breast height (DBH) and tree canopy cover as indicators of vegetation quality for primates. We based this on previous findings indicating that higher tree canopy cover means a higher-quality habitat for monkeys (Arroyo-Rodríguez & Mandujano, 2006), with the number and size of trees in a forest area linked to primate abundance (Mbora & Meikle, 2004; Ross & Srivastava, 1994).

Because anthropogenic deforestation is one of the principal threats reducing primate populations worldwide (Estrada et al., 2017), it is vital to more thoroughly understand how anthropogenic edges affect primates and impact their behaviour, including their communication behaviour. The present study investigates how primate long calling may be impacted by edge effects in a fragmented tropical forest landscape in Costa Rica, the La Suerte Biological Research Station (LSBRS). LSBRS is a forest fragment that represents one of the increasingly few forested areas in a region of Costa Rica that has been largely deforested since the 1970s, primarily due to cattle ranching and large-scale banana and pineapple production by major corporations (Garber, Molina, & Molina, 2010; Molina, 2015). Abrupt forest edges exist between many areas of LSBRS and the neighbouring properties, with barbed wire fences marking the sharp

transitions between protected rainforest and cattle pasture or road (Molina, 2015). These distinct forest edges make LSBRS an ideal site at which to investigate the relationship between anthropogenic edge effects and howling behaviour. This study explores how anthropogenic forest edges impact the long-calling behaviour of a folivorous primate species, the mantled howler monkey (*Alouatta palliata*).

Howler monkeys (*Alouatta* spp.) are group-living, large-bodied New World monkeys that mainly eat leaves, although they also feed on fruit and flowers when available (Asensio, Cristobal-Azkarate, Dias, Vea, & Rodríguez-Luna, 2007; di Fiore, Link, & Campbell, 2011; Glander, 1982). They are extremely inactive primates who spend most of their time resting, likely due to the energy restrictions of their mostly folivorous diet (Milton, 1980). They are known for their long calls ("howls"), which have a loud, deep roaring sound, and are produced only by adult males (Altmann, 1959). Adult males have enlarged hyoid bones, which enable them to produce howls at high amplitude and that carry more than 1 km through some environments (Baldwin & Baldwin, 1976; da Cunha, de Oliveira, Holzmann, & Kitchen, 2015).

The function of howling has been widely investigated in howler monkeys at both proximate and ultimate levels. Although proposed functions include mate defence (ursine howler [*A. arctoidea*], Sekulic, 1982; brown howler [*Alouatta guariba*], black-and-gold howler [*Alouatta caraya*], Holzmann, Agostini, & di Bitetti, 2012), group cohesion (e.g., brown howler [*A. guariba*], Steinmetz, 2005), predator deterrence (red-handed howler [*Alouatta belzebul*], Camargo & Ferrari, 2007) and advertisement of fighting ability to neighbouring groups (black howler [*Alouatta pigra*], Kitchen, 2004; Kitchen, Horwich, & James, 2004), howling is most widely thought to serve a group spacing function (ursine howler [*A. arctoidea*], Sekulic, 1982; brown howler [*A. guariba*], Chiarello, 1995; black-and-gold howler [*A. caraya*], da Cunha & Byrne, 2006; black howler [*A. pigra*], Van Belle, Estrada, & Garber, 2013). Males howl to generally maintain distance between groups and to avoid inter-group encounters, but evidence is preliminary as to whether males also howl to defend specific areas or resources (reviewed in Kitchen et al., 2015). In the ursine howler monkey, males howled and engaged in inter-group encounters at higher rates when near fig trees, which are preferred food resources (Sekulic, 1982), and in the brown howler monkey, inter-group encounters occurred at higher rates near preferred guapinol (*Hymenaea courbaril*) feeding and sleeping trees, likely in order to defend access to them (Chiarello, 1995). Seasonality affects howling patterns in other howler monkey species, with more howling during lower resource availability, potentially to defend available resources (ursine howler, Sekulic, 1982; black howler, Horwich & Gebhard, 1983; Guianan red howler, Drubbel & Gautier, 1993; brown howler, Chiarello, 1995). Howler monkeys also vary in howling behaviour within home ranges, with some species howling more often in core territory areas (black-and-gold howler, da Cunha & Byrne, 2006) and other species howling more often in border areas (black howler, Horwich & Gebhard, 1983; Guianan red howler, Drubbel & Gautier, 1993; brown howler, da Cunha & Jalles-Filho, 2007). The mantled howler monkey howled at greater rates

