



Anthropogenic edges impact howler monkey (*Alouatta palliata*) feeding behaviour in a Costa Rican rainforest

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Abstract

Anthropogenic forest fragmentation impacts many aspects of animal behaviour, including feeding ecology. With forests increasingly fragmented in tropical regions due to human development, the proportion of forest edge (≤ 100 m from clearcut regions) is higher relative to forest interior. Forest edges differ in vegetation from interior, making it important to better understand how anthropogenic edges impact the feeding behaviour of primates such as mantled howler monkeys (*Alouatta palliata*). We predicted that howler monkeys would feed on higher-quality plant resources, from a larger number of tree families, and from larger trees in forest interior compared to anthropogenic forest edge. We surveyed howler monkey feeding behaviour across forest zones in a fragmented rainforest in Costa Rica, La Suerte Biological Research Station. We observed individual monkeys for 30-minute periods, collecting data on their feeding behaviour and tree use at 2-minute intervals. We measured feeding trees and recorded the plant parts and taxonomy of resources consumed. Monkeys consumed more leaves and fewer stems and fed from a smaller number of tree families in the forest interior, while they consumed fewer leaves and more stems and fed from a larger number of tree families in the forest edge. Monkeys also fed from larger, taller trees in the forest interior than the edge. The differences in howler monkey feeding behaviour between forest zones attest to the impact of human disturbance on howler monkey feeding ecology.

Keywords Behavioural edge effects · Feeding ecology · Feeding tree DBH · Feeding tree height · Mantled howler monkey · Forest fragmentation

Introduction

Within tropical landscapes, forest edges are transition zones that differ from forest interior environments in abiotic and biotic characteristics (Laurance 1991; Laurance and Yensen 1991; Chen et al. 1999). Edges differ from forest interior in temperature, wind, moisture, and soil characteristics, which in turn impacts plant and animal species (Lovejoy et al. 1986; Harris 1988; Saunders et al. 1991; Stevens and

Husband 1998; Laurance et al. 2002). Human-modified edges typically have lower canopy connectivity and plant species richness, higher tree mortality, and smaller trees compared to the forest interior (Didham and Lawton 1999; Dislich and Pivello 2002; Tabarelli et al. 2008), which generally result in less food for animals, increased feeding competition, and lower overall biomass (Pardini 2004; Chaplin-Kramer et al. 2015). Primates are particularly affected by anthropogenic deforestation, with more than half of primate species worldwide currently facing extinction due to habitat destruction (Arroyo-Rodríguez and Dias 2010; Mittermeier et al. 2012; Estrada et al. 2017). Given these ongoing threats as well as the rising proportion of anthropogenic edges in remaining forest fragments (Saunders et al. 1991; Broadbent et al. 2008), it is important to better understand how primates may modify their feeding behaviour when in forest edges.

Previous research has shown that primate density and ranging patterns are impacted by edge effects, with dietary adaptations influencing where primates are located in forests

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(Lidicker 1999; Lenz et al. 2014). For example, some folivorous primate species prefer the forest edge [woolly lemur (*Avahi laniger*)], Lehman et al. 2006), likely due to higher light levels causing higher protein content in leaves (Ganzhorn 1995). In contrast, other folivores show no preference for forest edge or interior [sportive lemur (*Lepilemur microdon*)] Lehman et al. 2006; colobus monkey (*Procolobus rufomitratus*), Mbona and Meikle 2004; titi monkey (*Callicebus cupreus*), Kulp and Heymann 2015), likely due to the presence of leaves of sufficient nutritive quality throughout forest zones (Bolt et al. 2018). Few studies, however, have examined how other elements of primate feeding ecology relate to edge effects. The present study investigates the effects of anthropogenic forest edges on feeding behaviour and tree use in a folivorous-frugivorous platyrrhine primate, the mantled howler monkey (*Alouatta palliata*).

Howler monkeys (*Alouatta* spp.) are Neotropical primates that are well-known for their folivorous-frugivorous feeding ecology (Glander 1978; Milton 1980; Strier 1992; Dias and Rangel-Negrín 2015; Reynoso-Cruz et al. 2016). Although they typically live in social groups of 10–15 individuals (di Fiore et al. 2011), they minimize food resource competition with conspecifics through dietary flexibility, varying the proportions of fruit and leaves they consume based on resource availability (Espinosa-Gómez et al. 2013; Righini et al. 2017; McKinney 2019). Howler monkeys have dietary adaptations that enable them to neutralize the detrimental effects of secondary compounds such as tannins, thus allowing them to feed on larger proportions of mature leaves than other platyrrhines (Espinosa-Gómez et al. 2018), and to alter gut microbiota composition and activity to compensate for seasonal differences in energy and nutrient availability from dietary resources (Amato et al. 2014, 2015). Howler monkeys are also behaviourally adapted to compensate for periods with a low-energy diet. They move slowly, spend most of their daily activity budget resting (Estrada et al. 1999; di Fiore and Campbell 2007; Schreier et al. 2021) and produce long-distance vocalizations (howls), which are thought to spatially distance groups to further minimize feeding competition (Kitchen et al. 2015; Bolt et al. 2019, 2020a). Howler monkeys' ability to find adequate sustenance in a variety of forest habitats allows them to persist in disturbed environments, including forest fragments (Silver and Marsh 2003). However, despite this adaptability, howler monkeys are also constrained in their dietary flexibility. They lose weight when consuming diets with very high proportions of leaves (Espinosa-Gómez et al. 2013), suggesting that they should consume high-energy diets whenever possible.

