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Lone males: Solitary and group-living male howler monkey (*Alouatta palliata*) behavioral ecology in a Costa Rican rainforest

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Abstract

Objectives: Many group-living primate species have evolved the capacity for some individuals to live alone for part of their lives, but this solitary life stage has rarely been the subject of focused research. The mantled howler monkey (*Alouatta palliata*) is a social primate species with bisexual dispersal that lives in mixed-sex groups with low male-to-female sex ratios. Consequently, males often spend a long period of their lives as solitary individuals. This study compares the tree use, feeding, and long-distance vocalization behavior of solitary and group-living mantled howler monkey males living within a fragmented rainforest in Costa Rica, La Suerte Biological Research Station. Based on differences in competitive ability between solitary and group-living males, we predicted that lone males would be found in significantly smaller feeding and resting trees, consume more low-quality foods, and produce shorter howling bouts made at lower rates than group-living males.

Materials and methods: We collected data on tree use and feeding during 30-min focal samples on male focal animals, recording data at 2-min intervals. We measured the trees in which the monkeys fed and rested for two or more intervals, and recorded the plant parts consumed. We recorded howling behavior using all-occurrences sampling.

Results: Lone males used significantly smaller feeding and resting trees, consumed more low-quality foods, and howled at lower rates but had longer howling bouts triggered by anthropogenic noise more than group-living males.

Discussion: Our results demonstrate that lone males differ in their behavioral ecology compared to group-living males, thus improving understanding of the solitary male life stage in primates.

KEYWORDS

DBH, fallback food, feeding ecology, loud call, male life history

1 | INTRODUCTION

“As solitaires, they are secretive and do nothing to attract attention.” (Glander, 1992, p. 424)

In some group-living primate species, individuals have the capacity to spend part of their lives alone. Solitary males, for example, are

especially prevalent in species with one-male, multi-female (i.e., polygynous) mating or social structures, where young adult males typically disperse from natal groups at sexual maturity but are not yet physically capable of securing membership in a new mixed-sex group (e.g., langur [*Semnopithecus* spp.], Steenbeek, Sterck, de Vries, & van Hoof, 2000; blue monkey [*Cercopithecus mitis*], Roberts &

Cords, 2015; Roberts, Nikitopoulos, & Cords, 2014). In other primate species with solitary males, groups may be one-male or multi-male with multiple females, but have low male-to-female ratios (e.g., howler monkey [*Alouatta* spp.], Glander, 1992). In all primate species with solitary males, adult males face fierce agonistic competition for group membership with only the healthiest and strongest individuals succeeding, meaning that young solitary males need to bide their time as they mature and strengthen (Clarke & Glander, 2004; Glander, 1992; Roberts, 2017). Given this high level of male-male competition, it is adaptive for the smaller, weaker males to avoid competition (Zahavi, 1975) by remaining solitary until they develop the agonistic ability to effectively join a social group.

Dietary adaptations also relate to primate group size and the presence of solitary adults. The folivore's paradox suggests that leaf- and grass-eating primate species, which do not primarily consume clumped, contested resources, should live in large groups to avoid predation (Steenbeek & van Schaik, 2001). However, folivores are often found in small groups (Chapman & Rothman, 2009), with many species further adapted for some individuals to have a solitary life stage. Adult males across a range of folivorous, group-living primate species live as solitary individuals for part of their lives, including the mountain gorilla (*Gorilla beringei*, Watts, 2000; Robbins & Robbins, 2005), mantled guereza (*Colobus guereza*, Roberts, 2017), Thomas's langur (*Presbytis thomasi*, Steenbeek et al., 2000), and howler monkey (*Alouatta* spp., Bolin, 1981; Garber & Kowalewski, 2011; Glander, 1992; Sekulic, 1982a). In particular, the presence of solitary individuals has been widely documented across howler monkey species.

