

Mantled Howler Monkeys (*Alouatta palliata*) in a Costa Rican Forest Fragment Do Not Modify Activity Budgets or Spatial Cohesion in Response to Anthropogenic Edges

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Abstract

Forest fragmentation increases forest edge relative to forest interior, with lower vegetation quality common for primates in edge zones. Because most primates live in human-modified tropical forests within 1 km of their edges, it is critical to understand how primates cope with edge effects. Few studies have investigated how primates inhabiting a fragment alter their behaviour across forest edge and interior zones. Here we investigate how anthropogenic edges affect the activity and spatial cohesion of mantled howler monkeys (*Alouatta palliata*) at the La Suerte Biological Research Station (LSBRS), a Costa Rican forest fragment. We predicted the monkeys would spend greater proportions of their activity budget feeding and resting and a lower proportion travelling in edge compared to forest interior to compensate for

lower resource availability in the edge. We also predicted that spatial cohesion would be lower in the edge to mitigate feeding competition. We collected data on activity and spatial cohesion (nearest neighbour distance; number of individuals within 5 m) in forest edge and interior zones via instantaneous sampling of focal animals. Contrary to predictions, the monkeys spent equal proportions of time feeding, resting and travelling in forest edge and interior. Similarly, there were no biologically meaningful differences in the number of individuals or the distance between nearest neighbours in the edge (1.0 individuals; 1.56 m) versus the interior (0.8 individuals; 1.73 m). Our results indicate that *A. palliata* at LSBRS do not adjust their activity or spatial cohesion patterns in response to anthropogenic edge effects, suggesting that the monkeys here exhibit less behavioural flexibility than *A. palliata* at some other sites. To develop effective primate conservation plans, it is therefore crucial to study primate species' responses to fragmentation across their geographic range.

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Introduction

The destruction of tropical forests is a major threat to global biodiversity [Haddad et al., 2015]; clearing land for agriculture and cattle pastures are the leading sources of this degradation [Estrada, 2015]. In Costa Rica, for example, forests have been cut down, and their land has been appropriated for agriculture since the 1970s [Garber et al., 2010]. Consequently, remaining forest patches are separated from one another by a matrix of pasture and farmland, which negatively impacts some forest animals that live there, including primates. Habitat fragmentation is one of the main threats to primate species globally, with more than half of all primate species experiencing considerable population decline as a result [Boyle et al., 2013; Chapman et al., 2013; Nijman, 2013; Estrada et al., 2017].

Although in some cases forest fragments may be comparable to continuous forests in size and productivity [e.g., Zárate and Stevenson, 2014], many primate populations that inhabit forest fragments contend with decreased habitat size [Haddad et al., 2015; McKinney et al., 2015] and, consequently, reduced food availability [e.g., Arroyo-Rodríguez and Mandujano, 2006; Arroyo-Rodríguez et al., 2007; Chaves et al., 2012]. Primates generally rely on large, abundant trees [e.g., van Roosmalen, 1985; Chapman, 1988; Estrada et al., 1999b; Dunn et al., 2010; Bolt et al., accepted], but fragments have fewer tree species, and trees are less abundant and smaller than those in continuous forests [e.g., Didham and Lawton, 1999; Arroyo-Rodríguez and Mandujano, 2006; Dunn et al., 2009; Chaves et al., 2012]. Furthermore, forest fragmentation causes a greater amount of forest edge relative to forest interior [Laurance, 1991; Broadbent et al., 2008]. Abiotic conditions including temperature, moisture, sunlight, and wind differ at anthropogenic edges compared to forest interior [Laurance et al., 1998a; Chen et al., 1999], which can lead to plant and animal species loss nearer to the edge [Broadbent et al., 2008]. While in some cases forest vegetation is not impacted by edge effects [e.g., Phillips et al., 2006] and edge zones may experience increased recruitment of pioneer species and thus provide high-quality resources for herbivores [Laurance et al., 1998b; Meyer et al., 2009], vegetation quality for primates is generally lower at forest edges than interior with lower plant biomass and fewer tall trees closer to the edge [e.g., Estrada et al., 1999a; Arroyo-Rodríguez and Mandujano, 2006; Lehman et al., 2006]. Because most primate species live in human-modified forests within 1 km of the edge [Estrada et al., 2017], almost a third of which are within 100 m of forest edges [Haddad et al., 2015], it is critical to

understand how primates contend with edge effects in anthropogenically modified tropical forests.