near home range borders (Altmann, 1959); however, Hopkins (2013) found that howling bout responses were best understood in the light of inter-group dominance interactions coupled with food availability, with monkeys more often approaching other howling groups during times of food scarcity, presumably to gain access to their food-rich range area. Further, Whitehead (1989) found that mantled howler monkeys howled more often in frequently used home range areas, and thus may be broadcasting the location of primary food items to other groups. These findings suggest that we may expect mantled howler monkeys to howl more frequently in areas of richer resources. However, further research is needed to more fully elucidate how howler monkeys may be using howls within anthropogenically altered forest habitats.

1.1 | Hypothesis: Ecological resource defence

The ecological resource defence hypothesis predicts that howler monkeys howl to defend access to preferred resources, such as feeding trees and/or high-quality habitats containing a large number of preferred feeding tree species (reviewed in Kitchen et al., 2015). We predicted that the mantled howler monkeys at LSBRS would howl at higher rates in forest interior compared to anthropogenic forest edge in order to defend their access to the interior's higher-quality vegetation from other monkey groups. We further predicted that howling bouts in forest interior would be longer in duration and consist of a greater number of howls per bout than howling bouts at forest edge, to further advertise monkey presence and to defend access to higher-quality tree resources. Finally, we predicted that howling bouts would be preceded by different environmental precursors in forest edge compared to interior. If monkeys in the interior howl to alert other groups that areas containing high-quality feeding resources are already occupied, we predicted that more howling bouts would be triggered by howls from males in other social groups in forest interior than in forest edge.

2 | METHODS

2.1 | Study species

The mantled howler monkey ranges throughout Central America and lives in social groups containing 10–20 individuals, but up to 40 individuals, with adults typically in a 1:4 male-to-female ratio (di Fiore et al., 2011; Ryan, Starks, Milton, & Getz, 2008; Scott, Malmgren, & Glander, 1978). They live in single-male or multi-male groups with polygynous mating systems (Glander, 1980) where spatially clumped food resources may be defended by males, making them an ideal species on which to test the resource defence hypothesis for long calling (Wich & Nunn, 2002). Mantled howler monkeys have a large vocal repertoire with 9–20 different graded vocalizations fitting into 5–6 broad call families (Altmann, 1959; Baldwin & Baldwin, 1976; Carpenter, 1934), including the male-specific howl vocalization. Compared to other howler monkey species, mantled howler monkeys have simple howls with

short durations (reviewed in da Cunha et al., 2015). Their howls also have high amplitudes, low frequencies (300–1,000 Hz) and a noisy structure (see Baldwin & Baldwin, 1976, p. 88 for a spectrogram) which facilitates long-distance sound propagation. In previous research, howls have also been called “roars” (Altmann, 1959; Baldwin & Baldwin, 1976; Carpenter, 1934), “Type 1” vocalizations (Carpenter, 1934) and “Type A” vocalizations (Altmann, 1959; Baldwin & Baldwin, 1976). In the present study, although mantled howler monkeys made many vocalizations from various call families across forest zones at LSBRS, we restricted our investigation to the usage of the howl (type 1/type A/roar) vocalization. Other vocalizations were not examined because of their differences from the howl in form, amplitude and perceived adaptive function (Baldwin & Baldwin, 1976).

2.2 | Study site

We conducted this study at the LSBRS in northeastern Costa Rica (10°26'N, 83°46'W). LSBRS is a tropical lowland rainforest totaling approximately 3 square kilometers (km²) of primary and secondary forest (Garber et al., 2010; Pruetz & Leason, 2002). The forest fragment where we conducted research comprises two connected forest patches, “Large Forest” (0.935 km²) to the north and “Small Forest” (0.35 km²) to the south, as well as a partially cleared area for “camp” (0.071 km²; Molina, 2015, Figure 1).