Howler monkeys are a well-studied genus of group-living platyrrhine primates, characterized by both their folivorous, energy-minimizing behavioral ecology and their high-amplitude male-specific long-distance vocalizations (i.e., howls) (di Fiore, Link, & Campbell, 2011; Kitchen, da Cunha, Holzmann, & de Oliveira, 2015). Howler monkeys have also adapted the capacity for individuals to live outside of social groups for part of their life cycles; the black howler (*Alouatta pigra*) and black and gold howler (*Alouatta caraya*) have solitary males (Bolin, 1981; Garber & Kowalewski, 2011) and the red howler (*Alouatta seniculus*) and mantled howler (*Alouatta palliata*) have both solitary males and females (Crockett, 1996; Sekulic, 1982a; Young, 1982). Solitary howler monkeys have been described anecdotally and occasionally included in published research (e.g., Bolin, 1981; Crockett, 1996; Garber & Kowalewski, 2011; Glander, 1992; Sekulic, 1982a; Young, 1982); for example, in the red howler monkey, solitary individuals were reported to have lower-quality diets than group-living individuals (Pope, 1989, 2000). Despite a small number of such accounts, quantitative data and focused investigation on the behavioral ecology of these lone individuals are lacking. This study compares the behavior of solitary males to group-living male mantled howler monkeys in order to further our understanding of solitary male primates.

Mantled howler monkeys live in mixed-sex groups of typically 10–15 but up to 40 individuals (Bezanson, Garber, Murphy, & Premo, 2008; di Fiore et al., 2011; Ryan, Starks, Milton, & Getz, 2008), with 1:4 male-to-female sex ratios (Crockett & Eisenberg, 1987).

Mantled howler monkeys also have bisexual dispersal, with males and females typically leaving natal groups at between 1.5 and 4 years old (Clarke & Glander, 2008; Treves, 2001). After dispersing, both male and female solitary individuals initially remain within their natal group's range, then increase their distance, eventually approaching other groups (di Fiore et al., 2011; Glander, 1992). Females typically join other social groups within 6–12 months, while males may spend up to 36–40 months alone before joining a social group in which they often remain for the rest of their lives (Glander, 1992; but see Clarke & Glander, 2008, 2010). Males likely spend so much time as solitary individuals in order to sufficiently increase body size and strength (di Fiore et al., 2011; Glander, 1992), and many do not survive this life stage (Cristóbal Azkarate, Urbani, & Asensio, 2015; Crockett & Eisenberg, 1987). Once lone males are large enough to successfully challenge other adult males, a solitary male usually targets a specific group (Glander, 1992). The resident male(s) will attack the new male, and the solitary male will either win a fight against the highest-ranking male in the social group and become the new alpha male, or lose the fight and remain solitary (Clarke & Glander, 2004; Dias, Rangel-Negrin, Veà, & Canales-Espinosa, 2010; Glander, 1992). Alternately, solitary males may instead recruit or partner with other extra-group individuals to form new social groups rather than joining existing groups (Glander, 1992).

This investigation compares the tree use, feeding, and long-distance vocalization behavior of lone male mantled howler monkeys to group-living males within a fragmented tropical rainforest in north-eastern Costa Rica, the La Suerte Biological Research Station (LSBRS). Mantled howler monkey population density is much higher at LSBRS than at other sites, with 73.8 individuals/km² at LSBRS (Schreier & Bolt, 2020) compared to 5–20 individuals/km² elsewhere (Clarke, Crockett, Zucker, & Zaldivar, 2002; Estrada, 1982; Stoner, 1996). Monkeys may thus be crowding into LSBRS from surrounding areas, with individuals facing a high level of competition for access to food and membership in social groups (Schreier et al., accepted). This high density means that there may be a higher proportion of lone males at LSBRS than in other locations, making this investigation especially appropriate to undertake at this site.