To persist in forest edges, primates likely need to reduce feeding competition to secure sufficient food resources in these poorer-quality habitats [Bicca-Marques, 2003; Arroyo-Rodríguez and Mandujano, 2006]. One way to accomplish this is to alter their activity budgets to spend more time feeding to ensure sufficient food intake and to reduce energy expenditure by spending less time travelling and more time resting [Silva and Ferrari, 2009; Boyle and Smith, 2010]. While evidence is preliminary as to how primates alter their activity patterns in edge zones compared to forest interior [e.g. McGoogan, 2011; de Vries, 2017], research has been more focused on activity budgets in primates living in fragments compared with those in continuous forests. Among platyrrhines, Brazilian bearded saki monkeys (*Chiropotes satanas chiropotes*) spent more time resting and less time travelling in small fragments compared to large and continuous forests [Boyle et al., 2009], and Central American spider monkeys (*Ateles geoffroyi*) living in fragments in Mexico spent more time feeding and less time travelling compared to those living in continuous forest [Chaves et al., 2011]. Across three groups of mantled howler monkeys (*Alouatta palliata*) living in fragments of varying sizes in Los Tuxtlas, Mexico, time spent travelling increased with fragment size, although there were no clear differences in resting or feeding time [Juan et al., 2000]. *A. palliata* living in areas heavily modified by humans in the Curú Wildlife Refuge in Costa Rica spent more time feeding than those in areas less impacted by humans, although there was no difference in time spent resting [McKinney, 2019]. *A. palliata* activity patterns in edge versus interior zones of a forest fragment have not yet been examined.

In response to limited food availability in fragments, primates can also adjust their group size and spatial cohesion to reduce feeding competition [e.g., Chapman et al., 1995]. For example, group cohesion was lower in diademedsifakas (*Propithecus diadema*) living in fragments compared to those in continuous forest [Irwin, 2007]. Specifically, distances between nearest neighbours were greater in fragments than in continuous forest, with nearest neighbour differences across forest type most extreme in feeding contexts. In forest fragments, the sifakas relied more heavily on smaller, more dispersed resources like mistletoe, requiring them to spread out further across multiple food patches [Irwin, 2007]. In the Curú Wildlife Refuge in Costa Rica, *A. palliata* group cohesion was lower in areas more heavily modified by humans [McKinney, 2019]. Additional focused study on the effects of anthro-

pogenic edges on *A. palliata* spatial cohesion is critical to understanding if and how this species can persist in an increasingly fragmented landscape consisting of greater proportions of forest edge compared to interior.

In this study we examine anthropogenic edge effects on the activity patterns and spatial cohesion of *Alouatta palliata* at La Suerte Biological Research Station (LSBRS), a fragmented tropical rain forest in north-eastern Costa Rica. *A. palliata* are folivore-frugivores [di Fiore et al., 2011; Garber et al., 2015; Aristizabal et al., 2017; Righini et al., 2017] that live in large multimale, multifemale social groups of about 10–15 individuals, although group size can top 40 [Bezanson et al., 2008; Ryan et al., 2008; di Fiore et al., 2011]. Groups are typically spatially cohesive [Milton, 1980; Crockett and Eisenberg, 1987] but have been observed separating into subgroups in some instances [Leighton and Leighton, 1982; Chapman, 1990; Bezanson et al., 2008], probably to increase foraging efficiency [Dias and Rodríguez-Luna, 2006]. Howler monkeys spend most of their time resting [e.g., Estrada et al., 1999b], likely because leaves contain toxins and complex compounds that are difficult to digest [Milton, 1979, 1980].

