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Mantled Howler Monkey (*Alouatta palliata*) Demographic Structure in a Continuous Forest Compared to a Small Forest Fragment in Costa Rica

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Abstract: In the face of widespread habitat destruction and forest fragmentation, it is critical to understand primate demography to assess population viability across populations inhabiting continuous forests and fragmented landscapes. While mantled howler monkeys (*Alouatta palliata*) have traditionally been considered resilient to habitat destruction, their populations are declining and are now rated "Vulnerable" on the IUCN Red List of Threatened Species. In this study, we assessed the demography of the mantled howler monkey population at La Selva Research Station, a protected forest in northeastern Costa Rica—providing the first systematic study of population structure in 30 years. In 2022, we conducted a howler census to ascertain the number of groups at La Selva and recorded group size and composition for a subset of the groups. We then compared population density, group size and composition with a population in a nearby protected forest (La Suerte Biological Research Station, LSBRS) to help assess the viability of mantled howlers in a small forest fragment. The mantled howler population at La Selva has grown substantially since 1992 with, at the time of the survey, 25 groups and a population density of 23.4 individuals/km². Mean group size was 14.3 with a sex ratio of 1:2.2 and immature to adult ratio of 0.7—in line with mantled howler monkey populations throughout the species' range. The population density at La Selva was, however, almost five times lower than the forest fragment at LSBRS, although group size and composition did not differ across sites. Overall, our results highlight the importance of forest protection for mantled howler monkeys.
Keywords: population density, forest fragmentation, La Selva Research Station, La Suerte Biological Research Station, primate census, protected areas

Resumen: Ante la destrucción generalizada del hábitat y la fragmentación de los bosques, es fundamental comprender la demografía de los primates para evaluar la viabilidad de la población en las poblaciones que habitan bosques y continuos y paisajes fragmentados. Si bien los monos aulladores (*Alouatta palliata*) se han considerado tradicionalmente resistentes a la destrucción del hábitat, sus poblaciones están disminuyendo actualmente y ahora están clasificados como "vulnerables" en la Lista Roja de la UICN. En este estudio, evaluamos la demografía de la población de monos aulladores en la Estación de Investigación La Selva, un bosque protegido en el noreste de Costa Rica, proporcionando el primer estudio sistemático de la estructura de la población en 30 años. En 2022, realizamos un censo de aulladores para determinar la cantidad de grupos en La Selva y registramos el tamaño y la composición de los grupos para un subconjunto de los grupos. Luego comparamos la densidad de población, el tamaño de los grupos y la composición con un fragmento de bosque protegido cercano (Estación de Investigación Biológica La Suerte, LSBRS) para ayudar a evaluar la viabilidad de los aulladores en un pequeño fragmento de bosque. La población de aulladores en La Selva ha crecido sustancialmente desde 1992, con 25 grupos y una densidad de población de 23.4 individuos/km². El tamaño medio del grupo fue de 14.3 con una proporción de sexos de 1:2.2 y una proporción de inmaduros a adultos de 0.7, en línea con las poblaciones de monos aulladores en toda su área de distribución. La densidad de población en La Selva fue casi cinco veces menor que el fragmento de bosque en LSBRS, aunque el tamaño y la composición de los grupos no varió entre los sitios. Nuestros resultados destacan la importancia de la protección del bosque para los monos aulladores de manto.
Palabras clave: densidad poblacional, fragmentación del bosque, Estación Científica La Selva, Estación Científica Biológica La Suerte, censo de primates, áreas protegidas

Introduction

It is increasingly critical to understand primate demography in order to assess population viability (Lawler 2011; Klass *et al.* 2020a), especially in the face of widespread habitat destruction and forest fragmentation (Haddad *et al.* 2015). In Costa Rica, for example, forest fragmentation has increased over the past few decades largely due to conversion to banana and pineapple plantations (Garber *et al*. 2010). This habitat fragmentation greatly impacts wildlife, constituting a major cause of declining primate populations worldwide (Arroyo-Rodríguez and Dias 2010; Estrada *et al*. 2017). To ascertain whether primate populations are sustainable in forest fragments, it is essential to compare the demographic structure of primates living in forest fragments with those inhabiting continuous forests.

Research demonstrates an inverse relationship between habitat size and population density, with higher population densities typical in forest fragments compared to continuous forests across a variety of primate species (e.g., *Propithecus diadema*: Irwin 2007; *Alouatta palliata*: Arroyo-Rodríguez and Dias 2010; *Alouatta pigra*: Klass *et al.* 2020a). High density populations in forest fragments likely experience heightened feeding competition with a concomitant increase in stress, compared to those in larger, continuous forests (Arroyo-Rodríguez and Dias 2010; Chaves *et al.* 2011), which might impact a variety of population parameters including group size, sex ratio, and ratio of immatures to adult females (Richard *et al.* 2002; Gilbert 2003; Cristobal-Azkarate *et al.* 2005). In Brazil, for example, bearded saki (*Chiropotes satanas chiropotes*: now *C. sagulatus*) group size was directly related to fragment size, with the largest groups in continuous forest and the lowest group sizes in the smallest fragments (Boyle and Smith 2010). Klass *et al.* (2020b) reported that there were significantly fewer adult males in black howler monkey groups inhabiting forest fragments compared to a large, protected forest in Mexico.

Mantled howler monkeys are well-studied primates that range throughout Central America and northern South America (Di Fiore *et al.* 2011; Melin *et al.* 2020). They are folivore-frugivores (Aristizibal *et al.* 2017; Righini *et al.* 2017) that selectively feed in tall trees and prefer fruit and young leaves when they are available (Chapman 1988; Bolt *et al.* 2021a, 2023). Mantled howlers are known for their long calls ("howls"), which have a loud, deep roaring sound and are produced predominantly by adult males (Altmann 1959). They typically live in multimale-multifemale groups of ~10–15 individuals (Bezanson *et al.* 2008; Ryan *et al.* 2008; Di Fiore *et al.* 2011), and both males and females disperse from their natal groups (Glander 1992). Mantled howler monkey population density generally ranges from 15–30 individuals/km² (Di Fiore *et al.* 2011). For example, population density at Los Tuxtlas, Mexico, was 23.3 individuals/km² (Estrada, 1982), while in La Pacifica, Costa Rica, population density was 30 individuals/km² (Clarke *et al*. 2002).