1.1 | Hypothesis: Lone males' behavioral ecology will differ from group-living males

Mantled howler monkey habitats vary in food quality (Glander, 1981; Glander, 1982), and monkey groups have been observed actively defending clumped resources when other groups are present in areas of home range overlap (e.g., Carpenter, 1934; Chivers, 1969; but see Asensio, José-Domínguez, & Dunn, 2018; Crockett & Eisenberg, 1987). If mantled howler monkey groups defend forest areas with higher-quality vegetation, such as preferred larger trees (Chapman et al., 1992; Dunn, Cristóbal-Azkarate, & Veà, 2009; Estrada, Juan-Solano, Martínez, & Coates-Estrada, 1999) which generally contain more high-quality resources like fruit and flowers (Leighton & Leighton, 1982), group-living individuals are more likely to

gain access to these contested resources than lone males (Majolo, de Bortoli Vizioli, & Schino, 2008; Wrangham, 1980). We therefore predict that group-living males will feed and rest in larger trees than lone males (Chapman et al., 1992; Dunn et al., 2009; Estrada et al., 1999). We also predict that while feeding, lone males will consume more low-quality foods, including more stems, vines, and leaves, and less high-quality foods, including fruit, than group-living males.

Based on Glander's observation that solitary mantled howler monkeys are "secretive and do nothing to attract attention" (1992, p. 424), we also predict that solitary male howler monkeys will significantly differ from group-living males in howling behavior. Previous research at LSBRS suggested that mantled howler monkeys howl to defend access to preferred resources (Bolt et al., 2019; Bolt, Russell, et al., 2020). Given that it is likely more adaptive for lone males to avoid detection by predators than to advertise occupancy of an area (Bolt, 2016a) or to compete with larger groups for access to resources (Majolo et al., 2008; Wrangham, 1980), we expect that lone males will have lower howling rates and shorter howling bouts, triggered by different precursors, than group-living males.

2 | METHODS

2.1 | Study site

We conducted this study in northeast Costa Rica at the LSBRS (10°26'N, 83°46'W). This site is a 3 km² anthropogenically disturbed tropical lowland rainforest and shows seasonal variation in amount of rainfall (Bezanson, 2009; Brandt & Singleton, 2018). The main area where we collected data is formed of two linked forest fragments ("small forest" = 0.35 km² to the south and "large forest" = 0.94 km²

to the north) and a central clearing for "camp" (0.07 km²) (Schreier et al., accepted; Bolt et al., 2018; Bolt et al., 2019; Bolt, Russell, et al., 2020; Bolt, Schreier, Voss, Sheehan, & Barrickman, 2020; Garber, Molina, & Molina, 2010; Molina, 2015; Pruetz & Leason, 2002). Previous research on vegetation quality at the site found higher tree species richness and canopy cover and a trend toward larger trees in the undisturbed forest interior compared to 100 m anthropogenic edge areas (i.e., within 100 m of human-modified landscape such as cattle pasture or road) (Bolt et al., 2018, 2019). These vegetation features are positive indicators of habitat caliber for monkeys (Arroyo-Rodríguez & Mandujano, 2006; Ross & Srivastava, 1994), indicating that vegetation quality is higher in the forest interior at LSBRS.

We observed and collected data from 11 social groups of mantled howler monkeys at LSBRS (Schreier et al., accepted; Bolt et al., 2019; Bolt, Russell, et al., 2020) in addition to 12 individual lone males over the course of the study period (Table 1). Mean group size was 9.3 monkeys, with a mean of 2.4 adult males (range = 1–5) and 4 adult females (range = 1–12). The majority of the groups had multiple males, with a single one-male group during most field seasons (Table 1). The mantled howler monkey is sympatric with the Central American spider monkey (*Ateles geoffroyi*) and the white-faced capuchin monkey (*Cebus capucinus*) at LSBRS.

