B R I L L

# River edge feeding: Howler monkey feeding ecology in a fragmented riparian forest

Laura M. Bolt[a,d,*], Dorian G. Russell[b,d] and Amy L. Schreier[c,d]

[a]Department of Anthropology, University of Toronto Mississauga, Mississauga, ON, L5L 1C6, Canada
[b]Department of Environmental Science, American University, Washington, DC 20016, USA
[c]Department of Biology, Regis University, Denver, CO 80221-1099, USA
[d]The Maderas Rainforest Conservancy, P.O. Box 55-7519, Miami, FL 33255-7519, USA
*Corresponding author; e-mail: laurabolt@gmail.com
ORCID iDs: Bolt: 0000-0002-8275-6543; Schreier: 0000-0002-0379-3750

**Abstract** – Rivers are important components of animal habitats worldwide. The area near riparian edge (⩽100 m from the river) has different abiotic characteristics and vegetation than both forest interior and areas bordering human development, which may lead to differences in animal feeding behaviour. To better contextualize the impact of human-caused habitat destruction on animal feeding ecology, it is important to study both natural riparian and anthropogenic forest edges within the same habitat. We compared howler monkey (*Alouatta palliata*) feeding behaviour and tree use across four forest zones (riparian edge, anthropogenic edge, forest interior, and combined riparian and anthropogenic edge) in a fragmented riparian rainforest in Costa Rica, La Suerte Biological Research Station (LSBRS). We predicted that monkey feeding behaviour and tree use would differ across forest zones, and especially between riparian and anthropogenic edges due to higher vegetation quality near the river. We observed individual focal monkeys for 30-minute periods, collecting data on monkey feeding behaviour and tree use every 2 minutes. We recorded plant parts eaten and feeding tree taxonomy, and measured feeding trees. Monkeys ate more leaves in riparian edge than in other forest zones, and fed from fewer tree families in riparian edge and forest interior compared to anthropogenic edge. Monkeys also fed from trees with smaller DBH in riparian edge compared to other forest zones, but trees of similar height to forest interior and taller than anthropogenic edge. Our results indicate that riparian zones are rich habitats for howler monkeys and conservation efforts should prioritize their preservation.

**Keywords** – *Alouatta palliata*, Costa Rica, habitat zone, plant family, platyrrhine conservation.

## Introduction

Rivers are natural freshwater channels that flow towards other bodies of water, such as lakes, oceans, and other rivers. When present in a landscape, a river impacts the abiotic and biotic characteristics of surrounding habitat (Otani *et al*., 2020). For example, when a forest adjoins a river, the 50-100 m area of adjacent forest habitat typically has more soil moisture and less wind than areas of forest located further (i.e., greater than 100 m) from the same river (Grebner *et al*., 2013). The habitat area surrounding a river thus represents a naturally occurring transition zone between land-scape types, and can be termed a riparian edge zone (Cadenasso *et al*., 2003). While transitional (i.e., edge) zones between habitat types occur naturally, transition zones between landscapes may also be human-caused (Saunders *et al*., 1991). When edge zones are anthropogenic in origin, such as when a patch of forest is clearcut and the remaining forest fragment verges on a highway, more sudden transitions of abiotic elements are typically present than in natural edge zones (Cadenasso *et al*., 2003). These abrupt edges usually detrimentally affect plants and animals that are adapted to forest interior, leading to lower biomass in anthro-

pogenic edges as well as less preferred food available for some animal species (Estrada *et al.*, 1999; Arroyo-Rodríguez and Mandujano, 2006).

The differences in abiotic factors across various types of edge zones have profound effects on the biota found there. Riparian zones within forests typically include more water-tolerant vegetation with greater biodiversity than other types of edge zones (Grebner *et al.*, 2013). Increased sunlight due to canopy gaps at the river's edge mean that gap-specialist species are more successful than shade-adapted species, and these gap specialist trees tend to produce a larger number of leaves per tree as well as leaves with greater protein and water content than shade-adapted vegetation (Ganzhorn, 1995; Murcia, 1995). These leaf characteristics impact the animal species that range there, and many folivores find adequate nutrition in the leaves found in riparian zones despite the greater tree mortality and lower plant biomass compared to forest interior regions (Estrada *et al.*, 1999; Arroyo-Rodríguez and Mandujano, 2006). Animals may also favour riparian edge zones as general habitat zones within disturbed forest landscapes, since even in areas of heavy anthropogenic disturbance, vegetation is often left undisturbed along the water's edge (Lees and Peres, 2008) and can serve as a corridor between disparate forest fragments (Payne and Bryant, 1998). Understanding how animals feed in riparian zones is important, given both the prevalence of rivers in biodiverse landscapes and the ongoing anthropogenic destruction of habitats worldwide, particularly in areas of high species richness (Haddad *et al.*, 2015). Studying the differential effects of natural riparian and anthropogenic edges on animal feeding behaviour within the same landscape can increase understanding of the impact of anthropogenic edges, and can inform conservation strategy for fragmented habitats (Murcia, 1995).

