Crowded in a Fragment: High Population Density of Mantled Howler Monkeys (*Alouatta palliata*) in an Anthropogenically-disturbed Costa Rican Rainforest

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Abstract: Primate population size and demography are important to quantify as part of ongoing conservation efforts in tropical regions. The mantled howler monkey (*Alouatta palliata*) has a wide range from southern Mexico, through Central America to western Colombia, Ecuador and just into Tumbes, Peru. It is known to persist in anthropogenically-disturbed habitats, including forest fragments. As a Vulnerable species with a generally declining population, however, it is crucial to monitor their group size and population density at long-term study sites, particularly as habitats throughout their range are increasingly deforested. We present an updated group demography and population density estimate for the mantled howler monkey population at La Suerte Biological Research Station (LSBRS), Costa Rica, a long-term primate study site in a fragmented rainforest. From 2017–2022, we collected demographic data from 11 mantled howler monkey groups and several solitary individuals at LSBRS. Mean group size in 2022 was 13.1 individuals/group (±4.9 SD), adult male-to-female sex ratio was 1:2.2, and immature to adult female ratio (IFR) was 0.54. Estimated population density was 109.5 howlers/km^2, to our knowledge, the highest ever recorded for this species at any site. Our results indicate that mantled howler monkeys can persist at a very high density in a fragmented forest over multiple years. Ongoing deforestation in the area surrounding LSBRS has likely led to the migration of howlers into LSBRS, which, along with the lack opportunities for dispersal from LSBRS, has probably contributed to the high population density in this surviving forest fragment. Our findings attest to the ability of mantled howler monkeys to survive in very high densities, which is important to consider for conservation efforts on their behalf.

Resumen: Es importante cuantificar el tamaño y la demografía de la población de primates como parte de los esfuerzos de conservación en curso en las regiones tropicales. El mono aullador (*Alouatta palliata*) tiene una amplia distribución en todo el Neotrópico y es conocido por persistir en hábitats perturbados antropogénicamente, incluidos fragmentos de bosque. Sin embargo, como una especie vulnerable con una población generalmente en declive, es crucial monitorear el tamaño de su grupo y la densidad de población en los sitios de estudio a largo plazo, particularmente porque las áreas de hábitat a lo largo de su área de distribución están cada vez más deforestadas. Presentamos una demografía grupal actualizada y una estimación de densidad de población para la población de monos aulladores en la Estación de Investigación Biológica La Suerte (LSBRS), Costa Rica, un sitio de estudio de monos dentro de una selva tropical fragmentada. De 2017 a 2022, recopilamos datos demográficos de 11 grupos de monos aulladores y varios individuos solitarios en LSBRS. El tamaño medio del grupo en 2022 fue de 13.1 monos/grupo (±4.9 DE), la proporción de sexos entre machos y hembras adultos fue de 1:2.2 y la proporción entre hembras inmaduras y adultas (IFR) fue de 0.54. La densidad de población estimada fue de 109.5 monos/km², la más alta jamás registrada para esta especie en cualquier sitio que sepamos. Nuestros resultados indican que el mono aullador puede persistir en una densidad muy alta en un bosque fragmentado durante varios años. La deforestación en el área que rodea LSBRS probablemente ha llevado a la migración de monos a LSBRS, así como a la falta de dispersión de monos de LSBRS, aumentando la densidad de población en este fragmento de bosque sobreviviente. Nuestros hallazgos dan fe de la capacidad de los monos aulladores para sobrevivir en condiciones de muy alta densidad y pueden usarse para informar los esfuerzos de conservación en su nombre.