Like other howler monkey species, mantled howler monkeys eat nutrient-rich foods such as fruit and flowers when available, supplemented by leaves (Glander 1982; LaRose 1996; Asensio et al. 2007; di Fiore et al. 2011; Reynoso-Cruz et al. 2016; McKinney 2019). They also consume

nutrient-poor foods such as stems (Milton 1980; Glander 1981; Muñoz et al. 2006; Gotsch et al. 2015). Despite their seemingly broad diet, mantled howler monkeys are selective foragers. For example, they fed from only 15 plant families at a biodiverse tropical rainforest site at Los Tuxtlas, Mexico (Estrada 1984). Additionally, they prefer to feed from large trees (Chapman 1988a; Estrada et al. 1999), which are more common in forest interior regions than in human-disturbed forest edges (Didham and Lawton 1999; Bolt et al. 2018, 2019, 2020b; Russell 2018). Despite this selectivity (Glander 1982; Estrada 1984; Estrada et al. 1999), mantled howler monkeys are able to survive in many fragmented and low-quality forest habitats, demonstrating their dietary flexibility (Garber et al. 2006; Muñoz et al. 2006; Estrada 2015; Garber and Kowalewski 2015; McKinney et al. 2015). While mantled howler monkey feeding behaviour has been widely studied (Glander 1978, 1981, 1982; Milton 1980; Estrada 1984; Estrada and Coates-Estrada, 1984; Chapman 1987; Muñoz et al. 2006; Asensio et al. 2007; Reynoso-Cruz et al. 2016; McKinney 2019), few studies have specifically examined the impact of anthropogenic forest edges on their feeding ecology. Skrinyer (2016) found that mantled howler monkeys fed for greater proportions of total activity budget when in forest interior compared to forest edge at Piro Biological Station in the Osa Peninsula, Costa Rica. In contrast, Schreier et al. (2021) found no difference in proportion of activity budget dedicated to feeding behaviour when howler monkeys were in forest interior vs. anthropogenic edge at the La Suerte Biological Research Station (LSBRS), Costa Rica. However, neither study examined specific food resources consumed. Russell (2018) completed a short-term study on howler monkey feeding ecology at LSBRS and observed more feeding from larger trees in forest interior compared to anthropogenic edge, with different plant parts and species consumed in each zone. Our investigation builds on Russell's (2018) work at LSBRS, and will improve understanding of how mantled howler monkeys may modify feeding behaviour when in different regions of a fragmented and anthropogenically altered rainforest.

We hypothesized that howler monkey feeding behaviour and feeding tree use would differ when in forest interior vs. anthropogenic edge at LSBRS. Past investigations on vegetation quality at LSBRS found greater canopy cover, tree species richness, and larger trees in the forest interior, which includes areas surrounding the La Suerte river, compared to 100-m anthropogenic edge areas (within 100 m of disturbed landscape such as road or cattle pasture) (Bolt et al. 2018, 2019, 2020b). These vegetation features relate to habitat quality for monkeys (Ross and Srivastava 1994; Arroyo-Rodríguez and Mandujano 2006), indicating that forest interior at LSBRS is higher quality than anthropogenic edge. Previous research at LSBRS also showed that howler monkeys preferentially ranged in the forest interior zone

near the river (Bolt et al. 2020b), potentially because of the greater number of large feeding trees found there. With feeding tree size positively related to food quality (Leighton and Leighton 1982; Peters et al. 1988; Chapman et al. 1992) and mantled howler monkeys preferring larger trees than average for feeding (Estrada et al. 1999), we predicted that when in forest interior, monkeys would feed on higher-quality plant resources, such as flowers and fruit, from a larger number of different tree families, and from taller trees with larger diameter at breast height (DBH). Conversely, we predicted that when in anthropogenic forest edge, monkeys would feed on lower-quality plant resources, such as stems, from a smaller number of different tree families, and from shorter trees with smaller DBH.