As a result of their generalist diets and energy-minimizing lifestyles (Estrada *et al.* 1999; Schreier *et al.* 2021, 2022a), mantled howler monkeys can live in a wide range of habitats, from old growth forest to disturbed environments (Estrada 2015; Garber and Kowalewski 2015), and have thus been considered resilient to anthropogenic habitat change (e.g., Garber *et al*. 2006; McKinney *et al*. 2015). Some studies indicate, however, that howler monkeys are indeed susceptible to habitat destruction (Arroyo-Rodríguez and Dias 2010). In fact, mantled howler monkey populations are declining and they are now rated as "Vulnerable" on the IUCN Red List of Threatened Species (Cortés-Ortíz *et al.* 2021). It is thus crucial to document mantled howler demography at long-term study sites in forests of various sizes to provide a baseline from which to monitor population structure over time (Bolt *et al.* 2022b), and to compare populations inhabiting fragmented landscapes to those in larger forests to better understand the monkeys' ability to withstand habitat alteration.

We (L.M.B. and A.L.S.) recently reported an exceptionally high population density of the mantled howler monkey population in the study area at La Suerte Biological Research Station (LSBRS), a small forest fragment (3 km²) in northeastern Costa Rica (Bolt *et al.* 2022b). LSBRS is one of increasingly few protected forested areas in a region of Costa Rica that has been largely deforested since the 1970s, due mainly to cattle ranching and large-scale banana and pineapple production (Garber *et al*. 2010; Molina 2015). LSBRS is surrounded by cattle pasture and coconut plantations, forming distinct borders with the protected forest (Molina 2015). While the population density of 109.5 individuals/km² is the highest reported for this species to date (Bolt *et al.* 2022b), the mean group size of 13.1 is typical of mantled howlers (Bezanson *et al.* 2008; Di Fiore *et al.* 2011), suggesting that they may be effectively mitigating feeding competition in the face of an elevated density of individuals. However, the immature to adult female ratio (IFR) of 0.5 signifies a declining replacement rate. Heltne *et al.*'s (1975) model posits that an IFR greater than 1.5 is required for mantled howler populations to remain stable without immigration, which suggests the LSBRS population may not be sustainable based on birth rate alone at its current density.

To help assess the viability of the LSBRS population, in this study we examined the demography of the mantled howler monkey population at La Selva Research Station, a large forest in the same region of Costa Rica as LSBRS. While only 90 km apart and harboring a similar flora and fauna, La Selva is five times the size of LSBRS and forms a continuous forest with Braulio Carrillo National Park. This study marks the first demographic evaluation of the La Selva howler population in thirty years. In 1992, Stoner (1994) conducted a howler census that indicated 15 mantled howler monkey groups at La Selva. She also recorded detailed group size and composition data for seven groups in 1990, and reported a mean group size of 11, resulting in a population density of 7–15 individuals/km² (Stoner 1994). This is