2.2 | Monkey behavioral sampling data collection

We collected data on mantled howler monkey feeding and resting tree use, feeding, and howling behavior for a total of 10 months spanning both wet (May–August) and dry (December–January) seasons from 2017 to 2020: May to August 2017, May to August 2018,

TABLE 1 Behavioral sampling effort for solitary and group-living male mantled howler monkeys (*Alouatta palliata*) at LSBRS

Sampling season	Number of solitary males sampled	Number of multi-male groups	Number of one-male groups	Male to female ratio	Hours of lone male behavioral sampling	Hours of lone male howl sampling	Hours of group male behavioral sampling	Hours of group male howl sampling
May–August 2017	2	9	2	1:1.7	4.5	3.5	96.5	207
May–August 2018	4	10	1	1:1.6	17.5	14	147	361
December 2018–January 2019	1	10	1	1:1.8	3	1.5	16.5	15.5
June–August 2019	3	10	1	1:2	8	15.5	0	25
December 2019–January 2020	2	11	0	1:1.5	12	14	18.5	52.5
Total	12				45	48.5	278.5	661

Abbreviation: LSBRS, La Suerte Biological Research Station.

December 2018 to January 2019, June to August 2019, and December 2019 to January 2020 (Table 1). Between one and six people collected behavioral data during each day of sampling, and data collectors worked independently and deliberately rotated between various areas of the forest in order to ensure sampling of different monkeys and groups and representation of all forest areas. Data collectors used transect lines spaced approximately 150 m apart (see Bolt et al., 2018; Bolt, Schreier, et al., 2020; Russell, 2018) as reference points for locating individuals and groups, but additionally sampled monkeys opportunistically when encountered. Individual males were sampled once daily for 30 min but occasionally sampled a maximum of twice daily with samples separated by at least 2 hr (Schreier et al., accepted). While sampling groups, we used body characteristics and other identifying markings when present to prevent the resampling of individuals. Because individual identity is not reliably known in the population of howler monkeys at LSBRS, it is unknown how many times each individual was sampled across or between each study season. At the start of each 30-min sampling period, a GPS point was taken to mark the location of the sample using a Garmin GPSMAP 62s hand-held Navigator. Researchers actively searched for and sampled solitary and group-living males daily between 500 and 1800 hr. All monkeys were habituated and did not react to researcher presence.

We defined solitary males as those without any conspecifics within 40 m or within visible range for the duration of focal sampling of that individual. While it is possible that some group-living males may have been misidentified as solitary males, we minimized the chances of this by following solitary males for as long as possible when detected, and by omitting all behavioral samples from analysis when other howler monkeys were within visual range of the focal animal. Additionally, we were generally able to identify individual solitary males during each sampling season through their body and testes size and ranging patterns, further preventing misidentification of solitary males as group males. We similarly followed social groups for as long as possible when detected, collecting data on individual females and juveniles in addition to group-living males as part of a large-scale project on howler monkey behavioral ecology (e.g., Schreier et al., accepted). Our observation of each howler monkey group for as long as possible on a given day also minimized our chances of misidentifying a group-living male as a lone male. To assess interobserver reliability during data collection, researchers simultaneously scored monkey behaviors; we achieved a 94% reliability rate (Schreier et al., accepted).

2.3 | Monkey tree use and feeding behavior data collection

Data on tree use and feeding behavior were collected during 30-min focal samples on individual male howler monkeys, with instantaneous scan samples taken at 2-min intervals (Altmann, 1974). At the start of each sample, we noted whether the individual was a solitary male or a member of a social group and during each interval, we recorded the

focal animal's activity (i.e., resting, feeding, traveling, social, other; Schreier et al., accepted). During feeding, we recorded plant parts consumed (leaf, fruit, flower, stem, or vine [i.e., liana]) (following Russell, 2018). If an individual monkey fed or rested in the same tree for two or more consecutive 2-min samples, the tree was identified as a feeding or resting tree and its circumference was measured using a standard forestry tape reel. Tree diameter at breast height (DBH) was then calculated. Out of a total of 323.5 hr of individual male focal data (45 hr on lone males and 278.5 hr on group-living males), we measured 91 individual feeding trees and 307 individual resting trees, and recorded plant parts consumed from 364 discrete feeding bouts.