Methods

Study site

The La Suerte Biological Research Station (LSBRS) in northeastern Costa Rica exists within a forest fragment in a region of agricultural sprawl, mostly in the form of crop monoculture, that has occurred throughout the Eastern Caribbean slope since the 1970s (Molina 2015; Brandt and Singleton 2018). Surrounding areas include plantations and cattle ranches, which are separated from the LSBRS forest by barbed wire fences, creating distinct boundaries between land use zones. LSBRS includes a combination of primary and secondary growth tropical lowland rainforest. This fragment consists of two connected forest regions, the “Large Forest” (0.935 km²) to the north and “Small Forest” (0.35 km²) to the south, with the La Suerte river running throughout the fragment (Molina 2015). In one region of the site, there is a deforested area with maintained grass lawns for researcher and student housing referred to as “camp” (0.07 km²) (Fig. 1). We defined the anthropogenic edge as extending 100 m from human land use (Bolt et al. 2018, 2019, 2020b; Schreier et al. 2021). This included the LSBRS fragment border with agricultural activity as well as camp. In addition to mantled howler monkeys, LSBRS is home to white-faced capuchin (*Cebus imitator*) and Central American spider monkeys (*Ateles geoffroyi*).

Study subjects

We collected howler monkey feeding behaviour and feeding tree use data from 11 groups of mantled howler monkeys across both forest interior and anthropogenic edge zones at LSBRS. These same groups have also been the subjects for other behavioural investigations at the same site (Bolt et al. 2019, 2020a, 2021; Schreier et al. 2021). LSBRS has an unusually high population density of mantled howler

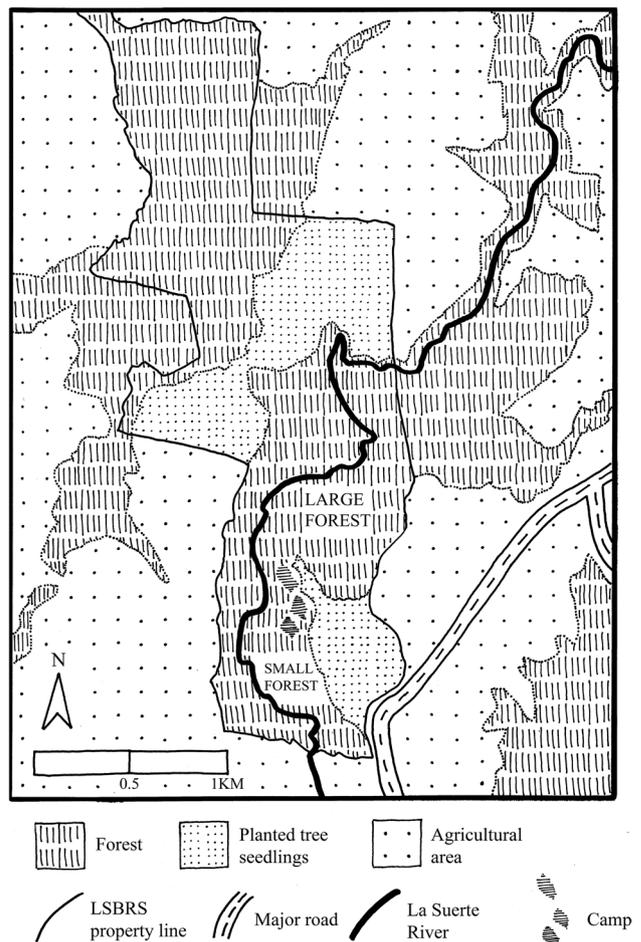


Fig. 1 Map of La Suerte Biological Research Station and surrounding area in Limón Province, Costa Rica

monkeys, with an estimated 73.8 individuals/km² at LSBRS (Schreier et al. 2021) compared to 5–30 individuals/km² at other neotropical sites (Estrada 1982; Stoner 1996; Clarke et al. 2002), suggesting that feeding competition at LSBRS should be higher and any differences in feeding across forest zones should be especially pronounced. Previous population estimates identified 8–11 groups of howler monkeys at LSBRS (Pruetz and Leason 2002; Garber et al. 2010). Current monkey groups could not be consistently identified between sampling seasons due to changing group demography, but 11 different groups were observed and sampled during each sampling period (Bolt et al. 2021). While group ranging patterns have not been studied, groups appear to have overlapping ranges spanning both forest edge and interior zones (Bolt et al. 2019; Schreier et al. 2021). Current group compositions range from three to 20 individuals of both sexes, with a mean of 9.3 individuals (Bolt et al. 2021). Various research teams have observed primates at this site for over 25 years (Bezanson 2009; Garber et al. 2010; Occhibove et al. 2015), and all mantled howler monkey

groups are habituated and do not react to observer presence (Bolt et al. 2019, 2020a, 2021; Schreier et al. 2021). We completed focal samples on individual monkeys and rotated focal subjects among adult males, adult females, and juveniles. Infants, who cannot feed and forage independently, were not sampled. Individuals from 1–5 different groups were sampled during each data collection day. Individuals were not sampled more than twice in 1 day, and samples of the same monkey were at least 2 h apart on the rare occasions of re-sampling (Bolt et al. 2021; Schreier et al. 2021). Although individual identities of monkeys were unknown in this population and some individuals were likely sampled multiple times over the study period, we avoided re-sampling of individuals on a daily basis by keeping track of individual sex, body size and tail characteristics within groups.