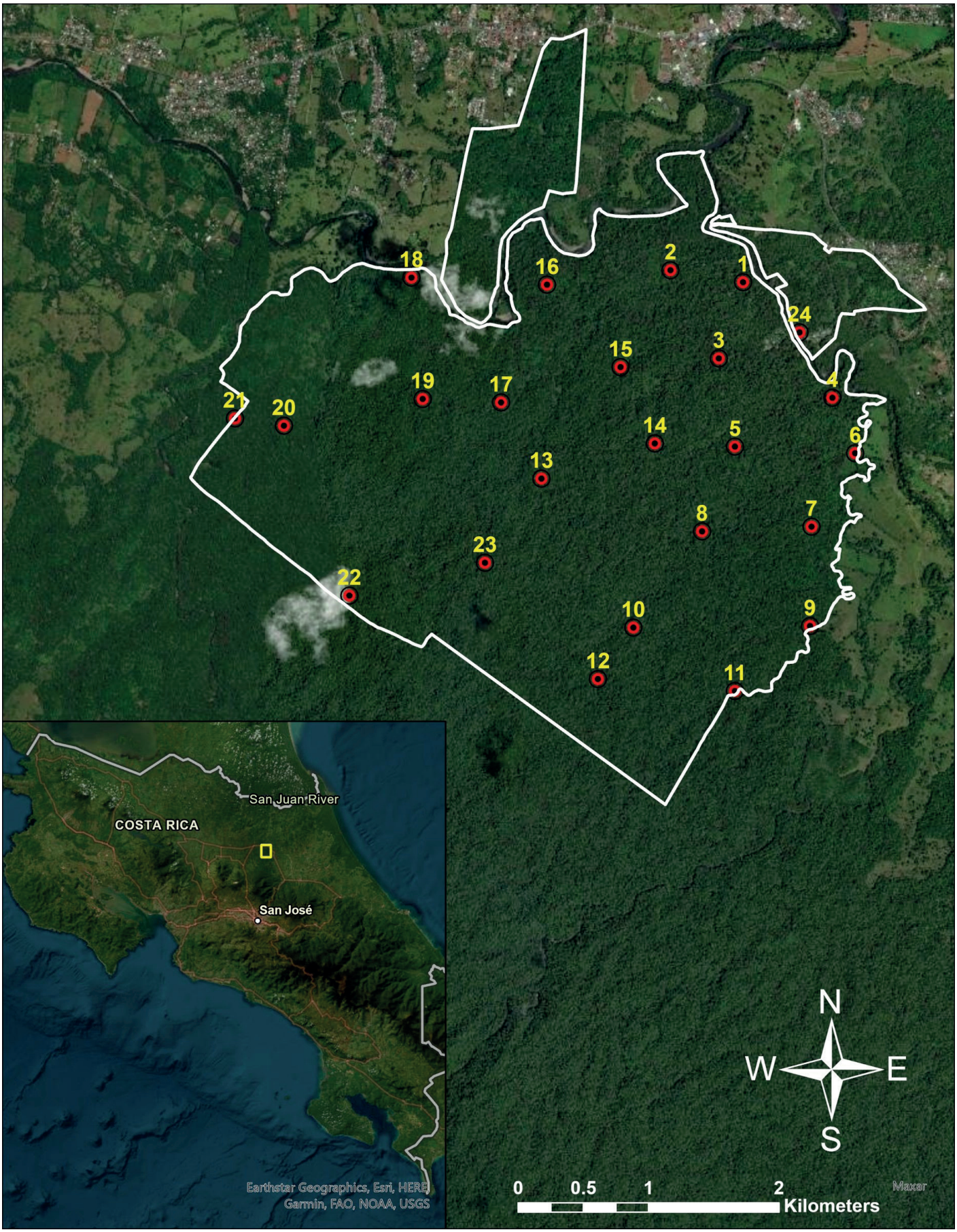

Figure 1. La Selva Research Station in Heredia Province, Costa Rica. Solid white lines indicate the La Selva property line; red circles show the locations of the 24 howler census observation sites.

at the low end of typical population densities for this species (Di Fiore *et al.* 2011), which may reflect a slow rebound from the yellow fever epidemic in the 1950s that decimated primate populations in Central America (Fishkind and Sussman 1987; Stoner 1994).

The goals of this paper are twofold: 1) to provide updated mantled howler monkey demographic data for La Selva Research Station, and 2) to compare howler demography between a continuous forest (La Selva) and a small forest fragment (LSBRS) in the same region of Costa Rica. In May 2022, we (C.E.J., M.D.W., and A.L.S.) carried out a population census at La Selva following the same methods as Stoner (1994) to ascertain if and how howler monkey demography had changed over the past thirty years. We (A.L.S.) also assessed group size and composition for a sample of the howler groups at La Selva. We expected the population to have increased in size given the time elapsed since the yellow fever outbreak.

Furthermore, we predicted that population density would be higher at LSBRS than La Selva based on studies demonstrating an inverse relationship between forest size and population density (e.g., Irwin 2007; Arroyo-Rodríguez and Dias 2010; Klass *et al.* 2020b). We also predicted that group size would differ across LSBRS and La Selva, although research is inconsistent, with some studies showing a direct association between group size and population density (Fedigan *et al.* 1998) and others suggesting that group size is lower in smaller areas (Gilbert 2003; Ewers and Didham 2006). Finally, we predicted a higher ratio of immatures to adult females (IFR) at La Selva compared to LSBRS. We predicted this due to the low IFR found at LSBRS coupled with the widespread deforestation in the areas surrounding the forest fragment, which likely limits dispersal opportunities for females which would consequently reduce the ratio of immatures to adult females (Bolt *et al.* 2022b).

Methods

Study site and study population

La Selva Research Station (10°26'N, 83°59'W), operated by the Organization for Tropical Studies, is located in northeastern Costa Rica where the ríos Sarapiquí and Puerto Viejo converge (McDade and Hartshorn 1994). La Selva, 15.4 km², comprises tropical wet forest (primary and secondary), pastures, areas managed for research and education (succession plots, arboretum), and research station infrastructure (laboratories and cabins) (Matlock and Hartshorn 1999). While most of La Selva's forest lies within the natural boundaries of the rivers (McDade and Hartshorn 1994), agricultural development and villages border the rivers and their tributaries on the northern, eastern, and western edges. The southern border of La Selva is adjacent and connected to Braulio Carrillo National Park which consists of ~440 km² of cloud and tropical rainforest (Bell and Donnelly 2006). The size of La Selva and the fact that it is continuous with a larger national park makes it ideal for comparing howler demography with the small forest fragment at LSBRS.

Three species of primates inhabit La Selva: mantled howler monkeys (*Alouatta palliata*), white-faced capuchins (*Cebus imitator*), and Geoffroy's spider monkeys (*Ateles geoffroyi*). The mantled howler monkey population has been systematically surveyed only once before, in 1992 (Stoner 1994). At that time, there were 15 groups of howlers at La Selva and mean group size was 11, resulting in a population density of 7–15 individuals/km². The sex ratio was 1:1.2 and the IFR was 0.9.

Demography data collection

We determined the number of mantled howler monkey groups inhabiting La Selva by conducting a howler census on 29 May 2022. Following the methods employed by Stoner (1994), we (A.L.S., C.E.J, M.D.W) along with 42 volunteers (students, researchers, and local community members) sampled howler long calls (howls) across 24 sites throughout the La Selva forest, with two data collectors stationed at each site from 4:00–7:00 (Fig. 1). We used the same site locations as Stoner (1994), although in a few cases we had to shift slightly given current forest conditions. Upon hearing howls, data collectors recorded: 1) the time the howl was heard, 2) the direction angle (in degrees) from the origin of the howl, and 3) the distance from the origin of the howl using three distance categories: close (0–50 m), near (50–1000 m), and far (1000+ m) (Johnson *et al.* accepted; Stoner 1994). Data collectors were trained in the days preceding the census.

In May–June 2022, A.L.S. collected group demography data for about a third of the La Selva howler monkey groups. The large size of La Selva and limited personnel precluded us from sampling all groups. For similar reasons, Stoner (1994) also conducted her population census throughout La Selva and then sampled seven of the groups; she calculated population density by multiplying the number of groups generated from the census by the mean group size of the groups she sampled, divided by the total size of the reserve. As part of a larger study examining monkey behavioral ecology across forest fragments and larger, continuous forests (Bolt *et al.* 2018, 2019, 2020a, 2020b, 2021a, 2021b, 2022a, 2022b, 2023; Bolt and Schreier 2022; Schreier *et al.* 2021, 2022a, 2022b), we collected howler monkey group demographic data between 6:00 and 17:00. Researchers located howler groups in the morning based on their vocalizations, known location the previous day, or opportunistically, and stayed with the group for as long as possible. We recorded the number of adult males, adult females, juveniles, infants, and unidentified adults during each sampling day and, to ensure accurate demographic data, we repeated our counts throughout the day, especially when the group traveled single-file across a trail. While we could not identify all individuals across groups, we distinguished groups from one another based on distinctive characteristics of group members (e.g., unique coloration patterns), location, and

demographic information (e.g., number of infants in the group) (Bolt *et al.* 2022b). To further ensure that we examined data from distinct groups, we only included in our analyses demographic data from groups that we followed for at least several consecutive days, and where we had multiple opportunities to record accurate group size and composition. This resulted in demographic data for eight howler monkey groups.