Many primate species are large-bodied mammals that live and feed in riparian zones worldwide, particularly in the tropics (Otani *et al.*, 2020). They are also severely impacted by anthropogenic landscape destruction, with the majority of primate species currently threatened with extinction due to habitat loss (Mittermeier *et al.*, 2012; Estrada *et al.*, 2017). As indicator species (Mace and Balmford, 2000) with diverse diets who live in both riparian and anthropogenic edges, primates make ideal subjects for investigating how different types of edge zone impact feeding behaviour. Previous investigations have shown that primate dietary adaptations impact the relative amounts of time they spend in edge vs. interior regions of forests (Lidicker, 1999; Skrinyer, 2016; Russell, 2018; Bolt *et al.*, 2018, 2020b, 2021a). Folivorous species, for example, are often edge-tolerant (e.g., colobus monkey [*Procolobus rufomitratis*], Mbora and Meikle, 2004; sportive lemur [*Lepilemur microdon*], Lehman *et al.*, 2006; Guianan red howler monkey [*Alouatta macconelli*], Lenz *et al.*, 2014), likely due to the greater level of solar energy in edges producing leaves with higher protein concentrations and feeding trees producing more leaves (Ganzhorn, 1995). This study investigates the feeding ecology of a group-living folivorous-frugivorous primate species, the mantled howler monkey (*Alouatta palliata*), across different edge zones of a fragmented forest at La Suerte Biological Research Station (LSBRS) in Costa Rica.

Vegetation characteristics differ across forest zones at LSBRS, with greater tree species richness, canopy cover, and mean tree diameter at breast height (DBH) in riparian edge compared to anthropogenic edge, and similar tree species richness and canopy cover but smaller tree DBH in riparian edge compared to forest interior (Bolt *et al.*, 2020a, b). These findings indicate that habitat quality for monkeys varies across forest zones at LSBRS, with tree abundance and size positively correlated with primate abundance (Mbora and Meikle, 2004) and greater levels of canopy cover indicating higher-quality primate habitat (Arroyo-Rodríguez and Mandujano, 2006). Based on these findings, we predicted that howler monkeys would consume more leaves and fewer flowers, fruits, and stems when feeding in the high-quality riparian zone at LSBRS compared to both low-quality anthropogenic edge and high-quality interior zones, due to the greater amount of leaves per tree

as well as more preferred, protein-rich leaves available in riparian edge compared to anthropogenic edge (Ganzhorn, 1995). Due to the "leaf flush" found in forest edges compared to interior (Murcia, 1995), we also predicted that howler monkeys would consume more leaves in riparian edge compared to forest interior. Following patterns of overall differences in tree species richness between zones (Bolt *et al.*, 2020a, b), we further predicted that monkeys would feed from a greater number of tree families in riparian edge compared to anthropogenic edge and a similar number of tree families in riparian edge and forest interior. Finally, we predicted that monkeys would feed from larger, taller trees in riparian edge compared to anthropogenic edge, and from shorter, smaller trees in riparian edge compared to forest interior, mirroring the overall tree size trends present at LSBRS (Bolt *et al.*, 2020a, b).

## Methods

### STUDY SITE

This study was undertaken at La Suerte Biological Research Station (LSBRS), a 3 km$^2$ tropical rainforest in northeastern Costa Rica that has been fragmented by anthropogenic disturbance, with agricultural fields, cattle pastures, and roads surrounding the site (Brandt and Singleton, 2018; Bolt *et al.*, 2021c; Schreier *et al.*, 2022). Barbed wire fences at the property line of the LSBRS forest fragment create marked boundaries between forested and adjacent deforested areas, and the La Suerte river runs northward through the site (Molina, 2015). In line with previous research at LSBRS, we defined forest edge as extending 100 m from any natural or anthropogenic boundary, including barbed wire fence and river's edge (Bolt *et al.*, 2020b). We divided the forest at LSBRS into four different zones for analysis: riparian forest edge (within 100 m of the La Suerte River), anthropogenic forest edge (within 100 m of deforested areas, including roads, cattle pasture, agriculture, and camp within LSBRS), forest interior (more than 100 m from any type of forest edge), and combined riparian and anthropogenic forest edge (i.e., combined edge; within

100 m of both the river and anthropogenically deforested area; Bolt *et al.*, 2020b). The LSBRS site is home to three monkey species: mantled howler (*Alouatta palliata*), white-faced capuchin (*Cebus imitator*), and Central American spider monkeys (*Ateles geoffroyi*).

### *Study subjects*

We collected data on mantled howler monkey feeding behaviour and tree use from 11 social groups across riparian edge, anthropogenic edge, forest interior, and combined edge zones at LSBRS. All groups are habituated and have been the focus of behavioural investigation since the 1990's (Garber *et al.*, 2010; Schreier *et al.*, 2021). Groups have overlapping ranges, and each group moves throughout the four forest zones surveyed at LSBRS (Bolt *et al.*, 2019; Bolt *et al.*, in press). Due to changes in group membership between sampling seasons, individuals and groups could not be consistently identified across seasons, but we have routinely observed 11 groups during sampling since 2017 (mean group size = 13.1 individuals, range = 5-21 individuals; Bolt *et al.*, in press).