Howler monkey feeding behaviour and feeding tree data collection

We collected howler monkey feeding behaviour and feeding tree use data over 10 months from 2017–2020: May–August 2017, May–August 2018, December–January 2018–2019, June–August 2019, and December–January 2019–2020, with data collected daily between 500 and 1800 hours. While more data were collected during wet seasons (May–August) compared to dry seasons (December–January), trends for edge vs. interior feeding behaviour remained consistent across seasons. We used the point sampling method, using 30-minute focal animal sampling with instantaneous recordings on feeding and other behaviours repeated at 2-minute intervals (Altmann 1974; Russell 2018; Bolt et al. 2021; Schreier et al. 2021). Between one and six people collected behavioural data during each day of sampling, and data collectors worked independently and deliberately rotated between various areas of the forest in order to ensure sampling of different monkey groups and representation of all forest areas. Data collectors used transect lines spaced approximately 150 m apart (Bolt et al. 2018, 2020b; Russell 2018) as reference points for locating groups, but additionally sampled monkeys opportunistically when encountered.

We collected a total of 870 hours of behavioural data on individual focal animals, 410 hours in the forest interior and 460 hours in the forest edge. During focal sampling, we recorded any of the following actions as feeding: approach food, manipulate food with hands, feet, or mouth, chew, swallow, or move through environment while intermittently consuming or manipulating food items (Russell 2018). During feeding behaviour, we noted any plant parts consumed, with food items recorded as flower, fruit, leaf, or stem (woody or herbaceous plant components including leaf petiole and pulvinus that serve as leaf attachment structures) (Glander 1981; Baum 2005; Russell 2018; Bolt et al. 2021),

and identified whether monkeys consumed plant parts from trees or lianas. We assessed plant parts consumed in forest interior and anthropogenic edge by the number of feeding scans for each type of food item, with 2665 instantaneous recordings of plant parts. We also taxonomically identified the vegetation consumed by howler monkeys whenever possible through collecting leaf or fruit samples and/or photographing plant parts consumed by monkeys, using plant identification guides to identify feeding trees (Gentry 1993), and consulting botany experts when needed. Although we could not identify any liana families due to the poor visibility of high canopy vegetation, we identified feeding trees to family level when possible and additionally noted genus and species when they could be determined. Out of a total of 1447 howler monkey feeding trees, we identified 511 feeding trees to family level. We recorded the location of each 30-minute behavioural sample using a Garmin GPSMAP 62s handheld navigator in order to designate whether each sample was located in anthropogenic edge or forest interior. To assess inter-observer reliability, researchers simultaneously scored monkey behaviours during pilot data collection. We achieved a 94% reliability rate before the onset of data collection for this study (Bolt et al. 2021; Schreier et al. 2021).

During behavioural sampling, we additionally collected size data on howler monkey feeding trees. We considered trees that monkeys fed in for two or more consecutive 2-minute scans as feeding trees, and recorded tree locations using GPS. When feeding trees were accessible, we measured their circumference using a standard forestry reel tape and then calculated tree DBH, and measured tree height using a Nikon Forestry Pro laser rangefinder. We measured circumference for 908 trees out of 1447 feeding trees in total. Feeding tree height was only measured in May–August 2017 and May–August 2018 ($n = 102$ feeding trees out of 1447 feeding trees).

Statistical analyses

We used two-way Pearson chi-squared tests (Bolt et al. 2021) to compare whether the feeding tree families and plant parts consumed by howler monkeys showed different distributions than expected by chance across forest interior and edge zones, assuming an equal distribution of tree families and plant parts across forest zones (Russell 2018). As post hoc tests to determine which feeding tree families and plant parts were consumed at higher or lower values than expected by chance in forest interior and edge, we examined adjusted residuals and identified z scores greater than ± 1.97 as significantly different. We used Mann–Whitney U tests to compare mean howler monkey feeding tree DBH and height across forest interior and 100 m anthropogenic edge zones. We used SPSS version 26 (IBM SPSS Statistics, IBM Corporation,

Armonk, NY, USA) for all statistical tests, and adopted an alpha level of 0.05.