Data analysis

To analyze the howler census data, we visualized the recorded howling location data using ArcGIS Pro 3.0 and conducted a point cluster analysis using the angle and distance category data. Using a cluster distance of 50 m, a group was identified by a cluster characterized by at least two calls heard by different volunteer pairs (Johnson *et al.* accepted). We calculated mean group size and SD by averaging group sizes of the eight howler groups for which we had accurate group composition data. Following Stoner (1994), we calculated the population density by multiplying the number of groups resulting from the howler census by the mean group size, and dividing that by the total size of La Selva.

We calculated the male:female sex ratio by dividing the mean number of adult females across groups by the mean number of adult males. Similarly, we calculated the immature to adult female ratio (IFR) by dividing the mean number of infants plus juveniles by the mean number of adult females (Zucker and Clarke 2003). To compare howler demography at La Selva in 2022 to that from 1990, we used the dataset from May–June 2022 and compared it to group composition data from June–July 1990 as reported in Table 2 in Stoner (1994). To compare current demography at La Selva to that at LSBRS, we used our La Selva dataset from May–June 2022 and the LSBRS group size and composition data from December 2021 – January 2022 reported in Table 2 in Bolt *et al.* (2022b). We used Mann-Whitney U tests to compare mean group size and mean number of adult females, males, juveniles, and infants across the La Selva datasets as well as between La Selva and LSBRS. We used SPSS version 26 for these analyses (IBM SPSS Statistics, IBM Corporation, Armonk, NY, USA) and statistical significance was set at $p < 0.05$.

Results

The point cluster analysis generated 27 distinct clusters, indicating 27 howler monkey groups at La Selva. Our data suggest that a couple of the howler groups may inhabit forest just over the La Selva border in Braulio Carrillo National Park, and we therefore conservatively report that there are 25 howler monkey groups within the La Selva forest. Mean group size at La Selva was 14.3 (±4.3) with a range of 9–21 (Tables 1 and 2). The howler monkey population density was therefore 23.4 individuals/km².

The mean number of adult males per group at La Selva was 3.0 (±1.2) with a range of 1–5, while the mean number of adult females was 6.5 (±2.5) ranging from 4–11 (Table 1). The adult male:female sex ratio was 1:2.2. The mean number of juveniles at La Selva was 2.4 (±1.6) ranging from 1–6, and the mean number of infants was 1.9 (±1.1) with a range of 0–3 (Table 2). The immature to adult female ratio (IFR) was 0.7 (Table 2).

There were 10 more groups at La Selva in 2022 than in 1992 (25 groups in 2022 vs. 15 groups in 1992), leading to higher population density in 2022 compared to 1992 (23.4 individuals/km² in 2022 vs. 7–15 individuals/km²; Stoner 1994). While mean group size was higher in 2022 compared to 1990 (10.9 ±3.5), this difference was not statistically significant (Table 2). There were significantly more adult females per group in 2022 compared to 1990 (4.0 ±1.0; $U = 8.0$; $p = 0.02$), but the mean number of adult males, juveniles, and infants did not differ significantly (Table 2). Consequently, the sex ratio was much lower in 1990 (1:1.2) than 2022 (1:2.2), while the IFR was higher in 1990 (0.9) than in 2022 (0.7).

With respect to demography across the LSBRS forest fragment and the larger forest at La Selva, the population density at LSBRS of 109.5 individuals/km² was almost five times that at La Selva. The sex ratio was the same across sites, while the IFR was higher at La Selva (Table 2). Mean group size and mean number of adult males, adult females, juveniles, and infants did not differ significantly across sites (Table 2).

Discussion

Overall, our results demonstrate that, as expected, the mantled howler monkey population density at La Selva has increased since 1992. Furthermore, in 2022 the population density at LSBRS was substantially higher than at La Selva. Most measures of group size and composition, however, were similar across thirty years at La Selva and between La Selva and LSBRS at the present time.

The howler population density at La Selva is now almost twice as high as it was thirty years ago, and it now falls within the species' typical range. The density of 23.4 individuals/km² is the same as in Los Tuxtlas, Mexico (Estrada 1999) and similar to the stable population at La Pacifica, Costa Rica (Clarke *et al.* 2002). Bigger groups often accompany higher population density (Fedigan *et al.* 1998), which is what has occurred at La Selva. The mean group size of 10.9 monkeys in 1990 is on the lower end of usual mantled howler monkey group sizes of ~10–15 individuals, while 14.3 is on the higher end (Di Fiore *et al.* 2011). The fact that both the population density and mean group size are currently typical for the species suggests that the howler population has effectively rebounded from a population dip following the past yellow fever epidemic and is currently thriving.

The population density at La Selva is almost five times lower than the population density at LSBRS. The population density at LSBRS, however, has been quite high for almost

Table 1. Mantled howler monkey group composition at La Selva Research Station in May-June 2022.

Group identification number	Total group size	No. of adult males	No. of adult females	No. of juveniles	No, of infants	No. of unknown adults
1	21	5	11	2	3	0
2	10	2	4	1	3	0
3	11	3	5	2	1	0
4	9	1	4	2	2	0
5	12	3	7	1	0	1
6	16	3	6	3	1	3
7	17	3	6	6	2	0
8	18	4	9	2	3	0

Table 2. Summary of mantled howler monkey group demography at La Selva Research Station and LSBRS.