The mantled howler monkey shares LSBRS with two sympatric monkey species: the white-faced capuchin monkey (*Cebus capucinus*) and the Central American spider monkey (*Ateles geoffroyi*). Population survey estimates for the mantled howler monkey suggest

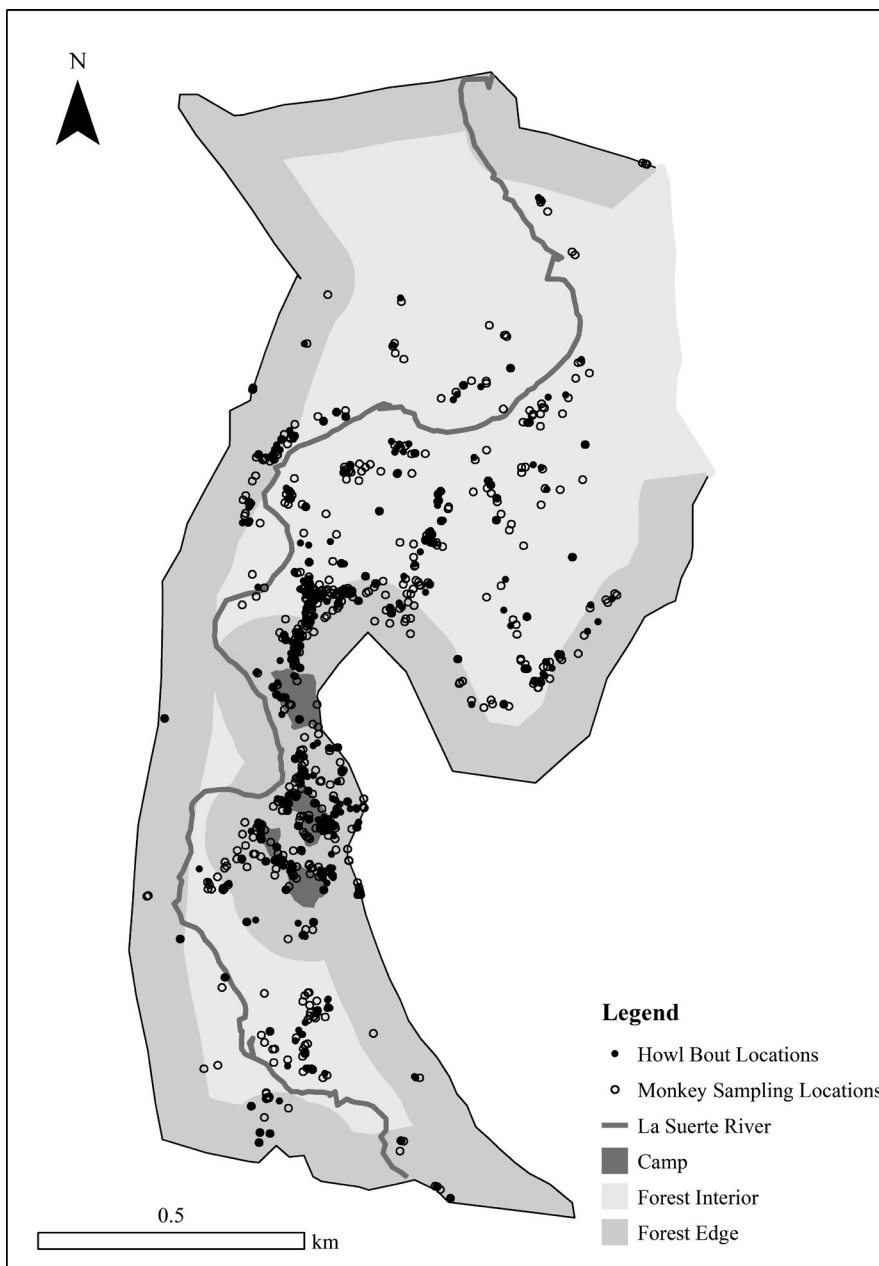


FIGURE 1 Map of La Suerte Biological Research Station showing howling bout locations and monkey sampling locations for each 30 min of sampling

that the Small Forest contains 2–3 groups, while the Large Forest contains 6–8 groups (Garber et al., 2010; Pruetz & Leason, 2002).