Keywords: *Alouatta*, howler, demography, population density, forest fragmentation, Costa Rica

Introduction

For both species- and area-focused conservation efforts, it is important to quantify population sizes to better understand how many individuals are sustainable in a given habitat. Non-human primates are indicator species in that their presence reflects the health of their habitat (Mace and Balmford 2000). They are particularly important to study in this regard, especially with the majority of primates now being threatened with extinction due to habitat destruction (Mittermeier *et al.* 2012; Estrada *et al.* 2017). The mantled howler monkey (*Alouatta palliata*) is wide ranging, extending from southern Mexico, through Central America, to western Colombia, and Ecuador and the northernmost tip of Peru in the Tumbes Region (Rylands *et al.* 2006). Although currently classified as Vulnerable and with a generally declining population (Cortes-Ortíz *et al.* 2021), this species is adapted to survive in a wide range of forest types (Garber *et al.* 2006; Muñoz *et al.* 2006), and has some degree of dietary flexibility as a frugivore-folivore, with the ability to eat a variety of widely available foods and to increase the proportion of leaves consumed when fruit is not available (Garber *et al.* 2006; Espinosa-Gómez *et al.* 2013; Righini *et al.* 2017; McKinney 2019).

As primates that regularly consume low-quality foods such as leaves (Espinosa-Gómez *et al.* 2018), mantled howler monkeys are energy minimizers that spend much of their daily activity budgets resting (Estrada *et al.* 1999; Schreier *et al.* 2021) and have small home ranges averaging 0.2 km² (Di Fiore *et al.* 2011). They have bisexual dispersal, with males and females being solitary for a time prior to joining social groups as adults (Glander 1992), and eventually live in multi-male, multi-female social groups of about 10–15 individuals (Bezanson *et al.* 2008; Ryan *et al.* 2008; Di Fiore *et al.* 2011). Groups tend to be cohesive (Milton 1980; Crockett and Eisenberg 1987), although they fission into smaller subgroups to forage in some environments (Leighton and Leighton 1982; Chapman 1990; Bezanson *et al.* 2008), likely to conserve energy and reduce feeding competition when in degraded habitats (Chapman *et al.* 1995; Dias and Rodriguez-Luna 2006). Due to these adaptive qualities, mantled howler monkeys are able to persist in many fragmented and anthropogenically-disturbed habitats (Arroyo-Rodríguez and Mandujano 2006; Garber *et al.* 2006; Arroyo-Rodríguez and Dias 2010).

While the mantled howler monkey is a generally resilient species (Di Fiore *et al.* 2011), it is important to monitor their group size and population density at long-term study sites because of forest loss and fragmentation (Garber *et al.* 2006). One such study site is La Suerte Biological Research Station (LSBRS) in Costa Rica, a fragmented tropical rainforest where the mantled howler monkey population has been studied for more than 25 years (Garber *et al.* 2010; Molina 2015; Bolt *et al.* 2021c; Fig. 1). Although LSBRS is protected, forest is being destroyed and fragmented in the surrounding area (Garber *et al.* 2010; Molina 2015). The howler monkey population in the study area at LSBRS was last systematically surveyed more than 20 years ago (Pruetz and Leasor 2002; Table 1). We present updated population density and group size estimates for the mantled howler monkeys at LSBRS.

Methods

Study site

We conducted this study at La Suerte Biological Research Station (LSBRS), a 3-km² tropical rainforest fragment in northeastern Costa Rica (10°26'N, 83°46'W) (Bezanson 2009; Brandt and Singleton 2018; Fig. 1). Although the forest's overall vegetation structure provides adequate food and habitat for howler monkeys (Bolt *et al.* 2020b; 2021a), the areas near the forest edge have less canopy cover, lower tree species richness, and smaller trees (Bolt *et al.* 2018; 2019; 2020b), indicating poorer habitat quality for howler monkeys (Ross and Srivastava 1994; Arroyo-Rodríguez and Mandujano 2006). The area surrounding LSBRS is largely deforested, with protected rainforest sharply transitioning to cattle pasture, road, and agricultural fields along many parts of the property line (Molina 2015; Fig. 1). The surrounding matrix therefore contains minimal habitat for primates (Bolt *et al.* 2018). We collected data in a 1.36-km² portion of the LSBRS forest fragment that has been reforested since the 1990's, previously consisting of separate forest fragments ('Small Forest' = 0.35 km² to the south which was linked to 'Large Forest' = 0.94 km² to the north; Molina, 2015; Fig. 2). This study area also has a cleared area for researcher housing in the middle ('camp' = 0.07 km²); the remainder of the LSBRS forest fragment was inaccessible to researchers due to governmental protections ('Far Forest' = 1.64 km²) (Garber *et al.* 2010; Molina 2015; Bolt *et al.* 2018, 2019, 2020a, 2020b, 2021a, 2021b, 2021c; Schreier *et al.* 2021, 2022; Fig. 1). Mantled howler monkeys share the site with two groups of white-faced capuchin monkeys (*Cebus imitator*) and a population of Central American spider monkeys (*Ateles geoffroyi ornatus*) (Pruetz and Leasor 2002; Garber *et al.* 2010; Bolt *et al.* 2018; 2020b).