Study site	Sampling season	No. of groups sampled	No. of one-male groups	No. of multi-male groups	Adult male to female ratio	Immature to adult female ratio (IFR)	Mean group size (± SD)	Pop. density No. of monkeys/km²
La Selva Research Station	May-June 2022	8	1	7	1:2.2	0.7	14.25 (4.3)	23.4
*La Selva Research Station	June-July 1990 July 1992	7	1	6	1:1.2	0.9	10.86 (3.5)	7-15
**LSBRS	Dec 2021 to Jan 2022	11	2	9	1:2.2	0.5	13.1 (4.7)	109.5

*Demography data reported in Table 2 of Stoner (1994)

**Demography data reported in Tables 1 and 2 of Bolt et al. (2022)

25 years. In 1999, the population density was 73.7 individuals/km² (Pruetz and Leasor 2002) and it remained relatively stable through 2018 (Bolt *et al.* 2022b). Since then, density increased rapidly to 94.1 individuals/km² in January 2020 and further to 109.5 individuals/km² in January 2022 (Bolt *et al.* 2022b). This upsurge occurred just after additional nearby forest was cleared for cattle pasture and pineapple plantations (Molina pers. comm.), which likely prompted monkeys from surrounding regions to migrate into the LSBRS forest (Bolt *et al.* 2022b). It remains to be seen how this recently elevated density will impact the population.

Given the considerable difference in population density across La Selva and LSBRS, we would expect mean group size to differ as well. However, there was no difference in mean group size, with current group sizes at both sites typical of mantled howler monkeys across their range (Bezanson *et al.* 2008; Di Fiore *et al.* 2011). It is important to note that group size prior to 2022 at LSBRS was lower than typical, with mean group size less than 10 in 1999 (Pruetz and Leasor 2002) and from 2017–2019 (Bolt *et al.* 2022b), which likely helped to reduce feeding competition (Chapman *et al.* 1995; Dias and Rodríguez-Luna 2006; Bolt *et al.* 2021a, 2023). It is possible that the monkeys have not been able to maintain low group sizes since the population density increase since 2019. While mantled howler monkey groups are generally spatially cohesive (Milton 1980; Crockett and Eisenberg 1987), in a few populations groups are known to separate into subgroups (Leighton and Leighton 1982; Chapman 1989), including at LSBRS (Bezanson *et al.* 2008; Schreier *et al.* 2021). We have not yet observed such group fissioning at La Selva (Schreier unpubl. data), although further research is needed to confirm this. Splitting into subgroups at LSBRS, therefore, may be sufficient for reducing feeding competition, allowing them to live in similar sized groups as at La Selva.

With respect to group composition at La Selva, there were significantly more adult females per group in 2022 compared to 1990, while the mean number of males stayed the same, resulting in a sex ratio that was twice as high in 2022. The 1:1.2 sex ratio from 1990 is one of the lowest ever reported for this species, whereas 1:2.2 in 2022 is within the typical range for mantled howler monkeys (Di Fiore *et al.* 2011). Elsewhere in Costa Rica, for example, Clarke *et al.* (2022) recorded three females for every male at La Pacifica in 1998, and Fedigan *et al.* (1998) recorded almost twice as many females as males in groups at Santa

Rosa National Park in Costa Rica in each year from 1983–1992. In 1986, the Organization for Tropical Studies (OTS) acquired the southernmost area of the property, which connected its forest to Braulio Carrillo National Park, allowing secondary growth and connectivity to increase since then (Schelhas and Sánchez-Azofeifa 2006). From 1987 to 1994, two years after Stoner (1994) conducted the census, areas southwest and north of the property were owned by OTS and protected, which further expanded the property and increased connectivity with the national park, thus increasing dispersal opportunities (McDade and Hartshorn 1994). The population growth at La Selva can be attributed to a rise in the number of adult females which may have occurred via increased dispersal from females from the bordering national park.

Across several species of howler monkeys, researchers have reported fewer adult males per group in forest fragments compared to continuous forests (Van Belle and Estrada 2006; Zunino *et al.* 2007), including in mantled howlers (Arroyo-Rodríguez and Dias 2010). There was no difference, however, in mean number of adult males and adult females or sex ratio between the fragment at LSBRS and continuous forest at La Selva in 2022, despite the fact that dispersal opportunities are likely limited at LSBRS by the surrounding plantations and pastures. The number of males per group at LSBRS may therefore be a consequence of the elevated density of solitary males compared to most other mantled howler sites (Bolt *et al.* 2021b); it is possible that there was an influx of lone males during the population surge in 2019, which then successfully joined groups by 2022.

The immature to adult female ratio (IFR) is a measure of reproductive rate, with high ratios indicating higher reproductive rates (Zucker and Clarke 2003). The IFR at La Selva was, however, only slightly higher in 1990 compared to 2022 despite the substantial increase in population size. While it is possible that the difference (0.9 vs. 0.7) is too small to be biologically meaningful, this may be further evidence that the population growth was due largely to more frequent female dispersal from adjacent areas as opposed to increased birth rates. It may also indicate that the population has approached carrying capacity and thus population growth is slowing. It will be important to study dispersal across La Selva and Braulio Carillo National Park to better understand migration patterns and group composition in this population. The IFR is lower at LSBRS (0.5) than at La Selva, which is consistent with low IFRs in other mantled howler populations inhabiting fragmented landscapes (Cristobol-Azkarate *et al.* 2005). However, the difference is akin to that at La Selva between 1990 and 2022, so it is unclear if this difference signifies differences in population health between the sites, especially considering that the IFR of the stable population at La Pacifica was 0.6, very similar to what we report for La Selva and LSBRS. It will be important to monitor birth rates and dispersal patterns more closely at both La Selva and LSBRS to better understand demography at both sites.