### DATA COLLECTION

We collected howler monkey feeding behaviour and feeding tree use data during five sampling seasons spanning ten months across both wet and dry seasons: May-August 2017, May-August 2018, December-January 2018-2019, June-August 2019, and December-January 2019-2020. We collected data between 500 and 1800 hours daily, using 30-min focal animal sampling and taking instantaneous recordings each 2 mins to document feeding behaviour and tree use (Altmann, 1974; Russell, 2018; Bolt *et al.*, 2021a, b; Schreier *et al.*, 2021). We recorded the location of each 30-min behavioural sample using a Garmin GPSMAP 62s hand-held navigator in order to determine the habitat zone that each sample was located in: riparian edge, anthropogenic edge, forest interior, or combined edge. We completed focal samples on individual monkeys of all age and sex classes with the exception of infants. Individuals were sampled a maximum of twice daily, with samples separated by at least two hours when re-sampled

(Bolt *et al*., 2021a, b; Schreier *et al*., 2021). Although we could not consistently determine the identity of individual monkeys across sampling seasons, we prevented over-sampling of individuals on a daily basis by keeping track of individual characteristics including body size, sex, colouration, and other notable traits within groups (Bolt *et al*., 2021a, b; Schreier *et al*., 2021).

We collected a total of 870 hours of behavioural data on individual focal animals: 221 hours in riparian edge, 245 hours in anthropogenic edge, 128 hours in forest interior, and 276 hours in combined edge. During focal sampling, any of the following actions were scored 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; Bolt *et al*., 2021a, b). During feeding behaviour, we identified the plant parts consumed (i.e., flower, fruit, leaf, or stem; Russell, 2018; Bolt *et al*., 2021a), and noted whether monkeys fed from trees or lianas. We assessed plant parts consumed across forest zones by the number of feeding scans for each type of food item, out of a total of 2622 instantaneous recordings of plant parts. We also taxonomically identified the vegetation consumed by howler monkeys whenever possible, and identified feeding trees to family level (Bolt *et al*., 2021a). No liana families could be identified due to poor visibility of the high canopy at LSBRS (Bolt *et al*., 2021a). We identified 599 feeding trees to family level out of 1447 howler monkey feeding trees in total. To assess inter-observer reliability, data collectors simultaneously scored monkey behaviours and achieved a 94% reliability rate prior to collecting data during each sampling season of this study (Bolt *et al*., 2021a, b; Schreier *et al*., 2021).

During focal sampling, we concurrently collected size data on howler monkey feeding trees and noted tree locations using GPS. Trees that monkeys fed in for a minimum of two 2 min instantaneous recordings during behavioural sampling were defined as feeding trees. We measured feeding tree circumference with a standard forestry reel tape before calculating tree DBH, and feeding tree height using a Nikon Forestry Pro laser rangefinder. Due to accessibility limitations, we measured circumference for 905 out of 1447 feeding trees. Data on feeding tree height were only collected during two sampling seasons, and we measured feeding tree height for 156 out of 1447 feeding trees.

## Statistical Analyses

To determine whether differences in plant parts and feeding tree families eaten by howler monkeys showed different distributions than expected by chance across the four forest zones (riparian edge, anthropogenic edge, forest interior, and combined edge), we used Pearson chi-squared tests (Bolt *et al*., 2020a, 2021a, b). We eliminated duplicate trees and duplicate plant part data points from specific trees in order to ensure that tree and plant part data were independent (Kramer and Schmidhammer, 1992). As post-hoc tests to determine which plant parts and feeding tree families were consumed in different proportions than expected across forest zones, we examined adjusted residuals and identified those with z-scores greater than ±1.97 as indicating significant differences. We used Kruskal-Wallis *H* tests to determine differences in mean feeding tree DBH and height across the four forest zones at LSBRS. For significant values, we performed pairwise asymptotic (2-sided) post-hoc tests with significance adjusted by the Bonferroni correction for multiple tests to determine which forest zones differed in howler monkey feeding tree DBH and height. 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

Howler monkeys fed from both trees (>99% of feeding) and lianas (<1% of feeding) at LSBRS. Monkeys consumed different proportions of plant parts than expected based on chance when in riparian edge, anthropogenic edge, forest interior, and combined edge zones ($x^2(9) = 105.6$, n = 2622 plant parts, p > 0.001, table 1). The strength of association

**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 riparian edge, anthropogenic edge, forest interior, and combined edge zones. Asterisks on z-scores show significant differences between zones (z > ±1.97). A negative z-score indicates that a plant was consumed less than expected by chance, while a positive z-score indicates that a plant was consumed more often than expected by chance.

| Forest zone | Flower | Fruit | Leaf | Stem |
|---|---|---|---|---|
| Riparian edge plant part consumed (z score) | 2.3% (−4.5*) | 9.6% (−1.0) | 87.5% (3.8*) | 0.6% (−0.8) |
| Anthropogenic edge plant part consumed (z score) | 9.8% (5.9*) | 11.9% (1.4) | 76.2% (−5.9*) | 2.1% (4.7*) |
| Forest interior plant part consumed (z score) | 6.4% (0.5) | 18.3% (4.9*) | 75% (−4.0*) | 0.3% (−1.2) |
| Combined edge plant part consumed (z score) | 4.4% (−2.0*) | 7.0% (−4.1*) | 88.6% (5.3*) | 0% (−3.1*) |

between variables was strong (Cramer's V test: $\varphi c = 0.116$, p > 0.001), and post-hoc examination of adjusted residuals indicated that when adjusted for sample size, monkeys consumed significantly more leaves and fewer flowers than expected in riparian edge, more flowers and stems and fewer leaves than expected in anthropogenic edge, more fruit and fewer leaves than expected in forest interior, and more leaves, fewer flowers, fewer fruit, and fewer stems than expected in combined forest edge (z > ±1.97, table 1). Other observed values for plant parts consumed did not differ from those expected by chance distribution across forest zones (z < ±1.97, table 1).