Results

Monkeys were observed feeding from both trees (99.3% of total food items consumed) and lianas (0.7% of total food items consumed) at LSBRS. Monkeys consumed different proportions of plant parts than expected based on chance when in forest interior vs. edge zones ($\chi^2(3)=11.18$, $n=2665$ plant parts, $p=0.011$, Table 1). The strength of association between variables was strong (Cramer's V test: $\phi c=0.065$, $p=0.011$), and post hoc examination of adjusted residuals indicated that when adjusted for sample size, monkeys consumed significantly more leaves than expected in the forest interior and fewer leaves than expected in the forest edge, while they consumed fewer stems than expected in the forest interior and more stems than expected in the forest edge ($z > \pm 1.97$, Table 1). Observed frequency of flowers and fruit consumed did not differ from expected values across forest zones ($z < \pm 1.97$, Table 1).

Of feeding trees that could be identified to family, genus, or species level (35.3% of total feeding trees), monkeys fed from trees from 11 different families (5 families in the forest interior and 11 families in the forest edge), at least 14 different genera, and 18 different species across the forest interior and edge at LSBRS (Table 2). Monkeys in the forest interior vs. anthropogenic edge zones consumed plant parts from significantly different tree families than expected based on a chance distribution of tree families across edge and interior at LSBRS ($\chi^2(10)=96.54$, $n=511$ feeding trees, $p < 0.001$, Table 3). The strength of association between variables was strong (Cramer's V test: $\phi c=0.44$, $p < 0.001$), and post hoc examination of adjusted residuals indicated that when adjusted for sample size, monkeys fed from the

tree families *Moraceae* and *Urticaceae* in the forest interior zone more often than expected by chance and less often than expected in forest edge ($z > \pm 1.97$, Table 3). Conversely, monkeys fed from the tree families *Lauraceae*, *Melastomaceae*, *Myristicaceae*, *Phyllanthaceae*, and *Rubiaceae* in the forest interior zone less often than expected by chance and more often than expected in the forest edge ($z > \pm 1.97$, Table 3). Observed frequency of feeding from other tree families, such as *Annonaceae*, *Fabaceae*, *Malvaceae*, and *Sapindaceae* did not differ from expected values across forest zones ($z < \pm 1.97$, Table 3).

We measured the circumference of 62.8% and the height of 7.0% of total feeding trees. Monkeys fed from trees with significantly larger mean DBH when in forest interior (81.1 cm, SD = 82.7, range = 340.6, $n=320$ feeding trees) compared to anthropogenic forest edge (60.8 cm, SD = 50.6, range = 353, $n=588$ feeding trees; Mann–Whitney U test: $U=82,161.5$, $z=-3.16$, $n=908$ feeding trees, $p=0.002$, Fig. 2). Similarly, monkeys fed from significantly taller trees in forest interior (19.0 m, SD = 4.9, range = 15.2, $n=54$ feeding trees) compared to anthropogenic edge (14.6 m, SD = 5.2, range = 16.6, $n=48$ feeding trees; Mann–Whitney U test: $U=649.5$, $z=-4.37$, $n=102$ feeding trees, $p < 0.001$, Fig. 3).

Discussion

In accordance with our predictions, mantled howler monkey feeding behaviour and tree use differed when in forest edge vs. interior at LSBRS. Howler monkeys ate more leaves than expected by chance when in forest interior (Table 1), likely due to the larger feeding trees found there and the likelihood that they have more leaves per tree (Chapman et al. 1992; LaRose 1996), allowing the monkeys to access a more abundant food source while minimizing their energetic expenditure on travel (Chapman 1988b). While leaves are generally considered a poorer-quality food source for mantled howler monkeys, young and mature leaves vary widely in nutritive quality, with young leaves containing more protein and fewer secondary plant metabolites that may irritate monkeys (Milton 1979; Glander 1981; di Fiore et al. 2011). Young leaves tend to be preferred by mantled howler monkeys along with flowers and fruit (LaRose 1996; Estrada et al. 1999; Baum 2005), so were likely consumed instead of mature leaves whenever available. Our study did not differentiate between young and mature leaves during data collection, which is a limitation, but previous study on the nutritive content in leaves at LSBRS found that mature leaves contained more sugars than young leaves as well as sufficient protein to sustain howler monkey metabolic needs and were therefore good sources of energy for mantled howler monkeys

Table 1 Mantled howler monkey (*Alouatta palliata*) plant parts consumed across forest zones at LSBRS showing percentages of plant parts consumed and z scores for adjusted residual values in interior and edge zones

Plant part	Interior forest zone plant parts consumed (z score)	Edge forest zone plant parts consumed (z score)
Flower	5.9% (−0.9)	6.8% (0.9)
Fruit	10.1% (−1.2)	11.5% (1.2)
Leaf	83.9% (2.0*)	80.8% (−2.0*)
Stem	0.1% (−2.9*)	0.9% (2.9*)