Previous research at LSBRS showed lower tree species richness, diameter at breast height (DBH) and canopy cover in anthropogenic edges (<100 m from forest boundary) compared to forest interior [Bolt et al., 2018, 2019]. Given that greater canopy cover and the presence of large trees provide high-quality primate habitat [Arroyo-Rodríguez and Mandujano, 2006; Dunn et al., 2009; Chaves et al., 2012], and tree DBH is a reliable proxy for fruit abundance [e.g., Leighton and Leighton, 1982; Peters et al., 1988; Chapman et al., 1992], vegetation quality for monkeys in forest edge zones at LSBRS is lower than that of forest interior. Furthermore, *A. palliata* population density at LSBRS is 73.8 individuals/km² [Schreier and Bolt, 2020], strikingly higher than at other mantled howler sites where density typically ranges from 5 to 30 individuals/km² [e.g., Estrada, 1982; Stoner, 1996; Clarke et al., 2002b]. This combination of high population density and reduced vegetation quality in edge zones suggests more substantial feeding competition at LSBRS than other *A. palliata* sites.

Previous studies at LSBRS reported that *A. palliata* group encounter rates did not differ significantly between anthropogenic forest edge and interior zones [Bolt et al., 2018, 2020b], although howling behaviour did vary across habitat zones. Howling bouts were longer and consisted of more howls in the forest interior, presumably to announce their presence to other howler monkey groups in

forest locations with high-quality vegetation [Bolt et al., 2019, 2020a]. These results suggest that while the monkeys inhabit anthropogenic edge and interior forest at LSBRS evenly despite vegetation differences across forest zones, anthropogenic edges affect howling behaviour and may therefore also influence other aspects of behaviour.

We hypothesize that *A. palliata* at LSBRS will alter their activity budget and spatial cohesion in response to forest edges. Given differences in vegetation quality across forest zones at LSBRS [Bolt et al., 2018, 2019, 2020a, b], coupled with the high population density that likely increases feeding competition, we predict that *A. palliata* will spend greater proportions of their activity budget feeding and resting, and a lower proportion of their activity budget travelling in the edge than the forest interior to ensure sufficient food intake and reduce energy expenditure. Furthermore, we predict that monkeys will be less spatially cohesive in the edge compared to the forest interior in order to reduce feeding competition.

Methods

Study Site

We conducted this study at LSBRS in north-eastern Costa Rica (10°26' N, 83°46' W). LSBRS is a tropical lowland fragmented rain forest totalling approximately 3 km² of primary forest, secondary forest and regenerating pastures [Pruetz and Leason, 2002; Garber et al., 2010]. The main forested area where we conducted research comprises two connected forest patches (“Large Forest” = 0.935 km² and “Small Forest” = 0.35 km²) as well as a partially cleared area for “camp” (0.071 km²) [Molina, 2015; Bolt et al., 2018]. The area around the reserve consists mainly of pasture and coconut plantations [Molina, 2015; Brandt and Singleton, 2018]. LSBRS is a model site at which to examine the effects of anthropogenic edges on *A. palliata* activity and spatial cohesion patterns because of the distinct edges surrounding the forest fragment. Barbed wire fences indicate the property perimeter, flagging the sharp boundary between preserved forest in LSBRS and surrounding developed land [Molina, 2015].

Along with mantled howler monkeys, white-faced capuchin (*Cebus capucinus*) and Central American spider monkeys (*A. Geoffroyi*) inhabit the forests at LSBRS. For the current study, we observed 11 groups of howler monkeys, 3 in the Small Forest and 8 in the Large Forest, which is consistent with previous population surveys [Pruetz and Leason, 2002; Garber et al., 2010]. The mean group size was 9.1 individuals (SD 3.2).