Group demography data collection

We collected demographic data on the mantled howler monkeys in the study area at LSBRS from 2017–2022. As part of a large-scale project on monkey behavioral ecology at LSBRS (Bolt *et al.* 2019; 2020a; 2021a; 2021b; Schreier *et al.* 2021; 2022), we collected howler monkey demography and group size data daily between 4:30 and 18:00 hours during six field seasons spanning 2017–2022: May – August 2017, May–August 2018, December 2018 – January 2019, June–August 2019, December 2019 – January 2020, and December 2021 – January 2022. We collected these data opportunistically from 2017–2020, and more intensively in December 2021 – January 2022 over 56 observation hours during this three-week-long field season. Researchers located individual monkeys and groups both visually and

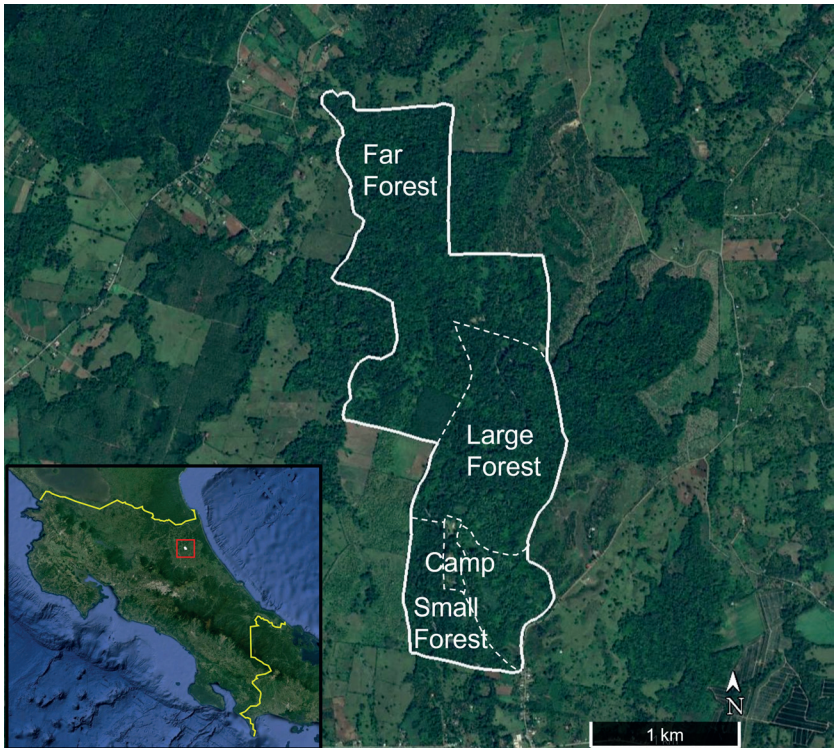

Figure 1. La Suerte Biological Research Station (LSBRS) in Limón Province, Costa Rica. Solid white lines indicate the LSBRS property lines; dotted white lines identify different regions within LSBRS. Google Earth, 2022.

by localizing howling behavior (Bolt *et al.* 2019, 2020a). Researchers then followed howler groups for as long as possible to record group demography and size, noting the total number of adult males, females, juveniles, infants, and unidentified adults per group during each sampling session. Researchers additionally recorded the locations of individuals and groups during sampling by taking a GPS point in the centre of the group or directly beneath a lone male during each 15 minutes of contact using a Garmin GPSMAP 62s hand-held navigator (Fig. 2).