Asterisks on z scores show significant differences between zones (values $> \pm 1.97$). Negative z score results indicate that a plant part was consumed less than expected by chance, while positive z score results indicate that a plant part was consumed more than expected by chance

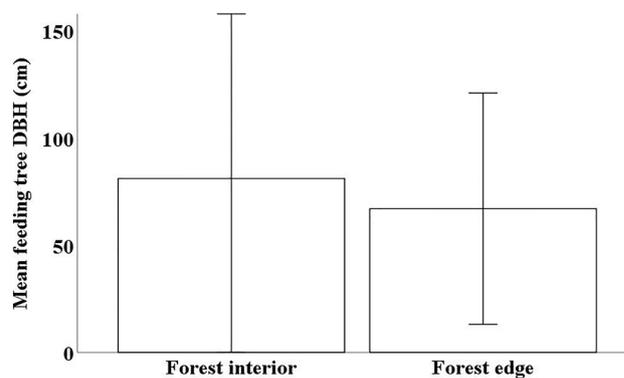
Table 2 Mantled howler monkey (*Alouatta palliata*) feeding tree families, genera, species, and plant parts consumed across forest zones at LSBRS

Feeding tree family	Feeding tree species	Plant parts consumed	Forest zone where feeding behaviour observed
<i>Annonaceae</i>	<i>Guatteria</i> spp.	Leaf	Edge
<i>Fabaceae</i>	<i>Dipteryx panamensis</i>	Leaf	Edge
<i>Fabaceae</i>	<i>Inga spectabilis</i>	Flower, leaf	Interior and edge
<i>Fabaceae</i>	<i>Pentaclethra maculoba</i>	Leaf	Interior and edge
<i>Lauraceae</i>	Unknown	Leaf	Edge
<i>Malvaceae</i>	<i>Apeiba membranacea</i>	Leaf	Interior and edge
<i>Malvaceae</i>	<i>Hampea appendiculata</i>	Leaf	Interior and edge
<i>Malvaceae</i>	<i>Luehea seemannii</i>	Leaf	Interior and edge
<i>Malvaceae</i>	Unknown	Leaf	Interior and edge
<i>Melastomaceae</i>	Unknown	Fruit, leaf	Edge
<i>Moraceae</i>	<i>Brosimum lactescens</i>	Leaf	Interior
<i>Moraceae</i>	<i>Ficus</i> spp.	Fruit, leaf	Interior and edge
<i>Moraceae</i>	<i>Ficus insipida</i>	Leaf	Interior and edge
<i>Moraceae</i>	<i>Ficus tonduzii</i>	Leaf	Interior and edge
<i>Moraceae</i>	<i>Miconia</i> spp.	Fruit, leaf	Edge
<i>Myristicaceae</i>	Unknown	Leaf	Interior
<i>Myristicaceae</i>	<i>Virola koschnyi</i>	Fruit, leaf	Interior and edge
<i>Myristicaceae</i>	<i>Virola sebifera</i>	Leaf	Interior and edge
<i>Phyllanthaceae</i>	<i>Hieronyma oblonga</i>	Leaf	Edge
<i>Rubiaceae</i>	<i>Palicourea guianensis</i>	Fruit	Edge
<i>Sapindaceae</i>	Unknown	Leaf	Edge
Unknown	Unknown	Flower, fruit, leaf, stem	Interior and edge
<i>Urticaceae</i>	<i>Cecropia insignis</i>	Fruit, leaf, stem	Interior and edge
<i>Urticaceae</i>	<i>Cecropia obtusifolia</i>	Leaf	Interior and edge

Table 3 Mantled howler monkey (*Alouatta palliata*) tree families consumed across forest zones at LSBRS showing percentages of trees consumed and z scores for adjusted residual values in interior and edge zones

Feeding tree family	Interior forest zone trees consumed (z score)	Edge forest zone trees consumed (z score)
<i>Annonaceae</i>	0% (-1.1)	0.4% (1.1)
<i>Fabaceae</i>	8.4% (0.9)	6.3% (-0.9)
<i>Lauraceae</i>	0% (-4.6*)	7.6% (4.6*)
<i>Malvaceae</i>	6.6% (1.0)	4.6% (-1.0)
<i>Melastomaceae</i>	0% (-4.9*)	8.4% (4.9*)
<i>Moraceae</i>	52.0% (2.8*)	39.5% (-2.8*)
<i>Myristicaceae</i>	2.2% (-2.9*)	7.6% (2.9*)
<i>Phyllanthaceae</i>	0% (-2.2*)	1.7% (2.2*)
<i>Rubiaceae</i>	0% (-4.6*)	7.6% (4.6*)
<i>Sapindaceae</i>	0% (-1.1)	0.4% (1.1)
<i>Urticaceae</i>	30.8% (3.9*)	15.9% (-3.9*)