Data Collection

We collected data on *A. palliata* activity and spatial cohesion patterns from May to August 2017, May to August 2018 and December 2018 to January 2019. Most of the groups we sampled inhabited either the edge or interior zone, although a few groups ranged across both forest zones. The monkeys were all habituated to the presence of researchers; they did not howl or move away from researchers when we approached and observed them. Re-

searchers sampled monkeys daily between 5.00 and 18.00 h. We aimed to collect approximately equal amounts of data across anthropogenic edge and interior forest zones. We defined edge as 100 m from any anthropogenic forest boundary, following previous edge effect studies [e.g., Laurance et al., 2002; Pohlman et al., 2009] and consistent with prior studies at LSBRS [Bolt et al., 2018, 2019, 2020b]. Indeed, results from vegetation surveys at LSBRS show that canopy cover and DBH are both lower within 100 m of the forest edge compared to forest greater than 100 m from the forest boundary [Bolt et al., 2018, 2019, 2020b].

We conducted 30-min samples on single howler monkeys (infants were not sampled), during which we conducted instantaneous scan samples at 2-min intervals [Altmann, 1974]. At each scan we recorded the focal animal's activity (i.e., *rest* – remain in one location on substrate; *feed* – manipulate food or water with hands, feet, mouth; *travel* – move along a substrate (not while feeding); *social* – includes grooming, playing, aggression, submission; or *other* – any behaviour not mentioned above) [Paterson, 2001]. To quantify spatial cohesion, we recorded the number of individuals within a 5-m radius of the focal subject during each scan [cf. Chapman, 1990] and estimated the distance (in metres) to the nearest monkey in any of the distance classes: 0, 0.5, 1, 2, 3, 4, 5, 6, 7, 8, 9, 10 m or >10 m, and age/sex class of neighbour monkeys was recorded whenever possible [Irwin, 2007]. During each 30-min sample, we recorded the location of the focal animal within LSBRS using a Garmin GPSMAP 62s hand-held navigator. Because individual monkey identities were unknown in this population, we cannot be certain how many times each individual was sampled over the course of the study period. We aimed to sample groups equally across forest zones with no more than 2 researchers collecting data on a single monkey group at any given time. At least 2 h had to elapse before resampling a monkey, and a single monkey could not be resampled more than twice in a day; in practice, it was rare that any monkey was sampled more than once in a 3-hour period. We used body size and tail length differences across group members, and more distinct characteristics when present, to prevent resampling individuals. If the monkey being sampled was out of view for 10 min or more of the 30 min sample, the sample was discarded. In preparation for this study, researchers conducted instantaneous sampling of focal animals simultaneously. We calculated interobserver agreement by calculating the number of scans in agreement across observers by the total number of scans, and data collection began once researchers reached 94% agreement.

Data Analysis

We base our analyses on 792 h of 30-min focal samples (1,629 30-min samples; 26,064 2-min scans), 427 h (878 30-min samples; 14,048 2-min scans) in anthropogenic edges and 365 h (751 30-min samples; 12,016 2-min scans) in forest interior. To test our hypothesis that *A. palliata* will alter their activity budget in response to forest edges, we fit 3 binomial generalized linear mixed models (GLMMER), one for each activity (i.e., resting, feeding, travelling) with fixed effect for forest zone. To quantify the effect of forest zone on spatial cohesion, we fit generalized linear mixed models (GLMM), with distributions chosen based on data type. For number of individuals within 5 m of the focal subject, we used a Poisson distribution with log-link function. For distance to nearest neighbour, we first log-transformed the data ($\log(x + 1)$) to meet assumptions of normality and used a Gaussian distribution with identity link function. For each model, we included a

random effect for each 30-min focal sample to control for the autocorrelation across 2-min scans in each 30-min focal sample. To test whether our response variables differed by forest zone, we also fit a null (i.e., intercept-only) model for each response (i.e., each activity, number of individuals within 5 m, distance to nearest neighbour) and compared Akaike information criteria (AICs) within each model pair (i.e., null and forest zone) [Burnham et al., 2011].

Exploratory data analyses showed consistent results across age-sex classes and we thus include adult males, adult females and juveniles in all analyses reported here. Similarly, spatial cohesion results did not differ significantly based on activity, and we thus include the complete data set (comprising all activity types) in our present analyses. All statistical analyses were conducted in open source statistical software R (version 3.4.1 [R Core Team, 2017]) with the following packages: “tidyr” and “dplyr” for data manipulation [Wickham et al., 2017; Wickham and Henry, 2017] and “lme4” for GLMM [Bates et al., 2015]. α -Values <0.05 were considered significant.