2.4 | Howling data collection

During all time spent with a mantled howler monkey group or solitary male, we used all-occurrences sampling (Altmann, 1974) to record group-wide and lone male howling behavior (following Bolt, 2013a, 2013b; Bolt et al., 2019; Bolt, Russell, et al., 2020; Hopkins, 2013). The group and/or individual male needed to remain consistently visible for sampling to continue, enabling us to reliably record when group-living or solitary males howled. When howling from a solitary male or from any member of a focal group was heard, we recorded the beginning and ending times of the howling bout, and any potential trigger(s) in the seconds preceding the howl (Bolt et al., 2019; Bolt, Russell, et al., 2020). Howls were defined as male-specific, high-amplitude Type 1/A loud calls (Altmann, 1974; Baldwin & Baldwin, 1976; Carpenter, 1934) separated from other long-distance vocalizations made by the caller or members of the same group by at least 2 s. If individual vocal utterances were continuous or separated by less than 2 s, they were considered part of the same howl vocalization (Bolt et al., 2019; Bolt, Russell, et al., 2020). Howls were contained within howling bouts, which consisted of one or more howls occurring less than 60 s apart (Bolt et al., 2019; Bolt, Russell, et al., 2020; Sekulic, 1982b). We base our analyses on 709.5 hr of all-occurrences of howling data: 48.5 hr collected on lone males and 661 hr on group-living males.

2.5 | Animal welfare note

This research adhered to the ABS Guidelines for the Use of Animals in Research and followed the recommendations of the ARRIVE guidelines. Our research met the legal requirements of Costa Rica and was conducted with the permission of the Molina family, who own the LSBRS site. Our research protocol was approved by the Regis University Animal Care Committee (IACUC permit #17-006).

2.6 | Data analysis

To compare differences in mean size of feeding and resting trees between lone males and group-living males, we used Mann-Whitney

U tests. We used a two-way Pearson chi-squared test to compare plant parts consumed by lone males versus group-living males. As a post hoc test to determine which plant parts were consumed by males more or less often than expected based on chance, we examined adjusted residuals and identified those with *z*-scores greater than ± 1.97 as indicating significant differences.

We also used Mann-Whitney *U* tests to determine differences between lone males and group-living males in mean howling rates and mean length of howling bouts. To compare whether howling triggers differed from those expected by chance in lone and group-living males, we used a two-way Pearson chi-squared test. As a post hoc test to determine which triggers varied between lone males and group-living males, we examined adjusted residuals and identified those with *z*-scores greater than ± 1.97 as indicating differences between observed and expected values based on chance. We used SPSS version 26 (IBM SPSS Statistics, IBM Corporation, Armonk, NY) for all statistical tests, and set the alpha level to .05.

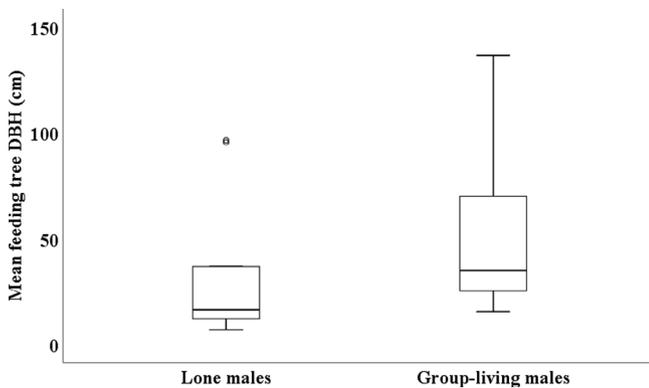


FIGURE 1 Mean feeding tree diameter at breast height (DBH) in cm for lone males versus group living males at LSBRS ($p = .042$). Boxes represent interquartile ranges, lines represent median values, whiskers represent maximum and minimum values, and dots represent outliers