We also plan to improve sampling of group size and group composition across the entirety of La Selva in the coming years. The current analyses are based on a subset of howler monkey groups at this site, as was the case thirty years ago (Stoner 1994). While in both sampling years (1990 and 2022) group size and composition were generally consistent with mantled howlers across their range, it is possible that the other groups in the forest differ from those we (and Stoner) sampled, potentially skewing our results. Furthermore, we were unable to use the same methods at both sites. At both La Selva and LSBRS, we determined the number of groups based on sampling the entire forest, as was the case for group size and composition at LSBRS. At La Selva, however, we could sample only a subset of groups due to limited personnel and the large size of the forest. Despite the fact that we used different methods at the two sites, the results still allow us to compare demography across a small forest fragment and a larger, continuous forest in the same year. Our results provide a useful baseline as we continue to monitor the health of these mantled howler monkey populations.

Overall, our results highlight the importance of forest protection given that forest structure and biodiversity impact howler monkey density (Peres 1997). The number of mantled howler monkey groups at La Selva has almost doubled since 1992, and group size has increased, resulting in a much larger population. It is critical that its protected status be maintained to ensure that this population continues to thrive. LSBRS is one of the few protected forest fragments in its vicinity, providing refuge for wildlife as nearby forest has been cleared for agriculture. The influx of monkeys in 2019 combined with reduced dispersal opportunities for those natal to LSBRS likely led to the extremely high population density there today (Schreier *et al.* 2021; Bolt *et al.* 2022b), which may not be sustainable, especially if deforestation continues apace. Costa Rica has committed to conservation, with protected areas covering 25% of the country (Sanchez 2018; Tafoya *et al.* 2020). The demographic structure at La Selva suggests that the monkeys at this site are currently effectively protected. The results from LSBRS are less clear. Given that group size and composition do not indicate poor population health at LSBRS, it is possible that the high density is sustainable; however, it is critical that deforestation near LSBRS cease in order to prevent the population density from increasing even more. It is also important for LSBRS to connect to other protected areas via corridors. A plan to develop a large-scale corridor linking Tortuguero National Park and Braulio Carillo National Park has been underway since 2018 (Programa Nacional de Corredores Biológicos de Costa Rica, 2019), and incorporates linking small forest fragments including LSBRS (Bolt *et al.* 2022a). Once complete, this corridor may alleviate pressure from the current high density at LSBRS.

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Ethical approval:

This research met the legal requirements of Costa Rica and was approved by the Sistema Nacional de Areas de Conservation (SINAC-ACC-PI-re-039-2022 and SINAC-ACC-PI-re-045-2022). Our research protocol was approved by Regis University's Institutional Animal Care and Use Committee (IACUC permit # 20-003).

Literature Cited

Altmann, S. 1959. Field observations on a howling monkey society. *J. Mammal.* 40: 317–330.

Aristizibal, J. F., J. M. Rothman, L.M. Garcia-Feria and J. C. Serio-Silva. 2017. Contrasting time-based and weight-based estimates of protein and energy intake of black howler monkeys (*Alouatta pigra*). *Am. J. Primatol.* 79: 1–8.

Arroyo-Rodríguez, V. and P. Dias 2010. Effects of habitat fragmentation and disturbance on howler monkeys: a review. *Am. J. Primatol.* 72: 1–16.

Bell, K. E. and M. A. Donnelly. 2006. Influence of forest fragmentation on community structure of frogs and lizards in northeastern Costa Rica. *Conserv. Biol.* 20: 1750–1760.

Bezanson, M., P. A. Garber, J. Murphy and L. Premo. 2008. Patterns of subgrouping and spatial affiliation in a community of mantled howling monkeys (*Alouatta palliata*). *Am. J. Primatol.* 70: 282–293.

Bolt, L. M. and A. L. Schreier. 2023. Student research collaboration as conservation education: a case study from the primate field school at Maderas Rainforest Conservancy. *Am. J. Primatol.* 85: 1–12.

Bolt, L. M., D. G. Russell and A. L. Schreier. 2023. River edge feeding: howler monkey feeding ecology in a fragmented riparian forest. *Folia Primatol.* 94: 1–11.

Bolt, L. M., A. L. Schreier, K. A. Voss, E. A. Sheehan, N. L. Barrickman, N. P. Pryor and M. C. Barton. 2018. The influence of anthropogenic edge effects on primate populations and their habitat in a fragmented rainforest in Costa Rica. *Primates* 59: 301–311.

Bolt, L. M., A. L. Schreier, D. G. Russell, Z. S. Jacobson, C. Merrigan-Johnson, M. C. Barton and E. M. C. Coggeshall. 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.

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

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

Bolt, L. M., D. G. Russell and A. L. Schreier. 2021a. Anthropogenic edges impact howler monkey (*Alouatta palliata*) feeding behaviour in a Costa Rican rainforest. *Primates* 62: 647–657.

Bolt, L. M., M. N. Cavanaugh and A. L. Schreier. 2021b. Lone males: solitary and group-living male mantled howler monkey behavioural ecology in a Costa Rican rainforest. *Am. J. Phys. Anthropol.* 174: 201–212.

Bolt, L. M., L. S. E. Brandt, R. L. Molina and A. L. Schreier. 2022a. Maderas Rainforest Conservancy: a One-Health approach to conservation. *Am. J. Primatol*. 84 e23293: 1–16.

Bolt, L. M., C. M. Hadley and A. L. Schreier. 2022b. Crowded in a fragment: high population density of mantled howler monkeys (*Alouatta palliata*) in an anthropogenically-disturbed Costa Rican rainforest. *Primate Conserv.* (36): 37–44.

Bolt, L. M., D. G. Russell and A. L. Schreier. 2023. River edge feeding: howler monkey feeding ecology in a fragmented riparian forest. *Folia Primatol.* 94: 1–11.

Boyle, S. A. and A. T. Smith. 2010. Behavioral modifications in northern bearded saki monkeys (*Chiropotes satanas chiropotes*) in forest fragments of central Amazonia. *Primates* 51: 43–51.

Chapman, C. A. 1988. Patterns of foraging and range use by three species of Neotropical primates. *Primates* 29: 177–194.

Chapman, C. A. 1989. Ecological constraints on group size in three species of Neotropical primates. *Folia Primatol.* 55: 1–9.