Results

Overall, *A. palliata* spent 67.5% of their activity budget resting, 12.5% feeding and 11.3% travelling. The monkeys spent equal proportions of their activity budget resting (67.8% in edge vs. 67.2% in interior), feeding (12.4% in edge vs. 12.5% in interior) and travelling (11.1% in the edge vs. 11.5% in interior) in anthropogenic edge and forest interior zones. There were no significant differences in the odds of resting ($p = 0.570$), feeding ($p = 0.572$) or travelling ($p = 0.735$; binomial GLMMER) across forest interior and anthropogenic edge. The forest zone models did not improve the model fits compared to the null models (as evidenced by higher AIC in the forest zone models than the null models for resting [AIC = 24,573.8 vs. 24,572.1], feeding [AIC = 14,647.3 vs. 14,645.7] and travelling [AIC = 16,537.9 vs. 16,536.0]; Table 1), further showing that forest zone is not a strong predictor of activity budget.

Across forest zones, the mean number of individuals within 5 m was 0.86 (range = 0–12; confidence interval, CI: 0.81–0.92). GLMM results indicated that the mean number of individuals within 5 m was 0.96 in the edge (CI: 0.84–1.09) and 0.77 in the interior (CI: 0.70–0.84; $p = 0.001$). AIC was lower in the forest zone model (AIC = 54,179.0) than the null model (AIC = 54,188.1; Table 2). The median distance to the nearest neighbour across forest zones was 1.64 m (range = 0–13 m; CI: 1.52–1.76). Results of GLMM showed that median distance did not differ between the forest interior (1.56 m; CI: 1.35–1.80) and anthropogenic edge (1.73 m; CI: 1.53–1.92; $p = 0.156$). Including forest zone did not improve the model

Table 1. Binomial generalized mixed model comparisons for activity budget of *Alouatta palliata* at La Suerte Biological Research Station

Activity	Model	AIC	log likelihood	Deviance	Residual df
Resting	Forest zone model	24,573.8	-12,283.9	24,567.8	25,367
	Null model	24,572.1	-12,284.0	24,568.1	25,368
Feeding	Forest zone model	14,647.3	-7,320.7	14,641.3	25,367
	Null model	14,645.7	-7,320.8	14,641.7	25,368
Travelling	Forest zone model	16,537.9	-8,266.0	16,531.9	25,367
	Null model	16,536.0	-8,266.0	16,532.0	25,368

AIC, Akaike information criterion; df, degree of freedom.

Table 2. Generalized mixed model comparisons for spatial cohesion of *Alouatta palliata* at La Suerte Biological Research Station

Spatial cohesion variable	Model	AIC	log likelihood	Deviance	Residual df
Individuals within 5 m, <i>n</i>	Forest zone model	54,179.0	-27,086.5	54,173.0	21,461
	Null model	54,188.1	-27,092.0	54,184.1	21,462
Distance to nearest neighbour	Forest zone model	26,023.7	-13,007.8	26,015.7	19,897
	Null model	26,023.6	-13,008.8	26,017.6	19,898

AIC, Akaike information criterion; df, degree of freedom.

fit compared to the null model (AIC = 26,023.7 vs. 26,023.6; Table 2), further demonstrating that forest zone does not predict distance to nearest neighbour.

Discussion

Our hypothesis that *A. palliata* inhabiting LSBRS, a Costa Rican forest fragment, would modify their activity budget and spatial cohesion patterns in response to anthropogenic edges due to the lower vegetation quality compared to forest interior was not supported. Despite vegetation at the LSBRS being richer in forest interior compared to the edge [Bolt et al., 2018, 2019, 2020a, b], and the high *A. palliata* population density at this site [Schreier and Bolt, 2020], the monkeys spent equal proportions of their activity budget resting, feeding and travelling in edge and interior forest zones. There were also no biologically meaningful differences in the number of individuals or distance between nearest neighbours in the edge versus the interior. These results suggest that the monkeys at LSBRS exhibit less behavioural flexibility than their conspecifics at some other sites [e.g., Clarke et al., 2002a; McKinney, 2019] and highlight the need to study primate species' responses to fragmentation across

their geographic ranges in order to develop effective primate conservation plans.