Asterisks on z scores show significant differences between zones (values $> \pm 1.97$). Negative z score results indicate that a tree family was consumed less than expected by chance, while positive z score results indicate that a tree family was consumed more than expected by chance

**Fig. 2** Feeding tree DBH across forest zones at LSBRS. Bars indicate mean values and whiskers show one SD. Monkeys fed from significantly larger trees in forest interior ($p = 0.002$)

(Occhibove et al. 2015). Both young and mature leaves may therefore be preferred dietary resources at LSBRS.

Howler monkeys consumed stems more often in the forest edge than expected by chance (Table 1). As plant parts containing few nutrients and a large proportion of cellulose as well as weaponry like thorns (Milton 1980; Glander 1981;

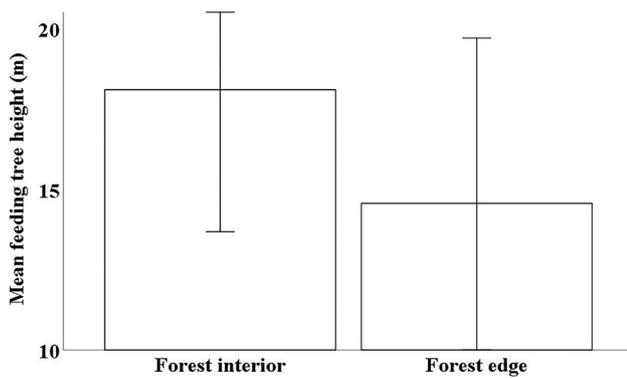


Fig. 3 Feeding tree height across forest zones at LSBRS. Bars indicate mean values and whiskers show one SD. Monkeys fed from significantly taller trees in forest interior ($p < 0.001$)

Baum 2005; Gotsch et al. 2015), stems are consumed at low rates in other tropical forest environments (Glander 1981; Muñoz et al. 2006) and are therefore likely to be howler monkey fallback foods (Marshall et al. 2009). With anthropogenic edge at LSBRS containing lower quality habitat for monkeys than forest interior (Bolt et al. 2018, 2019, 2020b), monkeys may increase stem consumption when in forest edge at LSBRS due to fewer feeding options in this forest zone. Other plant parts such as high-quality flowers and fruit (Glander 1981; Chapman et al. 1992; LaRose 1996) were consumed in the amount expected based on chance across forest zones, likely because high-quality plant parts were consumed wherever they were encountered, and these were equally found in both large and small trees in both habitat zones at LSBRS.

Monkeys at LSBRS also varied the tree families consumed across edge and interior forest zones. Despite greater tree species richness in forest interior compared to anthropogenic forest edge at LSBRS (Bolt et al. 2018, 2019, 2020b), of identified tree families, monkeys fed on trees from only 5 families in the forest interior and 11 families in the forest edge, and on different families than expected based on chance within each forest zone (Tables 2 and 3). In forest interior, howler monkeys consumed trees from the families *Moraceae* and *Urticaceae* more often than expected, although both families are well-represented throughout LSBRS (Russell 2018). The *Moraceae* and *Urticaceae* families were the taxa most often consumed by howler monkeys, with *Moraceae* comprising the largest percentage of food for howlers (Table 3). Both families contain well-known preferred howler monkey feeding tree genera such as *Ficus* spp. and *Cecropia* spp., which are two of the top genera that howler monkeys feed on throughout Central America (Milton 1980; Glander 1981; Estrada 1984; LaRose 1996; Kinzey 1997; Estrada et al. 1999) and are commonly consumed in both interior and edge zones at LSBRS (Russell

2018). At LSBRS, monkeys may feed more from *Moraceae* and *Urticaceae* feeding trees in forest interior due to the trees there being larger and containing more fruit and leaves (Chapman et al. 1992; LaRose 1996).