2.3 | Vegetation survey

We collected vegetation data at LSBRS from May to August 2015 and May to June 2017. These time periods all comprise the wet season at LSBRS, and therefore, seasonal differences are not a confounding factor in our analyses. The vegetation data we recorded are not expected to vary considerably over a couple of years and therefore can effectively be compared to howling data collected during May–August 2017 and 2018.

We conducted vegetation surveys along forest edge (within 100 m of anthropogenic forest edge) and interior transects (more than 100 m from forest edge). Each survey transect was 50 × 5 m; we aimed to distribute them evenly throughout the Large and Small Forests and camp. Overall, we conducted 17 edge and 12 interior transects (described in detail in Bolt et al., 2018). Along each transect and within 2.5 m on either side of the transect line, we recorded all trees with circumferences at breast height >10 cm and identified tree species when possible. We then calculated mean DBH for each transect. We estimated tree cover using a point sampling method. At each 1-m interval, we estimated tree cover by looking straight above and assigning a score of 1–4 (1 = 0%–25% coverage, 2 = 26%–50% coverage, 3 = 51%–75% coverage and 4 = 76%–100% coverage). We also determined tree species richness for transects located in the Large Forest.

2.4 | Howling data collection

Data on mantled howler monkey howling behaviour were collected from May to August 2017 and 2018 from approximately 11 groups of monkeys—eight groups primarily in the Large Forest and three groups primarily in the Small Forest. We collected data over 70 days in 2017 ($n = 208$ hr, $\bar{x} = 3.0$ hr/day) and 77 days in 2018 ($n = 361$ hr, $\bar{x} = 4.7$ hr/day). Researchers actively searched for and sampled monkeys daily between 500 and 1800 hr, collecting data approximately evenly throughout the day, but especially from 730 to 1200 hr and 1230 to 1600 hr. We aimed to collect approximately equal amounts of data across anthropogenic edge ($n = 336$ hr) and interior ($n = 233$ hr) forest zones. Because individual monkey identities were unknown in this population and group membership likely changed between summer 2017 and 2018 due to births, deaths and dispersals, we cannot be completely certain of individual group identities and compositions; based on our data, however, mean group size was 9.1 monkeys ($SD = 3.2$), mean male:female sex ratio was 1:1.6, and groups of monkeys ranged from three individuals to up to 20 individuals of both sexes (Table 1). We followed groups as they traveled across various habitat zones, and all occurrences of howling data were collected for continuous durations of time ranging from 30 min to 5 hr. Due to the high canopy, thick foliage and poor visibility at LSBRS, data collectors stayed as close as possible to monkey

TABLE 1 Mantled howler monkey (*Alouatta palliata*) group membership at La Suerte Biological Research Station

Group membership	Mean number per group	Range per group
Adult males	2.4	1–6
Adult females	3.8	1–8
Juveniles	1.4	0–3
Infants	0.7	0–6
Total	9.1	3–20

groups during sampling to ensure that monkey groups remained visible. All monkey groups were well-habituated and did not react to researchers.

During all time spent with a mantled howler monkey group, all-occurrences sampling (Altmann, 1974) was conducted for group-wide howling behaviour (following Bolt, 2013a, 2013b; Hopkins, 2013). When howling from one or more members of the focal group was heard, we recorded the start time and end time of the howling bout, the number of howls in the bout, the location of the howling bout (recorded the location of the howling male by noting the closest trail marker to him and taking a single GPS point as close to him as possible using a Garmin GPSMAP 62s Handheld GPS Navigator) and any potential precursor(s) in the seconds preceding the howl. These known howling precursors were recorded qualitatively, then placed into one of six categories for analysis: (a) no observed precursor, (b) other group howling, (c) environmental factor (e.g., rain, wind, thunder), (d) intra-group social behaviour (e.g., agonism, travel, non-howl vocalization), (e) inter-species interaction (e.g., dog, bird or other monkey species was seen by researchers and observed interacting with focal howler monkey group) and (f) anthropogenic noise (e.g., lawn mower, chainsaw, airplane) (Baldwin & Baldwin, 1976; Van Belle et al., 2013; reviewed in Kitchen et al., 2015).