Across forest zones, howler monkeys fed from trees from 11 different families (6 families in riparian edge, 10 families in anthropogenic edge, 5 families in forest interior, and 7 families in combined edge) across forest zones at LSBRS (table 2). Monkeys across forest zones consumed plant parts from significantly different tree families than expected based on a chance distribution of tree families across riparian edge, anthropogenic edge, forest interior, and combined edge at LSBRS ($x^2(30) = 197.8$, n = 599 feeding trees, p < 0.001, table 2). The strength of association between variables was strong (Cramer's V test: $\varphi c = 0.33$, p < 0.001), and post-hoc examination of adjusted residuals indicated that when adjusted for sample size, monkeys in riparian edge fed from the tree family Moraceae more often than expected

by chance, while feeding on the tree families Lauraceae, Malvaceae, Rubiaceae, and Uriticaceae less often than expected (z > ±1.97, table 2). In anthropogenic edge, monkeys fed from the tree families Lauraceae and Rubiaceae more often than expected, and the tree family Moraceae less often than expected (z > ±1.97, table 2). In forest interior, monkeys fed from the tree family Melastomaceae more often than expected, while feeding on the tree families Lauraceae, Myristicaceae and Rubiaceae less often than expected (z > ±1.97, table 2). In combined edge, monkeys fed from the tree families Myristicaceae, Phyllanthaceae, and Uriticaceae more often than expected, and the tree families Lauraceae, Moraceae, and Rubiaceae less often than expected (z > ±1.97, table 2). Other observed feeding tree families, such as Annonaceae, Fabaceae and Sapindaceae, did not differ from expected values across forest zones (z < ±1.97, table 2).

Howler monkeys used feeding trees with significantly different DBH across riparian, anthropogenic, interior, and combined forest zones (Kruskal-Wallis H3 = 46.1, p < 0.001, n = 905 feeding trees; fig. 1). Monkeys fed from trees with significantly smaller DBH at riparian edge (mean DBH = 55.9 cm, SD = 55.2, range = 3.5-356.7 cm, n = 240 trees) compared to anthropogenic edge (mean DBH = 57.6 cm, SD = 40.1, range = 7.0-348.4 cm, n = 323 trees), forest interior (mean DBH = 116.8 cm, SD = 107.9 cm, range = 4.8-345.5 cm, n =

**Table 2.** Mantled howler monkey (*Alouatta palliata*) feeding tree families consumed across forest zones at LSBRS showing percentages of trees consumed and z-scores for adjusted residual values in riparian edge, forest interior, combined edge, and anthropogenic edge zones. Asterisks on z-scores show significant differences between zones (z > ±1.97). A negative z-score indicates that a tree family was consumed less than expected by chance, while a positive z-score indicates that a tree family was consumed more often than expected by chance.

| Feeding tree family | Riparian edge forest zone trees consumed (z-score) | Anthropogenic edge zone trees consumed (z-score) | Forest interior zone trees consumed (z-score) | Combined edge zone trees consumed (z-score) |
|---|---|---|---|---|
| Annonaceae | 0% (−0.8) | 0.9% (1.9) | 0% (−0.7) | 0% (−0.7) |
| Fabaceae | 6.0% (−1.2) | 9.3% (0.7) | 12.6% (1.9) | 5.1% (−1.4) |
| Lauraceae | 0% (−2.5*) | 8.5% (5.8*) | 0% (−2.1*) | 0% (−2.1*) |
| Malvaceae | 2.7% (−2.3*) | 9.3% (1.8) | 9.3% (1.2) | 5.1% (−0.8) |
| Melastomaceae | 3.4% (0.0) | 1.9% (−1.5) | 8.4% (3.4*) | 0.9% (−1.7) |
| Moraceae | 62.4% (7.2*) | 25.2% (−4.7*) | 42.0% (1.1) | 24.8% (−3.2*) |
| Myristicaceae | 3.4% (−1.3) | 4.2% (−1.0) | 0% (−2.9*) | 16.2% (5.7*) |
| Phyllanthaceae | 0% (−1.3) | 0% (−1.7) | 0% (−1.1) | 4.3% (4.6*) |
| Rubiaceae | 0% (−2.5*) | 8.4% (5.8*) | 0% (−2.1*) | 0% (−2.1*) |
| Sapindaceae | 0% (−0.6) | 0.5% (1.3) | 0% (−0.5) | 0% (−0.5) |
| Uriticaceae | 22.1% (−2.7*) | 31.8% (0.4) | 27.7% (−0.8) | 43.6% (3.3*) |
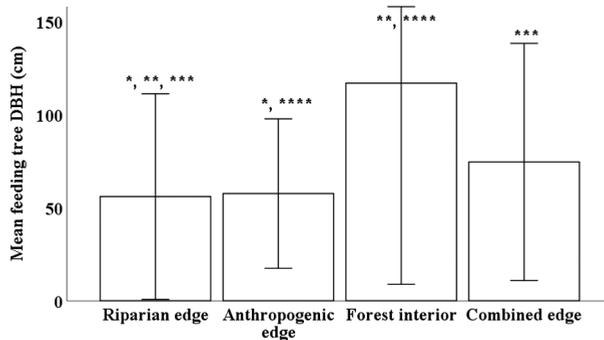


**Figure 1.** Mantled howler monkey (*Alouatta palliata*) feeding tree DBH across forest zones at LSBRS (p < 0.001). Bars indicate mean values and whiskers indicate one SD. Similar asterisks indicate paired differences between forest zones (riparian edge vs. anthropogenic edge, p = 0.013; riparian edge vs. forest interior, p < 0.001; riparian edge vs. combined edge, p < 0.001; anthropogenic edge vs. forest interior, p < 0.001). Monkeys fed from significantly smaller trees in riparian edge compared to other forest zones.