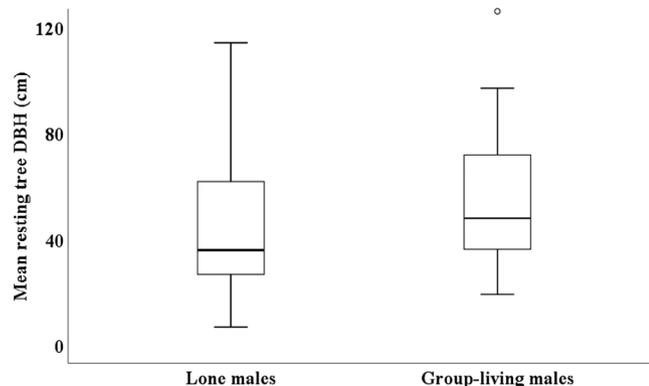


FIGURE 2 Mean resting tree diameter at breast height (DBH) in cm for lone males versus group living males at LSBRS ($p = .001$). Boxes represent interquartile ranges, lines represent median values, whiskers represent maximum and minimum values, and dots represent outliers

3 | RESULTS

Overall, mean male feeding tree DBH was 57.1 cm ($SD = 57.2$, range = 5.7–318.5 cm, $N = 91$ feeding trees), while mean male resting tree DBH was 70.1 cm ($SD = 61.2$, range = 5.1–445.9 cm, $N = 307$ resting trees). Lone males fed from trees with significantly smaller DBH than group-living males ($X + SD = 40.4 + 46.4$ cm, range = 7–156 cm, $N = 13$ lone male feeding trees vs. $X + SD = 59.9 + 58.6$ cm, range = 5.7–318.5 cm, $N = 78$ group-living male feeding trees;

TABLE 2 Mantled howler monkey (*Alouatta palliata*) food items consumed at LSBRS showing *z*-scores for adjusted residual values

	Leaves	Fruit	Flowers	Stems	Vines
Lone males	-2.2*	-0.1	1.1	3*	2.1*
Group-living males	2.2*	0.1	-1.1	-3*	-2.1*

Note: Asterisks show significant differences between lone males and group-living males (values $> \pm 1.97$). Negative results indicate that food items were consumed less than expected by chance, while positive results indicate that food items were consumed more than expected by chance.

Abbreviation: LSBRS, La Suerte Biological Research Station.

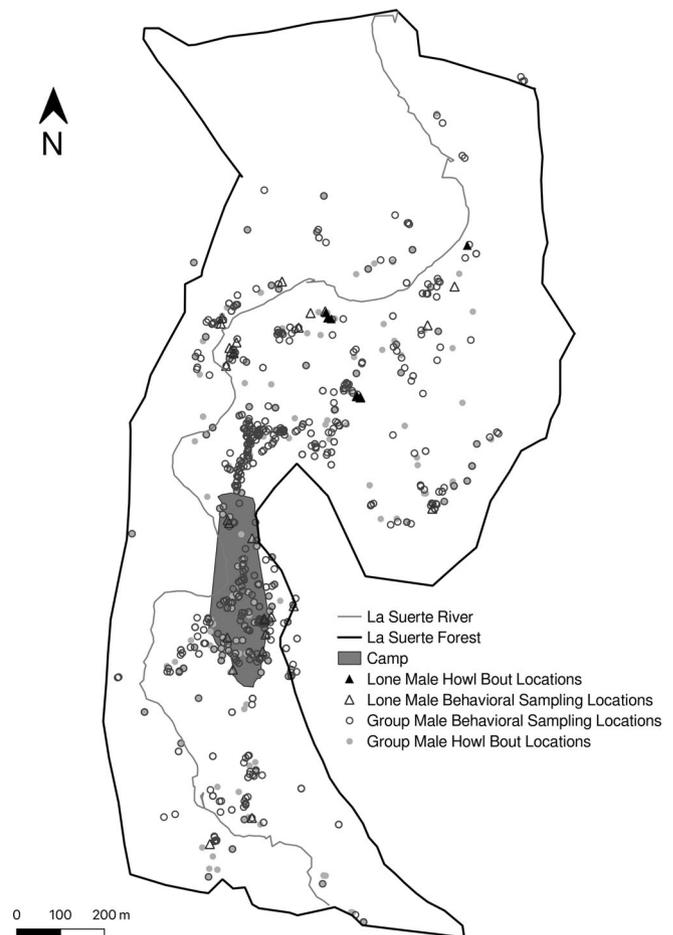


FIGURE 3 Map of La Suerte Biological Research Station showing howling bout locations and behavioral sampling locations for each 30 min of sampling, for both lone males and group-living males