Although it was difficult to consistently identify individual monkeys on different sampling days due to poor visibility in some areas of LSBRS (Bolt *et al.* 2019), groups could be identified during each sampling season by using the individual characteristics of group members (e.g., patterns of gold pigmentation on tails and legs; testicle size and coloration) as well as demography and location. Although groups could not be confidently identified between sampling seasons due to changing group demography, 11 different groups were uniformly observed during each sampling period (Bolt *et al.* 2021b), consistent with past howler monkey population estimates at LSBRS (Pruetz and Leasor 2002; Garber *et al.* 2010).

Data analysis

We determined adult male-to-female ratios by dividing the number of sexually mature adult female howler monkeys we observed each sampling season by the number of sexually mature adult males. To calculate the immature to adult female ratio (IFR), we divided the total number of infants and juveniles by the total number of sexually mature adult females observed at LSBRS each sampling season (Zucker and Clarke 2003). To determine the percentage of infants, juveniles, and adults in the population, we divided the total number of each respective age class observed during each sampling season at LSBRS by the total number of monkeys observed. We calculated mean group size and SD within each sampling season by averaging the total number of individuals in each of 11 social groups. To determine population density, we divided the total number of monkeys observed by the size of our study area in LSBRS. We used SPSS version 26 (IBM SPSS Statistics, IBM Corporation, Aramonk, NY, USA) to make all calculations.

Results

From 2017–2022, we observed 11 different groups of mantled howler monkeys at LSBRS. Mean group size across sampling seasons ranged from 7.8–13.1 individuals with 1–5 solitary individuals in the population (Table 1). We consistently identified the membership of 11 different howler monkey groups at LSBRS during intensive demography sampling in 2021–2022 (Table 2). Groups were located throughout LSBRS with some overlap (Fig. 2), and we observed a total of 149 individual howler monkeys, including group-living and solitary (Tables 1 and 2). Average group size in 2021–2022 was 13.1 individuals, with a range of 5–21, including 1–4 adult males and 3–11 adult