Howls were defined as male-specific, high-amplitude Type 1/A loud calls (Altmann, 1959; Baldwin & Baldwin, 1976; Carpenter, 1934) separated from other long-distance vocalizations made by the caller or members of the same group by at least 2 s. If individual vocal utterances were continuous or separated by <2 s, they were considered part of the same howl vocalization. Howls were contained within howling bouts.

A howling bout comprised howls occurring <60 s apart (following Sekulic, 1982). Howling bouts could therefore be seconds long and consist of a single howl vocalization by one male, or many minutes long and consist of a large number of howl vocalizations by multiple males from the same group. In addition to recording GPS points to note locations of howling bouts, a GPS point was taken at the location of every 30-min period we spent in the presence of a monkey group, regardless of whether howling occurred during the sample. These GPS sampling points were taken in the approximate centre of the monkey group and allowed us to determine behavioural sampling frequency across various forest zones at LSBRS (Figure 1).

2.5 | Data analysis

We compared mean tree species richness and mean tree DBH across edge and interior vegetation transects at LSBRS using Mann–Whitney U tests. We also compared mean howler monkey howling rate, mean length of howling bouts and mean number of howls in howling bouts in forest edge vs. interior zones using Mann–Whitney U tests. To compare whether howling precursors showed different distributions than expected by chance across forest zones, we used a Pearson chi-squared test. As a post hoc test to determine which precursors showed differences across forest zones, we examined adjusted residuals and identified those with z -scores greater than ± 1.97 as showing differences across forest zones. We used SPSS version 25 (IBM SPSS Statistics; IBM Corporation, 2013) for all statistical tests and set the alpha level to 0.05.

3 | RESULTS

Mean tree species richness was significantly higher in the forest interior ($\bar{x} = 6.1$ trees, $SD = 2.1$) than the anthropogenic edge ($\bar{x} = 3.8$ trees; $SD = 1.8$; $U = 22.5$, $p = 0.038$) at LSBRS. Mean tree cover was also higher in the interior than the edge, with 92.0% of 1-m intervals in the interior having between 51% and 100% cover compared with 73.6% of 1-m intervals in the edge. Mean tree DBH in interior transects (34.1 cm, $SD = 29.6$) was higher than mean DBH in the edge (22.4 cm, $SD = 11.6$), but this difference was not statistically significant ($U = 75.0$, $p = 0.245$).

Across habitat zones, mean howler monkey howling rate was 1.13 bouts/hr (range = 0–18 bouts/hr, $n = 569$ hr), while mean howling bout length was 122.4 s/bout (range = 1–2,882 s/bout, $n = 641$ bouts), and mean number of howls in a bout was 5.4 howls/bout (range = 1–176 howls/bout, $n = 433$ bouts). There was no difference in overall howling rate between anthropogenic edge and forest interior ($\bar{x} = 1.0$ bouts/hr in forest interior [range = 0–18 bouts/hr, $n = 233$ hr] vs. 1.2 bouts/hr in anthropogenic edge [range = 0–14 bouts/hr, $n = 336$ hr]; $U = 151,731.0$, $z = -1.114$, $r = -0.033$, $p = 0.265$). Howling bouts were significantly longer in forest interior than in anthropogenic edge ($\bar{x} = 149.4$ s in forest interior [range = 1–2,882 s, $n = 242$ bouts] vs. 106.1 s in forest edge [range = 1–1,641 s, $n = 399$ bouts]; $U = 43,382.5$, $z = -2.158$, $r = -0.0852$, $p = 0.031$, $n = 641$; Figure 2). There were also significantly more howls per bout in forest interior than in anthropogenic edge ($\bar{x} = 7.91$ howls/bout in interior [range = 1–176 howls/bout, $n = 143$ bouts] vs. 4.09 howls/bout in forest edge [range = 1–78 howls/bout, $n = 290$ bouts]; $U = 18,216.0$, $z = -2.179$, $r = -0.1047$, $p = 0.029$, $n = 433$; Figure 3). When examining the association between howling bout precursor and howling location (anthropogenic edge vs. interior), howling bouts in different forest zones had significantly different precursors ($\chi^2(5) = 31.489$, $p = 0.000$, $n = 624$). The strength of association between variables was strong (Cramer's V test: $\phi_c = 0.225$, $p = 0.000$), and post hoc examination of adjusted residuals