Chapman, C. A., L. J. Chapman and R.W. Wrangham. 1995. Ecological constraints on group size: An analysis of spider monkey and chimpanzee subgroups. *Behav. Ecol. Sociobiol.* 36: 59–70.

Chaves, O. M., K. E. Stoner and V. Arroyo-Rodríguez. 2011. Seasonal differences in activity patterns of Geoffroy's spider monkeys (*Ateles geoffroyi*) living in continuous and fragmented forests in southern Mexico. *Int. J. Primatol.* 32: 960–973.

Clarke, M., C. Crockett, E. Zucker and M. Zaldivar. 2002. Mantled howler population of Hacienda La Pacifica, Costa Rica between 1991 and 1998: effects of deforestation. *Am. J. Primatol.* 56: 155–163.

Cortés-Ortiz, L. *et al.* 2021. *Alouatta palliata* (amended version of 2020 assessment). The IUCN Red List of Threatened Species 2021: e.T39960A190425583.

Cristóbal-Azkarate, J., J. Vea, N. Asensio and E. Rodríguez-Luna. 2005. Biogeographical and floristic predictors of the presence and abundance of mantled howlers (*Alouatta palliata mexicana*) in rainforest fragments at Los Tuxtlas, Mexico. *Am. J. Primatol*. 67: 209–222.

Crockett, C. M. and J. F Eisenberg. 1987. Howlers: variations in group size and demography. In: *Primate Societies*, B. B. Smuts, D. L. Cheney, R. M. Seyfarth, R. W. Wrangham and T. T. Struhsaker (eds.), pp. 54–68. University of Chicago Press, Chicago, IL.

Dias, P. and E. Rodríguez-Luna. 2006. Seasonal changes in male associative behavior and subgrouping of *Alouatta palliata* on an island. *Int. J. Primatol*. 27: 1635–1651.

Di Fiore, A., A. Link and C. Campbell. 2011. The atelines: behavioral and sociological diversity in a New World monkey radiation. In: *Primates in Perspective*, C. J. Campbell, A. Fuentes, K. C. MacKinnon, M. Panger, and S. K. Bearder (eds.), pp. 155–188. Oxford University Press, New York.

Estrada, A. 1982. Survey and census of howler monkeys (*Alouatta palliata*) in the rain forest of "Los Tuxtlas," Veracruz, Mexico. *Am. J. Primatol.* 2: 363–372.

Estrada, A. 2015. Conservation of *Alouatta*: social and economic drivers of habitat loss, information vacuum, and mitigating population declines. In: *Howler Monkeys: Behavior, Ecology, and Conservation*, M. Kowalewski, P. A. Garber, L. Cortés-Ortiz, B. Urbani and D. Youlatos (eds.), pp. 383–409. Springer, New York.

Estrada, A., A. Anzures and R. Coates-Estrada. 1999. Tropical rain forest fragmentation, howler monkeys (*Alouatta palliata*), and dung beetles at Los Tuxtlas, Mexico. *Am. J. Primatol.* 48: 253–262.

Estrada, A. *et al.* 2017. Impending extinction crisis of the world's primates: why primates matter. *Sci. Adv.* 3: e1600946

Ewers, R. M. and R. K. Didham. 2006. Confounding factors in the detection of species responses to habitat fragmentation. *Biol. Rev.* 81: 117–142.

Fedigan, L., L. Rose and R. Avila. 1998. Growth of mantled howler groups in a regenerating Costa Rican dry forest. *Int. J. Primatol.* 19: 405–432.

Fishkind, A. S. and R. W. Sussman. 1987. Preliminary survey of the primates of the Zona Protectora and La Selva Biological Station, northeast Costa Rica. *Primate Conserv*. (8): 63–66.

Garber, P. A. and M. Kowalewski. 2015. New challenges in the study of howler monkey behavioral ecology and conservation: where we are and where we need to go. In: *Howler Monkeys: Behavior, Ecology, and Conservation*, M. Kowalewski, P. A. Garber, L. Cortés-Ortiz, B. Urbani and D. Youlatos (eds.), pp. 413–428. Springer, New York.

Garber, P. A., A. Molina and R. Molina. 2010. Putting the community back in community ecology and education: the role of field schools and private reserves in the ethical training of primatologists. *Am. J. Primatol.* 72: 785–793.

Garber, P. A., A. Estrada and M. Pavelka. 2006. New perspectives in the study of Mesoamerican primates: concluding comments and conservation priorities. In: *New Perspectives in the Study of Mesoamerican Primates: Distribution, Ecology, Behavior and Conservation*, A. Estrada, P. A. Garber, M. Pavelka and L. Luecke (eds.), pp. 563–584. Kluwer Academic/Plenum Publishers, New York.

Gilbert, K. A. 2003. Primates and fragmentation of the Amazon Forest. In: *Primates in Fragments*, L. K. Marsh (ed.), pp. 145–158. Kluwer Academic/Plenum, New York.

Glander, K. 1992. Dispersal patterns in Costa Rican mantled howling monkeys. *Int. J. Primatol.* 13: 415–435.

Haddad, N. M. *et al*. 2015. Habitat fragmentation and its lasting impact on Earth's ecosystems. *Sci. Adv.* 1: e1500052.

Heltne, P. G., D. C. Turner and N. J. Scott Jr. 1975. Comparison of census data on *Alouatta palliata* from Costa Rica and Panama. In: *Neotropical Primates: Field Studies and Conservation*, R. W. Thorington Jr and P. G. Heltne (eds.), pp. 10–19. National Academy of Sciences, Washington, DC.

Irwin, M. T. 2007. Living in forest fragments reduces group cohesion in diademed sifakas (*Propithecus diadema*) in eastern Madagascar by reducing food patch size. *Am. J. Primatol.* 69: 434–447.

Johnson, C. E., A. L. Schreier, O. Vargas, and M. D. Wasserman. Accepted. The mantled howler monkey (*Alouatta palliata*) population at La Selva Research Station, Costa Rica: comparing censuses in 1992 and 2022.