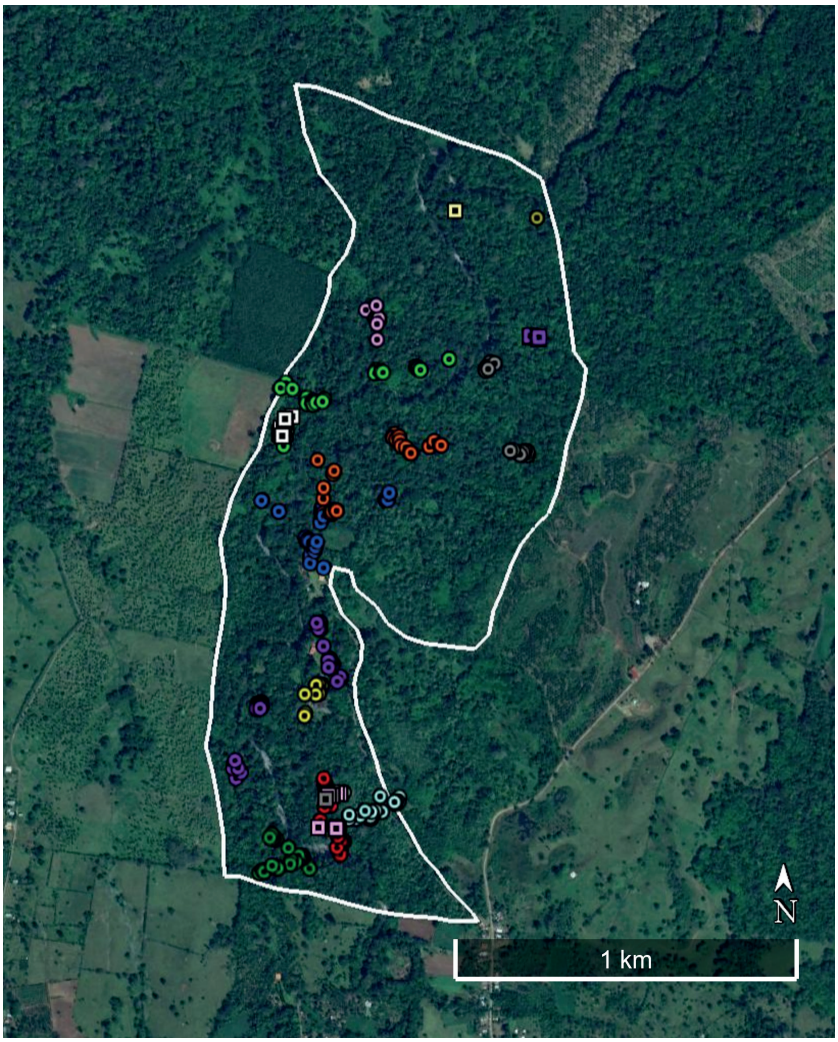

Figure 2. Study area showing the sampling locations of 11 mantled howler monkey (*Alouatta palliata*) groups and 5 solitary males in December 2021 – January 2022. Circles indicate howler monkey groups and squares indicate solitary males; different colors indicate different groups and individuals. Each marker represents 15 minutes of sampling. Google Earth, 2022.

Table 1. Summary of mantled howler monkey group demography at LSBRS from 1999* and across 2017–2022 study seasons.

Sampling season	No. of groups	No. of one-male groups	No. of multi-male groups	Adult male to female ratio	Immature to adult female ratio (IFR)	% of infants/ juveniles/ adults in the population	Mean group size (± SD)	No. of solitary males observed	No. of solitary females observed	Pop. size (total no. of individuals observed)	Pop. density (no. of monkeys/ km²)
Jun-Aug 1999*	10-11*	-	-	-	-	-	4.8*	-	-	-	73.7*
May-Aug 2017	11	2	9	1:1.7	0.61	10.8%/ 17.9%/ 71.3%	9.6 (2.7)	2	0	108	79.4
May-Aug 2018	11	1	10	1:1.6	0.38	6.6%/ 13.7%/ 79.7%	9.2 (3.9)	4	0	105	77.2
Dec 2018-Jan 2019	11	1	10	1:1.8	0.5	10.4%/ 15.9%/ 73.7%	8.7 (1.2)	1	0	97	71.3
Jun-Aug 2019	11	1	10	1:2	0.5	15.4%/ 11.5%/ 73.1%	7.8 (2.0)	3	0	89	65.4
Dec 2019-Jan 2020	11	0	11	1:1.5	0.55	10.8%/ 15.7%/ 73.5%	11.4 (5.1)	2	1	128	94.1
Dec 2021-Jan 2022	11	2	9	1:2.2	0.54	11.8%/ 13.9%/ 74.3%	13.1 (4.9)	5	0	149	109.5

*Demography data reported in tables 2 and 4 of Pruetz and Leasor (2002).

females per group (Tables 1 and 2). With our study area at LSBRS comprising a forest fragment of 1.36 km², our results indicate a population density of 109.5 individuals/km² at LSBRS.