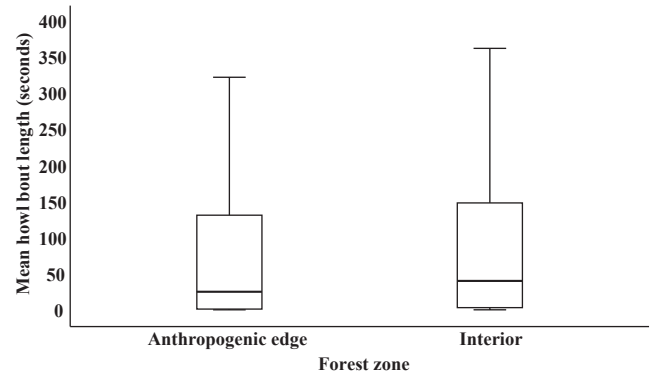


FIGURE 2 Mean howling bout length in forest interior vs. anthropogenic edge at La Suerte Biological Research Station ($p = 0.031$). Boxes represent inter-quartile ranges, lines represent median values, and whiskers represent maximum and minimum values. Outliers were removed for graphical purposes

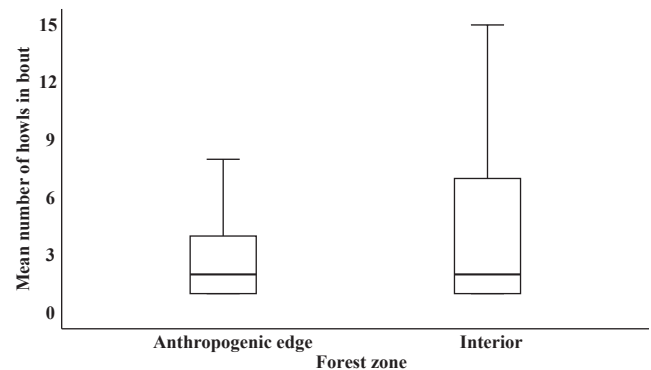


FIGURE 3 Mean number of howls per howling bout in anthropogenic edge vs. forest interior at La Suerte Biological Research Station ($p = 0.029$). Boxes represent inter-quartile ranges, lines represent median values, and whiskers represent maximum and minimum values. Outliers were removed for graphical purposes

indicated that when adjusted for sample size, monkey howling bouts in the forest interior zone were more frequently preceded by howls from other groups and inter-species interactions than expected, while they were less frequently preceded by no precursor and environmental factors than expected ($z > \pm 1.97$, Table 2). The reverse pattern was seen for howling bouts sampled in forest edge zones. Observed values such as intra-group interaction and anthropogenic noise did not differ from expected values across forest zones ($z < \pm 1.97$, Table 2).

4 | DISCUSSION

Our results partially supported the predictions of the ecological resource defence hypothesis for howler monkey howling behaviour. Vegetation transects confirmed higher resource quality in forest interior, and while overall howling rate did not differ between forest zones, howling bouts were significantly longer and consisted of a greater number of howls per bout in forest interior compared to

TABLE 2 Mantled howler monkey (*Alouatta palliata*) howling precursors at La Suerte Biological Research Station showing z-scores for adjusted residual values

	No howling precursor	Howl from other group	Environmental factor	Intra-group social behaviour	Inter-species interaction	Anthropogenic noise
Interior Forest Zone	-2.8 [*]	4.1 [*]	-2.1 [*]	-1.8	2.8 [*]	-1.2
Edge Forest Zone	2.8 [*]	-4.1 [*]	2.1 [*]	1.8	-2.8 [*]	1.2