Our results that activity patterns did not vary in response to forest fragmentation are not consistent with work from Los Tuxtlas, Mexico, where *A. palliata* spent more time travelling as fragment size increased [Juan et al., 2000], and the Curú Wildlife Refuge in Costa Rica where the monkeys spent more time feeding in areas more heavily modified by humans [McKinney, 2019]. However, in line with our results, Cristóbal-Azkarate and Arroyo-Rodríguez [2007] found no relationship between howler activity patterns and fragment size in Los Tuxtlas, nor did Bicca-Marques [2003] in his survey of 6 different howler monkey species across 27 study sites throughout Central and South America.

Therefore, both our results at LSBRS as well as those from elsewhere in the geographic range of *A. palliata* suggest that some howler populations can subsist in areas with reduced resource availability without modifying their activity budgets. This may be due to the fact that leaves are readily available even in poorer-quality habitats. At LSBRS, leaves made up about 60% of the monkeys' diet in both forest edge and interior [Russell, 2018], indicating availability of foliage across forest zones. Thus, there may be no need to increase feeding time in the edge.

It is also possible that howler monkeys are constrained in their ability to alter their activity budgets compared to other primates [Arroyo-Rodríguez and Dias, 2010]. While howler gut morphology is not particularly specialized for a leaf-heavy diet, their gut retention time is long, enabling efficient digestion of leaves [Milton, 1980, 1998]. Howler monkeys, therefore, need to devote the majority of their time to resting to ensure effective digestion regardless of habitat quality, limiting how much they can vary time spent engaged in other activities. Another way howler monkeys might deal with reduced food availability in fragments is by diversifying their diet and increasing the number of tree species they consume [Silver and Marsh, 2003]. We hope to address this hypothesis at LSBRS in the near future when we have a robust howler diet data set.

Spatial cohesion did not vary across anthropogenic edges and forest interior either. There was no difference in the median distance between nearest neighbours across forest zones; while the mean number of individuals within 5 m was statistically significantly different between anthropogenic edges and forest interior, we argue that this variation is not biologically meaningful (0.8 vs. 1.0 of a monkey are both, after all, essentially one monkey, and the significant value is likely an artefact of large sample size). These results are consistent with those of Stevenson et al. [2015] who found that adult woolly monkeys (*Lagothrix* spp.) were found within 5 m of other adults at the same frequency across two forest sites that differed in size and continuity, suggesting there were sufficient resources in the smaller fragment to maintain the same level of social cohesion. The fact that *A. palliata* at LSBRS did not vary their cohesion patterns across forest zones despite lower vegetation quality in the edge may be explained by the fact that, overall, they fed and rested from trees that were much larger than the average tree size at LSBRS. Mean DBH of both feeding and resting trees was almost 5 times that of average tree DBH in the interior and 4 times as large in the edge [Schreier and Bolt, unpubl. data], and feeding trees were taller than the average tree height at LSBRS in both forest zones [Russell, 2018; Bolt et al., accepted]. The howler monkeys therefore selected the largest trees in both the edge and interior. *A. palliata* at other fragmented sites also prefer larger trees than the average size in their forests [Munoz et al., 2006]. While the higher DBH and canopy cover in the forest interior at the LSBRS [Bolt et al., 2018; Bolt et al., 2019] shows that there are fewer large trees spread further apart in the edge, selecting the very largest trees likely allows the monkeys to remain in and near the limited number of preferred

trees in this forest zone. By feeding on the largest trees – that accommodate many monkeys at once – in both forest zones, the monkeys may not need to vary spatial cohesion to reduce feeding competition. The presence of large feeding trees throughout LSBRS may therefore enable howler monkeys to spend equal proportions of their activity budget feeding and to maintain consistent spatial cohesion patterns across forest zones.