97 trees), and combined edge (mean DBH = 74.5 cm, SD = 63.7, range = 8.3-318.5 cm, n = 245 trees; fig. 1). Monkeys also fed from trees with significantly smaller DBH in anthropogenic edge compared to forest interior (fig. 1). However, monkeys did not feed from trees with different DBH when anthropogenic edge and combined edge, or when forest interior and combined edge were compared (fig. 1).

Howler monkeys also fed from trees with significantly different heights across riparian, anthropogenic, interior, and combined edge forest zones (Kruskal-Wallis H3 = 61.3, p < 0.001, n = 156 feeding trees; fig. 2). Monkeys fed from significantly taller trees at river edge (mean height = 18.7 m, SD = 4.4, range = 7.2-26.4 m, n = 51 trees), forest interior (mean height = 18.8 m, SD = 0, range = 18.8-18.8 m, n = 9 trees), and combined edge (mean height = 20.1 m, SD = 5.8, range = 11.8-27 m, n = 49) compared to anthropogenic edge (mean height = 12.3 m, SD = 3.05, range = 9.8-19.2 m, n = 47 trees; fig. 2). However, monkeys
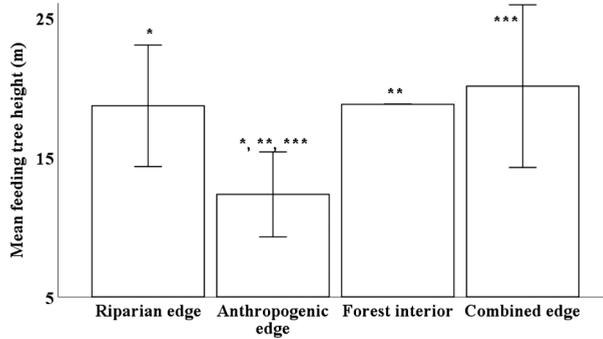
**Figure 2.** Mantled howler monkey (*Alouatta palliata*) feeding tree height across forest zones at LSBRS (p < 0.001). Bars indicate mean values and whiskers indicate one SD. Similar asterisks indicate paired differences between forest zones (riparian edge vs. anthropogenic edge, p < 0.001; anthropogenic edge vs. forest interior, p < 0.001; anthropogenic edge vs. combined edge, p < 0.001). Monkeys fed from significantly shorter trees in anthropogenic edge compared to all other forest zones.

did not feed from trees with significantly different heights when river edge and forest interior, river edge and combined edge, or forest interior and combined edge were compared (fig. 2).

## Discussion

Our results indicate that mantled howler monkeys consumed different plant parts and tree families in feeding trees of varying DBH and height in riparian edge zones compared to other forest zones at LSBRS. As predicted, mantled howler monkeys ate more leaves and fewer flowers than expected based on chance when in the riparian edge zone (table 1). Similarly, monkeys consumed more leaves than expected in the combined edge zone. Leaf consumption results are likely due to the greater availability of young, protein-and-water-rich leaves at water's edge, with canopy gaps allowing more solar energy to reach trees, and riparian proximity leading to extra water content in leaves in both riparian and combined edge zones at LSBRS (Ganzhorn, 1995; Matsuda *et al.*, 2019). In addition to leaves, monkeys are likely to consume rich foods like flowers and fruit when available (LaRose, 1996; Baum, 2005), suggesting that the riparian zone at LSBRS contains fewer tree species with edible flowers than other forest areas, while containing the expected amount of fruit trees. Howler monkeys also consumed stems in the proportion expected in riparian edge at LSBRS. As nutrient-poor fallback foods, stems tend to be eaten at low rates when other food options are present (Baum, 2005; Marshall *et al.*, 2009). Their consumption in expected proportion suggests that the riparian edge at LSBRS may not be as rich a feeding area as previously suggested (Bolt *et al.*, 2020b), with monkeys needing to rely on at least some low-quality foods to supplement other available food items.

Mantled howler monkeys also fed from different tree families across forest zones. While our prediction that monkeys in riparian edge would feed from a similar number of tree families as forest interior was supported, contrary to predictions, monkeys in riparian edge fed from fewer tree families compared to anthropogenic edge. Monkeys may feed from fewer tree families in riparian edge and interior due to a greater abundance of preferred feeding taxa in these zones, with monkeys preferentially feeding from these families when available (Glander, 1981; LaRose, 1996). Mantled howler monkeys are selective about plant taxa consumed, and fed from only 15 families in a species-rich rainforest in Mexico (Estrada, 1984). Our results suggest that the monkeys at LSBRS may be similarly selective, particularly in more species-rich riparian edge and interior zones (Bolt *et al.*, 2020b).

Across forest zones at LSBRS, monkeys fed from the plant families Moraceae and Uriticaceae the most frequently (table 2), which is consistent with findings from other rainforest sites (Estrada, 1984). At LSBRS, monkeys fed from Moraceae more often than expected in riparian edge and less often than expected in anthropogenic and combined edge (table 2), while feeding from Uriticaceae more often than expected in combined edge and less often than expected in riparian edge (table 2), likely attesting to differences in availability of these preferred tree families across habitat zones at LSBRS. The Moraceae family contains widely consumed feeding genera like *Ficus* spp., while the Uriticaceae family contains the similarly-desirable *Cecropia* spp.; both are favoured food for howler monkeys throughout the Neotropics (LaRose, 1996; Estrada *et al*., 1999; Muñoz *et al*., 2006), and are found throughout LSBRS (Russell, 2018).