$U = 328.0$, $z = -2.0$, $p = .042$, Figure 1). Lone males also rested in trees with significantly smaller DBH than group-living males ($X + SD = 53 + 51.1$ cm, range = 7–279 cm, $N = 38$ lone male resting trees vs. $X + SD = 72.6 + 62.2$ cm, range = 5.1–445.9 cm, $N = 269$ group-living male resting trees; $U = 3,473.5$, $z = -3.2$, $p = .001$, Figure 2).

Lone males and group-living males consumed significantly different amounts of plant parts than expected based on chance ($\chi^2_4 = 15.3$, $N = 364$ plant parts consumed, $p = .004$, Table 2). The strength of association between variables was strong ($\phi_c = 0.2$, $p = .004$), and post hoc examination of adjusted residuals indicated that when adjusted for sample size, lone males consumed significantly more stems (6% of total food items) and vines (4% of food items) and fewer leaves (74% of food items) than expected, while group-living males consumed significantly fewer stems (0.6% of food items) and vines (0.6% of food items) and more leaves (86% of food items) than expected based on chance (Table 2). Lone males and group-living males ate fruit (8 vs. 8.3% of food items) and flowers (8 vs. 4.5% of food items) in the amounts expected based on chance (Table 2).

Overall, mean howler monkey howling rate was 1.1 bouts/hr (range = 0–40 bouts/hr, $N = 709.5$ hr), while mean howling bout length was 127.4 s/bout (range = 1–2,882 howls/bout, $N = 769$ bouts). Lone males had significantly lower howling rates than group-living males ($X = 0.8$ bouts/hr, range = 0–40 bouts/hr, $N = 48.5$ hr for lone males vs. $X = 1.1$ bouts/hr, range = 0–18 bouts/hr, $N = 661$ hr for group-living males; $U = 53,339.0$, $z = -3.5$, $p < .001$; Figure 3). Mean howl bout

length also differed significantly between lone males and group-living males ($U = 5,195.5$, $z = -2.0$, $N = 769$ howl bouts, $p = .043$; Figure 4), with longer howl bouts by lone males compared to group-living males ($X = 306.2$ s; range = 2–1,783 s; $N = 19$ bouts for lone males vs. $X = 122.9$ s; range = 1–2,882 s; $N = 750$ bouts for group-living males; Figure 4). Howling bouts between lone males vs. group-living males had significantly different triggers ($\chi^2_4 = 11.9$, $N = 706$ howl bouts, $p = .018$). The strength of association between variables was strong ($\phi_c = 0.13$, $p = .018$), and post hoc examination of adjusted residuals indicated that when adjusted for sample size, howls by lone males were more frequently preceded by anthropogenic noise than expected based on chance, while howls by group-living males were less frequently preceded by anthropogenic noise than expected based on chance (Table 3). Observed values for other triggers, such as no observed precursor, other group howling, environmental factor, and interspecies interaction did not differ from expected values (Table 3).