Discussion

Our results indicate that LSBRS has an unusually high population density of mantled howler monkeys—to our knowledge, the highest ever reported. While our most recent population density estimate from intensive sampling in 2021–2022 was the highest, all population density estimates since 2017 are comparable to the historical LSBRS population density estimate from 1999 (73.7 individuals/km² average across fragments, Pruetz and Leasor 2002). These results suggest that LSBRS currently has a population density three times higher than other mantled howler monkey sites and may have consistently maintained a high population density for more than 20 years. At other sites, density ranges from 5–30 individuals/km² (e.g., Estrada 1982; Stoner 1994; Clarke *et al.* 2002) and forest size is also larger (range of 7–108 km² at other sites vs. 3 km² at LSBRS). Population density was 23.3 individuals/km² in a 7-km² rainforest Los Tuxtlas, Mexico (Estrada 1982), while in Costa Rica, population density was 30 individuals/km² in an 11.8 km² forest at La Pacifica (Clarke *et al.* 2002), grew from 4.9 to 7.9 individuals/km² in a 108 km² forest at Santa Rosa National Park (Fedigan *et al.* 1998), and was 7–15 individuals/km² in a 15 km² rainforest at La Selva despite the group sizes and sex ratios being similar to those at LSBRS (Stoner 1994; Schreier and Bolt 2020). These results are consistent with other studies that show that mantled howler population density is inversely related to forest size (Cristóbal-Azkarate *et al.* 2005; Mandujano and Escobedo-Morales 2008). Higher population density is also generally associated with larger groups (Fedigan *et al.* 1998) but at LSBRS density is extremely high while group size, at an average of 13, is within the 10–15 range typically found at other sites (Tables 1 and 2; Bezanson *et al.* 2008; Di Fiore *et al.* 2011). At LSBRS, group size appears to be linked to density, with increases in population density mirrored by increases in group size, and vice versa (Table 1). It is also noteworthy that prior to 2019, average group size at LSBRS was lower than the 10–15 range typically found at other sites, despite higher density at LSBRS (Table 1; Bezanson *et al.* 2008; Di Fiore *et al.* 2011). Maintaining these smaller group sizes at LSBRS when possible may be adaptive for minimizing feeding competition in this disturbed habitat (Chapman *et al.* 1995; Dias and Rodriguez-Luna 2006; Bolt *et al.* 2021a). Additionally, howler groups at LSBRS fission during foraging (Bezanson *et al.* 2008; Schreier *et al.* 2021), which further reduces effective group size. Group fissioning may have helped mitigate feeding competition at LSBRS since 2019, when group sizes were larger (Table 1).

Across the 2017–2022 sampling period, howler monkey population size and density appeared to change at LSBRS, with the number and density decreasing between May 2017 and August 2019, then steeply increasing until the end of our sampling season in January 2022, while the number of groups remained constant at 11 (Table 1). While some of the differences in the number of howler monkeys observed across the 2017–2022 sampling seasons may be due to changes in visibility in different areas of LSBRS as well as varying levels of reporting confidence by researchers, habitat change in the area surrounding LSBRS likely impacted the number of monkeys observed. Around 2017, an oil palm plantation located within 2 km of LSBRS expanded, with trees planted on former cattle pasture (Molina, pers. comm.) potentially creating some usable habitat for howler monkeys. This may have caused some of the howler monkeys

Table 2. Mantled howler monkey group composition at LSBRS in December 2021-January 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	Sampling effort (hours)
1	11	2	6	1	2	0	3.25
2	10	2	4	1	2	1	6.5
3	14	4	8	1	1	0	8
4	10	2	4	1	2	1	3
5	18	4	8	3	2	1	8.25
6	16	4	6	2	2	2	5.5
7	19	4	9	4	2	0	5.5
8	11	3	5	2	1	0	6.75
9	5	1	3	1	0	0	1.75
10	21	4	11	3	3	0	5
11	9*	1*	5*	1*	0*	2*	1.75*

*Group 11 demography from December 2019-January 2020. This group was seen in the same location in December 2021-January 2022 and was comparable in total group size to the data presented here, but poor visibility prevented more accurate sampling in 2021-2022.

at LSBRS to disperse to this area, thus lowering the population density at LSBRS. By 2019, however, additional areas of landscape within 5 km of LSBRS were deforested to create more pineapple plantations and areas for cattle grazing (Molina, pers. comm.), which could have caused more monkeys to crowd into LSBRS due to a reduced availability of usable habitat in the surrounding area. Regardless of any year-to-year changes in the howler monkey population and density during our study period, our results show that LSBRS consistently maintained a very high howler monkey population size and population density from 2017–2022.