*Significant differences between zones (values $>\pm 1.97$). Negative results indicate that howling occurrence following a precursor was lower than expected by chance, while positive results indicate that howling occurrence following a precursor was higher than expected by chance.

anthropogenic edge. Howling precursors also differed across forest zones as predicted, with more focal group howls preceded by howls from other groups in forest interior than in forest edge. Taken together, these results support our prediction that mantled howler monkeys may be howling more when in forest interior, potentially to advertise to other groups that their high-quality habitat is already occupied.

Howls, like the long calls made by other animal taxa, are thought to be energetically expensive to produce (Bradbury & Vehrencamp, 1998; da Cunha et al., 2015; Prestwich, 1994; Wich & Nunn, 2002), with longer howling bouts requiring more energy. Males will howl for longer durations of time in certain habitat zones if doing so provides them with some fitness advantage, such as maintaining their access to the higher-quality trees in the forest interior. Howler monkeys are known to be limited by food supply (Jones, 1980) and to be selective feeders that mostly eat from trees (Estrada, 1984, but see Dunn, Asensio, Arroyo-Rodríguez, Schnitzer, & Cristóbal-Azkarate, 2012; Arroyo-Rodríguez, Asensio, Dunn, Cristóbal-Azkarate, & Gonzalez-Zamora, 2015). For example, howler monkeys ate from 27 tree species from 15 families at a rainforest site in Mexico (Estrada, 1984). At LSBRS, preliminary investigation of howler monkey feeding tree species use in forest interior compared to 50 m anthropogenic edge at LSBRS (Russell, 2018) showed that monkeys fed from at least nine different tree species in forest interior compared to only four species in forest edge. With both number of observed feeding tree species (Russell, 2018) and overall tree species richness (this study) higher in forest interior at LSBRS, it may be adaptive for mantled howler monkeys to howl for longer durations of time while in the interior to prolong access to this higher-quality food resource zone. Our results find support from other howler monkey species including the ursine howler (Sekulic, 1982) and the brown howler (Chiarello, 1995), both of which howled at higher rates in areas of higher-quality food resources.

The differences in howl bout length at LSBRS may additionally be due to differences in long call sound propagation properties across forest zones. Given that the sound reverberation (i.e., sound being reflected by static objects and dispersed during propagation, see Naguib & Wiley, 2001; da Cunha et al., 2015) of long calls is typically stronger in dense forest habitats than in open areas (Waser & Brown, 1986), this limits the long-distance communication potential of howls in forest interior. If mantled howler monkeys are howling to communicate their location to other conspecific groups for any reason, they may increase the length and number of howls contained in their howling bouts when in forest interior in order to ensure that other groups can effectively

receive and locate their signal. It is adaptive for males to spend more energy producing longer howling bouts in interior locations if doing so minimizes their number of face-to-face inter-group encounters, which are often violent and can lead to severe injury or death for mature males (Chiarello, 1995; Sekulic, 1982). Although howls carry for long enough distances that they can likely be heard by neighbouring groups across forest zones, regardless of whether howls are uttered in forest edge or interior, males may howl for longer durations of time while in the interior to compensate for sound reverberation. Reverberation and other acoustic properties of howls have not been measured in forest edge and interior zones at LSBRS; future study will more fully assess the range of environmental factors that could be driving differences in howl bout length across forest zones.