In the forest edge, howler monkeys fed from *Lauraceae*, *Melastomaceae*, *Myristicaceae*, *Phyllanthaceae*, and *Rubiaceae* families more often than expected by chance. Monkeys consumed these families for much smaller percentages of total feeding budgets than taxa like *Moraceae* and *Urticaceae* (Table 3), suggesting that howler monkeys are less reliant on these edge taxa and fed on them opportunistically as they travelled through lower-quality forest edge zones (Bolt et al. 2018, 2019, 2020b). At some sites, mantled howler monkeys were not observed feeding on any plants from these families (Muñoz et al. 2006) or consumed only very small amounts of *Lauraceae* (Estrada 1984; Estrada et al. 1999) or *Rubiaceae* (Glander 1981; LaRose 1996). Tellingly, although these five plant families were found across both forest interior and edge zones at LSBRS (Russell 2018), monkeys did not feed from four of them at all in the forest interior (only fed on *Myristicaceae* in both zones, Table 3), suggesting that these plant families are fallback feeding options in forest areas where preferred taxa are not available (Marshall et al. 2009). With monkeys at LSBRS also feeding from a greater number of plant families when in the forest edge—despite lower overall tree species richness (Bolt et al. 2018, 2019, 2020b)—they may compensate for the reduced availability of preferred foods in forest edges by diversifying their diet and feeding from a wider variety of tree taxa, as has been found for black howler monkeys (*Alouatta pigra*) in forest fragments (Silver and Marsh 2003). However, our results on plant families consumed should be regarded as preliminary due to the small proportion of feeding trees (35.3%) we were able to identify. Further work is needed to provide a more complete picture of the taxonomy of plant resources consumed by howler monkeys at LSBRS.

Finally, howler monkeys fed from larger, taller trees when in the forest interior compared to the forest edge (Figs. 2 and 3). Monkeys' use of larger feeding trees in the forest interior at LSBRS likely reflects both the larger overall tree size in the forest interior (Bolt et al. 2018, 2019, 2020b) and howler monkey preferences for large feeding trees (Chapman 1988b; LaRose 1996; Dunn et al. 2009). Large trees with ≥ 60 cm DBH are preferred by howler monkeys because they produce more food than smaller trees (Chapman et al. 1992; LaRose 1996; Dunn et al. 2009), enabling monkeys to feed in the same tree for longer spans of time. With mean feeding tree DBH at LSBRS > 60 cm in both edge and interior forest zones, our overall feeding tree results are comparable to those from investigations at other tropical sites spanning a range of vegetation types, including the dry forest at Santa Rosa National Park, Costa Rica (LaRose 1996) and

the lowland rainforest at Los Tuxtlas, Mexico (Dunn et al. 2009). As an energy-minimizing species (Milton 1980; di Fiore et al. 2011), mantled howler monkeys are adapted to limit energy expenditure by reducing travel. They may therefore prefer to spend disproportionately more time in specific large trees at LSBRS that contain bountiful and high-quality food resources, such as young leaves and fruit, as has been found at other research sites (Glander 1981; Estrada et al. 1999).

Howler monkey feeding ecology at LSBRS was also likely influenced by inter-specific interactions between sympatric primate species. White-faced capuchin and Central American spider monkeys are both known to outcompete mantled howler monkeys for access to preferred food resources like fruiting trees (Rose et al. 2003; Cristóbal-Azkarate et al. 2015), with howler monkeys typically losing access to larger trees (Arroyo-Rodríguez and Mandujano 2006; Cristóbal-Azkarate et al. 2015) and consuming fall-back foods such as eggs when in environments with poor-quality vegetation (Bicca-Marques et al. 2009), particularly in fragmented habitats. At LSBRS, while howler monkeys range more in the forest interior, capuchins range more in anthropogenic edge zones and spider monkeys range equally throughout the site (Bolt et al. 2020b). Howler monkeys therefore face feeding competition throughout LSBRS, but face the highest level of competition for large trees and preferred foods when in the anthropogenic edge. While we did not collect data on interspecific feeding interactions at LSBRS, we commonly observed howler monkeys fleeing feeding trees when capuchin or spider monkeys approached, lending credence to this idea (Schreier and Bolt, unpublished data). Howler monkey feeding behaviour at LSBRS was also likely impacted by a variety of other factors, including differences in biochemical properties between plant parts and families in the forest edge and interior (Ganzhorn 1995), and differences in predation pressure across forest zones (Bolt et al. 2019). These and other factors should be tested in future research.

Our results show that mantled howler monkeys modify their feeding behaviour when in forest areas adjacent to human-altered landscapes. While our study is limited due to the proportion of feeding trees we could measure and identify to species level and some of our results should therefore be regarded as preliminary, our data as presented are sufficient to demonstrate differences in feeding ecology across anthropogenic edge and interior forest zones at LSBRS. These changes to howler monkey feeding behaviour will become increasingly widespread as the deforestation of tropical forests throughout Central America continues (Garber et al. 2010; Haddad et al. 2015). Understanding how howler monkeys modify their diets when in anthropogenic edge regions is vital to informing continued conservation efforts on their behalf.

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Declarations

Ethical approval Our research met the legal requirements of Costa Rica and was conducted with the permission of the Molina family. Our research complied with the ethical standards in the treatment of animals corresponding with the guidelines laid down by the Primate Society of Japan, NIH (US), and EC, and our research protocol was approved by the Regis University Animal Care and Use Committee.

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