Klass, K., S. Van Belle and A. Estrada. 2020a. Demographic population structure of black howler monkeys in fragmented and continuous forest in Chiapas, Mexico: implications for conservation. *Am. J. Primatol.* 82: e23163.

Klass, K., S. Van Belle, A. Campos-Villanueva, F. Mercado Malabet and A. Estrada. 2020b. Effects of variation in forest fragment habitat on black howler monkey demography in the unprotected landscape around Palenque National Park, Mexico. *PeerJ* 8: e9694.

Lawler, R. 2011. Demographic concepts and research pertaining to the study of wild primate populations. *Yrbk. Phys. Anth.* 54: 63–85.

Leighton, M. and D. Leighton. 1982. The relationship of size of feeding aggregate to size of food patch: howler monkeys (*Alouatta palliata*) feeding in *Trichilia cipo* fruit trees on Barro Colorado Island. *Biotropica* 14: 81–90.

Matlock, R. and G. S. Hartshorn. 1999. La Selva Biological Station (OTS). *Bull. Ecol. Soc. Am.* 1999: 188–193.

McDade, L. A. and G. S. Hartshorn. 1994. La Selva Biological Station. In: *La Selva: Ecology and Natural History of a Neotropical Rain Forest*, L. McDade, K. Bawa, H. Hespenheide and G. S. Hartshorn (eds.), pp. 6–14. The University of Chicago Press, Chicago, IL.

McKinney, T., J. L. Westin and J. C. Serio-Silva. 2015. Anthropogenic habitat modification, tourist interactions and crop-raiding in howler monkeys. In: *Howler Monkeys: Behavior, Ecology, and Conservation*, M. Kowalewski, P. A. Garber, L. Cortés-Ortiz, B. Urbani and D. Youlatos (eds.), pp. 281–311. Springer, New York.

Melin, A. D. *et al*. 2020. Primate life history, social dynamics, ecology, and conservation: contributions from long-term research in Área de Conservación Guanacaste, Costa Rica. *Biotropica* 52: 1041–1064.

Milton, K. 1980. *The Foraging Strategies of Howler Monkeys*. Columbia University Press, New York.

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*, F. Huettman (ed.), pp. 199–214. Springer, New York.

Peres, C. A. 1997. Effects of habitat quality and hunting pressure on arboreal folivore densities in Neotropical forests: a case study of howler monkeys (*Alouatta* spp.). *Folia Primatol.* 68: 199–222.

Programa Nacional de Corredores Biológicos de Costa Rica (2019). Elaboración de la justificación técnica para el diagnóstico de cuatro iniciativas de creación de Corredores Biológicos en el marco de la Estrategia de Adaptación de la Biodiversidad al Cambio Climático. Contratción Directa No. 2018CD-000076-0006800001.

Pruetz, J. and H. Leasor. 2002. Densities of primate species in forest fragments at La Suerte Biological Field Station, Costa Rica. *Neotrop. Primates* 10: 4–9.

Richard, A. F., R. E. Dewar, M. Schwartz and J. Ratsirarson. 2022. Life in the slow lane? Demography and life histories of male and female sifaka (*Propithecus verreauxi verreauxi*). *J. Zool., Lond.* 256: 421–436.

Righini, N., P. A. Garber and J. Rothman. 2017. The effects of plant nutritional chemistry on food selection of Mexican black howler monkeys (*Alouatta pigra*): the role of lipids. *Am. J. Primatol.* 79: e22524.

Ryan, S., P. Starks, K. Milton and W. Getz. 2008. Intersexual conflict and group size in *Alouatta palliata*: a 23-year evaluation. *Int. J. Primatol.* 29: 405–420.

Sanchez, R. V. 2018. Conservation strategies, protected areas, and ecotourism in Costa Rica. *J. Park Rec. Admin.* 36: 115–128.

Schelhas, J. and G. A. Sanchez-Azofeifa. 2006. Post-frontier forest change adjacent to Braulio Carrillo National Park, Costa Rica. *Hum. Ecol.* 34: 407–431.

Schreier, A. L., L. M. Bolt, D. G. Russell, Z. S. Jacobson, T. S. Readyhough, C. Merrigan-Johnson and E. M. C. Coggeshall. 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 Primatol.* 92: 49–57.

Schreier, A. L., K. A. Voss and L. M. Bolt. 2022a. Behavioral responses to riparian and anthropogenic edge effects in mantled howler monkeys (*Alouatta palliata*) in a disturbed riverine forest. *Primates* 63: 659–670.

Schreier, A. L., K. A. Voss and L. M. Bolt. 2022b. A mathematical modelling approach to functionally defining forest edge and its utility for primate behavioural edge effects. *Int. J. Primatol.* 43: 460–479.

Stoner, K. 1994. Population density of the mantled howler monkeys (*Alouatta palliata*) at La Selva Biological Reserve, Costa Rica: a new technique to analyze census data. *Biotropica* 26: 332–340.

Tafoya, K. A., E. S. Brondizio, C. E. Johnson, P. Beck, M. Wallace, R. Quiros and M. D. Wasserman. 2020. Effectiveness of Costa Rica's conservation portfolio to lower deforestation, protect primates, and increase community participation. *Front. Environ. Sci.* 8: 580724.

Van Belle, S. and A. Estrada. 2006. Demographic features of *Alouatta pigra* populations in extensive and fragmented forests. In: *New Perspectives in the Study of Mesoamerican Primates: Distribution, Ecology, Behavior, and Conservation*, A. Estrada, P. A. Garber, M. S. M. Pavelka and L. Luecke (eds.), pp.121–142. Springer, New York.

Zucker, E. and M. Clarke. 2003. Longitudinal assessment of immature-to-adult ratios in two groups of *Alouatta palliata*. *Int. J. Primatol.* 24: 87–101.

Zunino, G. E., M. M. Kowalewski, L. I. Oklander and V. Gonzalez. 2007. Habitat fragmentation and population size of the black and gold howler monkey (*Alouatta caraya*) in a semideciduous forest in northern Argentina. *Am. J. Primatol.* 69: 1–10.

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