The monkeys' spatial cohesion patterns may also be a consequence of the high density of *A. palliata* at LSBRS. While the population density of 73.8 individuals/km² [Schreier and Bolt, 2020] is comparable to that of other howler monkey species in a few sites [e.g. González et al., 2002; Palma et al., 2011], it is substantially higher than at other sites. Population density of *A. palliata* at Los Tuxtlas, for example, is only 23.3 individuals/km² [Estrada, 1982]. In Costa Rica, population density is 30 individuals/km² at La Pacifica [Clarke et al., 2002b], grew from 4.9 to 7.9 individuals/km² at Santa Rosa National Park [Fedigan et al., 1998] and is 7–15 individuals/km² at La Selva Biological Station despite the similar group sizes and sex ratios as at LSBRS [Stoner, 1996; Bolt et al., 2019]. These results are consistent with other work that shows *A. palliata* density is inversely related to forest size [Cristóbal-Azkarate et al., 2005; Mandujano and Escobedo-Morales, 2008]. The especially high density of monkeys at the LSBRS may necessitate members of both edge and interior groups to remain in close proximity simply due to the high number of individuals and limited space.

Our results that *A. palliata* at LSBRS do not modify their activity budgets or spatial cohesion patterns in response to edge effects are consistent with the species' reputation for being tolerant to habitat disturbance [Arroyo-Rodríguez and Dias, 2010]. However, unlike *A. palliata* at other sites that alter their behaviour in response to anthropogenic habitat modification [e.g., Clarke et al., 2002a; McKinney, 2019], those at LSBRS exhibit limited behavioural flexibility in response to lower vegetation quality. It is possible that recent habitat destruction to make way for banana and pineapple plantations in the area surrounding LSBRS has necessitated an influx of monkeys into this remaining forest fragment, leading to the very high *A. palliata* population density here. That the monkeys inhabit edge zones and forest interior equally [Bolt et al., 2018] may only be a current phenomenon due to overcrowding.

Future behavioural observations at LSBRS will shed light onto whether the monkeys begin to modify their activity and spatial cohesion patterns in edges over time in response to the lower habitat quality. It is important to

note that previous work showed that howling behaviour differs across edge and interior zones at LSBRS [Bolt et al., 2019, Bolt et al., 2020a], suggesting that *A. palliata* are flexible in at least some aspects of their behavioural repertoire. Differences in howling behaviour across various forest regions may be sufficient for reducing feeding competition at LSBRS; if so, it might obviate the need to alter activity and/or spatial cohesion patterns. Future work should examine the relationship between howling and feeding to determine whether changes in howling behaviour effectively mitigate feeding competition at the LSBRS. With most primates worldwide living in close proximity to a forest edge [Estrada et al., 2017], it is crucial to understand how primates deal with edge effects. This study explicitly examines how primates behaviourally cope with edge effects and underlines the importance of studying primate responses to forest fragmentation across species' geographic ranges to effectively inform conservation plans.

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Statement of Ethics

Permission to conduct research at the LSBRS was granted by the Maderas Rainforest Conservancy, and the research adhered to the legal requirements of Costa Rica. Protocols were approved by the Regis University Institutional Animal Care and Use Committee.

Conflict of Interest Statement

The authors have no conflicts of interest to declare.

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Author Contributions

A.L.S. was responsible for project design, data collection, data analysis and interpretation, and writing and revising the manuscript. L.M.B. was responsible for project design, data collection, data analysis and interpretation, and writing and revising the manuscript. D.G.R. collected and analysed data, and contributed to the writing and revision of the manuscript. T.S.R. analysed data and contributed to the writing and revision of the manuscript. Z.S.J. collected data and contributed to the writing and revision of the manuscript. C.M.-J. collected data and contributed to the writing and revision of the manuscript. E.M.C. collected data and contributed to the writing and revision of the manuscript. All authors approved the final version of the submitted paper.

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