Across forest zones at LSBRS, the third most frequently consumed tree family was Fabaceae (table 2). The Fabaceae family contains the fallback feeding tree species *Pentaclethra macroloba*, which is ubiquitous throughout the largely secondary-growth, degraded LSBRS site, and was the main Fabaceae species consumed across forest zones during this study (Bolt *et al*., 2021a; Schreier and Bolt, unpubl, data). Lambert (1998) suggested that *P. macroloba*, which is rarely consumed at other sites (Stoner, 1996), is a back-up food for mantled howler monkeys at LSBRS during times when they lack more compelling food options, particularly during the dry season in December-January, which our data collection period encompassed. It is notable that the mantled howler monkeys in our study consumed a fair amount of *P. macroloba* leaves in riparian edge (Schreier and Bolt, unpubl. data), suggesting that, like with stem consumption, monkeys near the LSBRS river do rely on sub-standard dietary resources to some degree despite being in a generally rich vegetation zone (Bolt *et al*., 2020a, b).

Mantled howler monkey feeding behaviour was also likely influenced by feeding tree size. Contrary to predictions, monkeys fed from tall trees with the smallest DBH in riparian edge compared to other forest zones (figs. 1 and 2). Howler monkey feeding tree selection thus did not reflect the overall vegetation structure in riparian edge, with trees taller and larger than in anthropogenic edge but shorter and smaller than forest interior (Bolt *et al*., 2020b). Riparian edge feeding trees may have had the smallest DBH of all forest zones due to factors such as preferred taxa being gap specialists that grow tall but narrow near the river, or differences in biochemical properties of plant parts from various tree families in different locations (Ganzhorn, 1995). Our results may also reflect a sampling limitation, since we could not access and were unable to measure some feeding trees growing on the steep incline at water's edge. In addition to feeding tree DBH being smaller at riparian edge than all other habitat zones, we found that feeding tree DBH was smaller in anthropogenic edge compared to forest interior, supporting previous findings at LSBRS (Bolt *et al*., 2021a) and mirroring overall vegetation characteristics at the site (Bolt *et al*., 2020b). However, it is important to note that while mantled howler monkeys prefer large feeding trees with DBH $\geqslant 60$ cm (Chapman *et al*., 1992; LaRose, 1996; Dunn *et al*., 2009), such as those found in forest interior at LSBRS (Bolt *et al*., 2021a), feeding trees across all forest zones at LSBRS approached or exceeded this value (fig. 1). General trends for large feeding tree preference in mantled howler monkeys were therefore still seen across LSBRS, despite these zonal differences in feeding tree size.

Our results have implications for the role of riparian edge zones within mantled howler monkey conservation initiatives. Despite our sample size being small for some variables, our results demonstrated differences in mantled howler monkey feeding ecology across various edge and interior habitat zones at LSBRS. Howler monkeys at LSBRS spend more time ranging in riparian zones than in other forest areas (Bolt *et al*., 2020b), and while there, they feed on more leaves and more trees from the Moraceae family than in other forest zones. Monkeys in riparian edge also feed from tall trees with similar DBH compared to feeding

trees from other sites (Dunn *et al*., 2009), suggesting that within riparian zones, large trees from the Moraceae family should be prioritized for preservation and Moraceae trees should be selected for replanting during reforestation efforts near rivers. When howler monkey feeding behaviour was compared across riparian and anthropogenic edges at LSBRS, plant parts and tree families consumed and feeding tree characteristics clearly differed across natural and human-caused forest edges, with natural riparian edges generally representing higher-quality feeding habitats. Creation of new anthropogenic edges should therefore be minimized and the vegetation in riparian edges preserved in the interest of mantled howler monkey conservation. By protecting Neotropical riparian zones with special focus on the vegetation that is key to mantled howler monkey feeding ecology, the abundance of mantled howler monkey populations can be perpetuated for future generations.

## Acknowledgements

## Statement of ethics

All applicable institutional and/or national guidelines for the care and use of animals were followed. This study was approved by the Regis University Animal Care and Use Committee (IACUC permit #17-006) and conducted with the permission of the Molina family in accordance with the legal requirements of Costa Rica.

## Disclosure statement

The authors have no conflict of interest to declare.

## Funding sources

## Author contributions

LMB, DGR, and ALS originally formulated the idea, developed methodology, collected data, analysed data, and wrote the manuscript.

## References

Altmann J (1974). Observational study of behavior: sampling methods. *Behaviour* 49: 227–265. DOI: 10.1163/156853974X00534.

Arroyo-Rodríguez V, Mandujano S (2006). Forest fragmentation modifies habitat quality for *Alouatta palliata*. *International Journal of Primatology* 27: 1079–1096. DOI: 10.1007/s10764-006-9061-0.

Baum J (2005). Foraging behaviors of *Alouatta palliata*, mantled howling monkeys. *Nebraska Anthropologist* 1: 129–140.