Mantled howler monkey groups at LSBRS also differed in their demography compared to other populations. With male-to-female sex ratios of 1:4 being typical in mantled howler monkey groups (Di Fiore *et al.* 2011), LSBRS had a much higher male-to-female sex ratio (1:2.2 in 2022; Table 1), suggesting an increased number of males gaining membership in groups and/or fewer sexually mature males dispersing from natal groups. In concert with this high male group membership, LSBRS also had solitary males that seemed to be more visible and were likely located at a much higher population density than at other sites (Bolt *et al.* 2021b; Table 1). This suggests that some males may potentially gain group membership at LSBRS due to a lack of other available habitat areas in the vicinity compounded by a decreased ability of group members to withstand the inundation.

Another measure of population structure, immature to adult female ratio (IFR), indicates replacement rates in a population (Zucker and Clarke 2003), with values of <1.5 indicating a decline (Heltne *et al.* 1975). At LSBRS, the IFR value was consistently much lower than this 1.5 threshold throughout the study period (IFR value of 0.54 in 2022, Tables 1 and 2), and was also lower than at other sites surveyed in Costa Rica with stable populations, such as La Pacifica (IFR value of 0.62, Zucker and Clarke 2003). The increase in population size at LSBRS, then, is likely primarily due to immigration and/or natal retention rather than high birth rate, although more research is needed to further explore these possibilities.

It is also important to note that our demographic data (Table 2) represent a minimum population estimate at LSBRS. Given that howler monkey groups at LSBRS break into small subgroups to forage (Bezanson *et al.* 2008), it is possible that some of the smaller groups we observed (e.g., Groups 9 and 11; Table 2) may have been sub-groups, with additional group members not counted. Each of these groups were also observed for less sampling time than other groups (Table 2); sampling these groups for longer times may result in the discovery of additional group members. We also likely failed to observe some solitary individuals due to the difficulty in finding and following them (Bolt *et al.* 2021b). With LSBRS having a total size of 3 km², it is also possible that the remaining 1.64 km² of forest has an even greater number of monkeys and groups (Figs. 1 and 2). This 'Far Forest' (i.e., the unstudied portion of LSBRS) is less anthropogenically-disturbed than our study area due to its governmental protection status (Molina 2015; Bolt *et al.* 2021c); it thus likely has richer vegetation and better monkey habitat (Ross and Srivastava 1994; Arroyo-Rodríguez and Mandujano 2006), possibly resulting in them preferring it to our study area and concentrating there in even higher density. While the howler monkey population in the 'Far' area of LSBRS has not been studied, our population count (Tables 1 and 2) based on the most disturbed forest region of LSBRS is very likely an underestimate of howler monkey density for the entire site.

Ongoing deforestation in the vicinity of LSBRS (Molina, 2015; Brandt and Singleton 2018; Bolt *et al.* 2021c) has likely precipitated an influx of monkeys dispersing into LSBRS both prior to and during our study period, as well as causing more of the monkeys born in LSBRS to remain in their natal groups for longer periods of time. Both factors have likely led to a spike in population density in this surviving forest fragment (Schreier *et al.* 2021). Mantled howler monkeys are well-known for their ability to persist in less-than-ideal conditions, including degraded habitats (Arroyo-Rodríguez and Mandujano 2006; Asensio *et al.* 2007; Arroyo-Rodríguez and Dias 2010), like the forest at LSBRS. In addition to quantifying the highest population density ever reported for the mantled howler monkey, our results indicate that this species can persist at very high density in a fragmented forest over multiple years (Table 1). However, in the absence of population welfare data, it is unknown whether howler monkeys are successfully coping with the degradation of the landscape surrounding LSBRS or if they are merely subsisting. It remains to be seen if this is a temporary population high prior to a sharp decline, or if LSBRS will continue to support such a high density of howler monkeys for the foreseeable future. Our findings attest to the ability of the mantled howler monkey to survive in degraded habitats and can be used to inform conservation efforts on their behalf.

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Ethical approval: Our research was conducted with the permission of the Molina family and met the legal requirements of Costa Rica. Our research protocol was approved

by Regis University's Institutional Animal Care Committee (IACUC permit #17-006).

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