Males may have also howled for longer durations of time in forest interior compared to forest edge due to differing predation pressures across forest zones. Monkeys in anthropogenic edge areas had shorter howling bouts with fewer howls per bout, potentially to avoid being detected by predators in this area of less dense canopy cover. In this study, male howling in both forest edge and interior was preceded by interactions with other species including dogs (*Canis familiaris*), capuchin and spider monkeys, turkey vultures (*Cathartes aura*) and the green ibis (*Mesembrinibis cayennensis*). Of these, dogs are the only known howler monkey predators (Baldwin & Baldwin, 1976; Carpenter, 1934; Raguét-Schofield, 2008), but the presence of unfamiliar or unexpected animals also appears to trigger howling in howler monkeys at other sites (Baldwin & Baldwin, 1976; Carpenter, 1934; Sekulic, 1982). Calling animals are more likely to attract the attention of potential predators (reviewed in Bolt, 2016), as are animals that call for longer periods of time. Thus, in areas of increased threat, it may be adaptive for howler monkey males to howl for shorter lengths of time, as they did on the edge at LSBRS. Howling in forest interior at LSBRS, however, was preceded by interactions with other species more often than would be expected by chance. The response of monkeys may be more marked (i.e., longer howling bouts, greater number of howls per bout and greater number of howls preceded by inter-species interaction) in forest interior due to greater tree cover helping to conceal monkeys from predators and increased sound reverberation helping to obscure the locations of howling males from other animals (Naguib & Wiley, 2001; Waser & Brown, 1986). Because calling monkeys are likely more difficult for predators to localize and target in dense forest interior than in open edge areas, they may howl for longer durations of time in the interior without substantially increasing their risk of predation.

Another possibility, that differences in mantled howler monkey population density across forest zones may be motivating differences in howling behaviour, has little support. Mantled howler monkey density has been suggested to relate to inter-group aggression in some populations, with higher monkey density in some areas leading to increased aggression (Kitchen et al., 2015) and howling rate. However, at LSBRS, howler monkey groups were encountered equally in anthropogenic edge and interior (Bolt et al., 2018), suggesting no difference in monkey group density between forest zones.

We collected howling data from May to August, during the wet season in northeastern Costa Rica. Howl sampling conducted at other times of year, including during the dry season, may yield different results for howling rate and bout characteristics at LSBRS. However, because seasonal variation is not expected to impact range use or food item selection in the mantled howler monkey (Bolt et al., 2018; Chapman, 1988), we would not necessarily expect it to influence the edge vs. interior spatial patterns of howling in our study.

We tested the ecological resource defence hypothesis in relation to overall tree species richness, DBH and canopy cover, but did not test how other forms of resource defence, such as feeding/resting tree species richness or abundance, may relate to howling behaviour. We also did not investigate potential variation in vegetation quality in areas within edge and interior forest zones. Some forest interiors at other tropical sites have core areas containing higher-quality vegetation (e.g., da Silva Júnior et al., 2009; Asensio, Lusseau, Schaffner, & Aurel, 2012), and it is unknown whether interior forest at LSBRS shows similar features. We also did not evaluate howler monkey preferred feeding tree abundance or usage between edge and interior. Future study should examine a broader range of ecological factors that may influence habitat use in the mantled howler monkey.

Our results have conservation implications. Howling bout properties and characteristics differed between anthropogenic edge and forest interior, which in turn indicates that proximity to anthropogenic edge is likely altering mantled howler monkey behaviour. Although it is unclear how this may affect howler monkey fitness, our findings suggest that long-term initiatives for mantled howler monkey conservation should prioritize both preservation of forest interior zones and regeneration of forest edges exposed to anthropogenic activity. Forest destruction should be minimized to mitigate any alterations to mantled howler monkey communication behaviour caused by human impact.

Finally, it is important to note that howl bout length in mantled howler monkeys may vary across edge and interior habitat zones due to a range of factors which are not mutually exclusive. As Kitchen et al. (2015) observe, howler monkey long calls have likely evolved in response to a variety of competing selective pressures. Mantled howler monkeys may utter howl bouts with different temporal characteristics across habitat zones due to a variety of adaptive functions, including—but not limited to—resource defence, group spacing and predator avoidance. Our findings may be interpreted in the light of other functions, but when our results for tree characteristics in edge and interior zones at LSBRS are considered, our howling behaviour results support the ecological resource defence function of

howling among other possibilities. Our findings thus contribute to the existing literature addressing the potential function(s) of howler monkey long calls (reviewed in Kitchen et al., 2015) and provide one of the first focused investigations of how primate communication behaviour is impacted by anthropogenic edge effects.

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