Bolt L, Schreier A, Voss K, Sheehan E, Barrickman N, Pryor N, Barton M (2018). The influence of anthropogenic edge effects on primate populations and their habitat in a fragmented rainforest in Costa Rica. *Primates* 59: 301–311. DOI: 10.1007/s10329-018-0652-0.

Bolt L, Schreier A, Russell D, Jacobson Z, Merrigan-Johnson C, Barton M, Coggeshall E (2019). Howling on the edge: mantled howler monkey (*Alouatta palliata*) howling behaviour and anthropogenic edge effects in a fragmented tropical rainforest in Costa Rica. *Ethology* 125: 593–602. DOI: 10.1111/eth.12886.

Bolt L, Russell D, Coggeshall E, Jacobson Z, Merrigan-Johnson C, Schreier A (2020a). Howling by the river: howler monkey (*Alouatta palliata*) communication in an anthropogenically-altered riparian forest in Costa Rica. *Behaviour* 157: 77–100. DOI: 10.1163/1568539X-00003582.

Bolt L, Schreier A, Voss K, Sheehan E, Barrickman N (2020b). Down by the riverside: riparian edge effects on three monkey species in a fragmented Costa Rican forest. *Biotropica* 52: 541–553. DOI: 10.1111/btp.12769.

Bolt L, Russell D, Schreier A (2021a). Anthropogenic edges impact howler monkey (*Alouatta palliata*) feeding behaviour in a Costa Rican rainforest. *Primates* 62: 647–657. DOI: 10.1007/s10329-021-00904-y.

Bolt L, Cavanaugh M, Schreier AL (2021b). Lone males: solitary and group-living male mantled howler monkey behavioural ecology in a Costa Rican rainforest. *American Journal of Biological Anthropology* 174: 201–212. DOI: 10.1002/ajpa.24152.

Bolt L, Brandt L, Molina R, Schreier A (2021c). Maderas rainforest conservancy: a one health approach to conservation. *American Journal of Primatology* 84: e23293. DOI: 10.1002/ajp.23293.

Bolt L, Hadley C, Schreier A (in press). Crowded in a fragment: High population density of mantled howler monkeys (*Alouatta palliata*) in an anthropogenically-disturbed Costa Rican rainforest. *Primate Conservation*.

Brandt L, Singleton M (2018). Record of Baird's tapir *Tapirus bardii* at the La Suerte Biological Field Station in the caribbean lowlands of Costa Rica. *PeerJ* 6: e27128v1. DOI: 10.7287/peerj.preprints.27128v1.

Cadenasso M, Pickett S, Weathers K, Jones C (2003). A framework for a theory of ecological boundaries. *BioScience* 53: 750–758. DOI: 10.1641/0006-3568(2003)053[0750:AFFATO]2.0.CO;2.

Chapman C, Chapman L, Wrangham R, Hunt K, Gebo D, Gardner L (1992). Estimators of fruit abundance of tropical trees. *Biotropica* 24: 527–531. DOI: 10.2307/2389015.

Dunn J, Cristóbal-Azkarate J, Vea J (2009). Differences in diet and activity patterns between groups of *Alouatta palliata* associated with the availability of big trees and fruit of top food taxa. *American Journal of Primatology* 71: 654–662. DOI: 10.1002/ajp.20700.

Estrada A (1984). Resource use by howler monkeys in the rain forest of Los Tuxtlas, Veracruz, Mexico. *International Journal of Primatology* 5: 105–131. DOI: 10.1007/BF02735736.

Estrada A, Anzures A, Coates-Estrada R (1999). Tropical rain forest fragmentation, howler monkeys (*Alouatta palliata*), and dung beetles at Los Tuxtlas, Mexico. *American Journal of Primatology* 48: 253–262. DOI: 10.1002/(SICI)1098-2345(1999)48:4<253::AID-AJP1>3.0.CO;2-D.

Estrada A, Garber P, Rylands A, Roos C, Fernandez-Duque E, Di Fiore A, *et al.* (2017). Impending extinction crisis of the world's primates: why primates matter. *Science Advances* 3: e1600946. DOI: 10.1126/sciadv.1600946.

Ganzhorn J (1995). Low-level forest disturbance effects on primary production, leaf chemistry, and lemur populations. *Ecology* 76: 2084–2096. DOI: 10.2307/1941683.

Garber P, Molina A, Molina R (2010). Putting the community back in community ecology and education: the role of field schools and private reserves in the ethical training of primatologists. *American Journal of Primatology* 72: 785–793. DOI: 10.1002/ajp.20837.

Glander K (1981). Feeding patterns in mantled howling monkeys. In *Foraging Behavior: Ecological, Ethological, and Psychological Approaches* (Kamil K, Sargent K, eds.), pp. 231–259. New York, Garland Press.

Grebner D, Bettinger P, Siry J (2013). *Introduction to Forestry and Natural Resources*. New York, Academic Press.

Haddad N, Brudwig L, Clobert J, Davies K, Gonzalez A, Holt R, *et al.* (2015). Habitat fragmentation and its lasting impact on Earth's ecosystems. *Science Advances* 1: e1500052. DOI: 10.1126/sciadv.1500052.

Kramer M, Schmidhammer J (1992). The chi-squared statistic in ethology: use and misuse. *Animal Behaviour* 44: 833–841.

Lambert J (1998). Secondary metabolites in *Pentaclethra macroloba*: a dominant canopy species fed on by mantled howling monkeys (*Alouatta palliata*) in northeastern Costa Rica. *Brenesia* 49/50: 103–108.

LaRose F (1996). Foraging strategies, group sizes and food competition in the mantled howling monkey, *Alouatta palliata*. PhD dissertation, Department of Anthropology, University of Alberta, Edmonton, Alberta, Canada.

Lees A, Peres C (2008). Conservation value of remnant riparian forest corridors of varying quality for Amazonian birds and mammals. *Conservation Biology* 22: 439–449. DOI: 10.1111/j.1523-1739.2007.00870.x.

Lehman S, Rajaonson A, Day S (2006). Edge effects and their influence on lemur density and distribution in southeast Madagascar. *American Journal of Biological Anthropology* 129: 232–241. DOI: 10.1002/ajpa.20241.

Lenz B, Jack K, Spironello W (2014). Edge effects in the primate community of the biological dynamics of Forest Fragments Project, Amazonas, Brazil. *American Journal of Biological Anthropology* 155: 436–446. DOI: 10.1002/ajpa.22590.

Lidicker W (1999). Responses of mammals to habitat edges: an overview. *Landscape Ecology* 14: 333–343. DOI: 10.1023/A:1008056817939.

Mace G, Balmford A (2000). Patterns and processes in contemporary mammalian extinction. In *Future Priorities for the Conservation of Mammalian Diversity* (Entwhistle A, Dunstone N, eds.), pp. 27–52. Cambridge, Cambridge University Press.

Marshall A, Boyko C, Feilen K, Boyko R, Leighton M (2009). Defining fallback foods and assessing their importance in primate ecology and evolution. *American Journal of Biological Anthropology* 140: 603–614. DOI: 10.1002/ajpa.21082.

Matsuda I, Nababayashi M, Otani Y, Wai Y, Tuuga A, Wong A, Bernard H, Wich S, Kubo T (2019). Comparison of plant diversity and phenology of riverine and mangrove forests with those of the dryland forest in Sabah, Borneo, Malaysia. In *Primates in Flooded Habitats* (Nowak K, Barnett AA, Matsuda I, eds.), pp. 15–28. Cambridge, Cambridge University Press.

Mbora D, Meikle D (2004). Forest fragmentation and the distribution, abundance and conservation of the Tana River red colobus (*Procolobus rufomitratus*). *Biological Conservation* 118: 67–77. DOI: 10.1016/j.biocon.2003.07.009.

Mittermeier R, Schwitzer C, Rylands A, Taylor L, Chiozza F, Williamson E, Wallis J (2012). Primates in peril: the world's 25 most endangered primates 2012-2014. IUCN/SSC Primate Specialist Group (PSG), International Primatological Society (IPS), Conservation International (CI), Bristol Conservation and Science Foundation, Bristol, pp. 1–40.

Molina R (2015). A brief history of the Molina family, and the birth of the Maderas Rainforest Conservancy at the La Suerte and Ometepe Field Stations – a narrative. In *Central American Biodiversity: Conservation, Ecology and a Sustainable Future* (Huettman F, ed.), pp. 199–214. New York, Springer Science + Business Media.

Muñoz D, Estrada A, Naranjo E, Ochoa S (2006). Foraging ecology of howler monkeys in a cacao (*Theobroma cacao*) plantation in Comalcalco, Mexico. *American Journal of Primatology* 68: 127–142. DOI: 10.1002/ajp.20211.

Murcia C (1995). Edge effects in fragmented forests: implications for conservation. *Trends in Ecology & Evolution* 10: 58–62. DOI: 10.1016/S0169-5347(00)88977-6.

Otani Y, Bernard H, Wong A, Tangah J, Tuuga A, Hanya G, Matsuda I (2020). Factors influencing riverine utilization patterns in two sympatric macaques. *Scientific Reports* 10: 15749. DOI: 10.1038/s41598-020-72606-2.

Payne N, Bryant F (1998). *Wildlife Habitat Management of Forest Lands, Rangelands, and Farmlands*. Krieger Publishing Co.

Russell D (2018). The influence of edge effects on mantled howler monkey (*Alouatta palliata*) food resource use and availability in a fragmented forest. Master thesis, Department of Environmental Science, American University, Washington, DC, USA.

Saunders D, Hobbs R, Margules C (1991). Biological consequences of ecosystem fragmentation: a review. *Conservation Biology* 5: 18–32. DOI: 10.1111/j.1523-1739.1991.tb00384.x.

Schreier A, Bolt L, Russell D, Jacobson Z, Readyhough T, Merrigan-Johnson C, Coggeshall E (2021). Mantled howler monkeys (*Alouatta palliata*) in a Costa Rican forest fragment do not modify activity budgets or spatial cohesion in response to anthropogenic edges. *Folia Primatologica* 92: 49–57. DOI: 10.1159/000511974.

Schreier A, Voss K, Bolt L (2022). A mathematical modelling approach to functionally defining forest edge and its utility for primate behavioural edge effects. *International Journal of Primatology* 43: 460–479. DOI: 10.1007/s10764-022-00289-9.

Skrinyer A (2016). Living on the edge: an assessment of habitat disturbance and primate use on the Osa Peninsula, Costa Rica. Master thesis, Department of Anthropology, Kent State University, Kent, Ohio, USA.

Stoner K (1996). Habitat selection and seasonal patterns of activity and foraging in mantled howling monkeys (*Alouatta palliata*) in northeastern Costa Rica. *International Journal of Primatology* 17: 1–30. DOI: 10.1007/BF02696156.