4 | DISCUSSION

We found support for our hypothesis that lone male mantled howler monkeys would differ in behavioral ecology from group-living males. Although males were sampled approximately equally across forest regions of varying overall vegetation quality (Bolt et al., 2018, 2019; Bolt, Russell, et al., 2020; Bolt, Schreier, et al., 2020; Russell, 2018), lone males consistently used significantly smaller trees with generally lower-quality food resources to feed and rest in than group-living males. Mantled howler monkey feeding trees produce varying amounts of nutrients and secondary compounds, leading to differences in quality between individual trees and tree species (Glander, 1981; Glander, 1982). Feeding tree size is also important, with mantled howler monkeys consistently using and preferring large trees for feeding (Chapman, 1988a; Estrada et al., 1999), particularly those with ≥ 60 cm DBH (Chapman, 1988b; Dunn et al., 2009; LaRose, 1996), which produce greater amounts of food than smaller trees (Chapman et al., 1992) and allow monkeys to feed in the same tree for a longer duration of time (Chapman, 1988b). As an energy-minimizing species (di Fiore et al., 2011; Milton, 1980), it is adaptive for howler monkeys to conserve energy whenever possible by curtailing travel.

Similarly, monkeys also probably spend more time resting in large trees due to increased ability to hide from predators within their denser foliage. With terrestrial predators like the ocelot (*Leopardus*

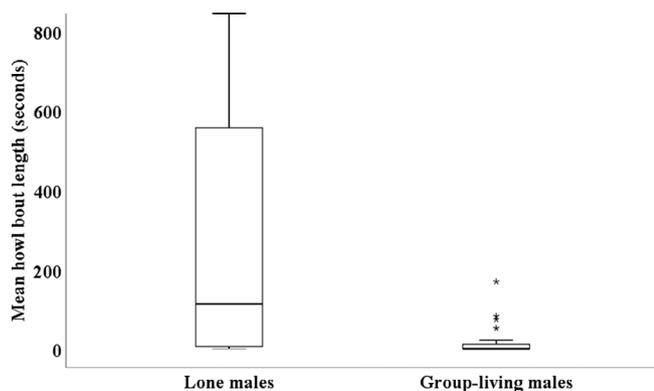


FIGURE 4 Mean howl bout length in lone males versus group-living males at La Suerte Biological Research Station (LSBRS) ($p = .043$). Boxes represent interquartile ranges, lines represent median values, whiskers represent maximum and minimum values, and asterisks represent extreme outliers

TABLE 3 Mantled howler monkey (*Alouatta palliata*) howling precursors at LSBRS showing z-scores for adjusted residual values

	No howling precursor	Howl from other group	Environmental factor	Interspecies interaction	Anthropogenic noise
Lone males	-1.5	1.6	-0.3	-1.1	2.8*
Group-living males	1.5	-1.6	0.3	1.1	-2.8*

Note: Asterisks show significant differences between lone males and group-living males (values $> \pm 1.97$). Negative results indicate that howling occurrence following a precursor was lower than expected by chance, while positive results indicate that howling occurrence following a precursor was higher than expected by chance.

Abbreviation: LSBRS, La Suerte Biological Research Station.

pardalis) and aerial predators like the harpy eagle (*Harpia harpyja*) present at LSBRS (Bolt, Russell, et al., 2020; Cristóbal-Azkarate, Urbani, & Asensio, 2015; Molina, 2015), groups can likely conceal themselves more effectively when in larger trees. While solitary animals are generally more vulnerable to predation than group-living animals (e.g., Bertram, 1978), they likely do not require as large a tree to conceal themselves as would a group. With resting comprising the majority of howler monkey daily activity budgets at LSBRS (Schreier et al., accepted; Occhibove et al., 2015), it makes sense for group-living monkeys to preferentially rest in trees that are large enough to accommodate entire social groups and to therefore minimize individual chances of predation through the dilution effect (Alatalo & Helle, 1990; Bertram, 1978).

Tree use differences are likely related to variation in competitive ability between lone males and group-living males. Based on the inferior competitive ability of individuals compared to groups (Majolo et al., 2008; Mosser & Packer, 2008; Parker, 1974; Wrangham, 1980), lone males are less likely to be able to feed or rest in preferred mature trees for any length of time if a group is nearby, so it may be more adaptive for lone males to spend time in smaller feeding and resting trees across forest regions. Lone males may therefore be using a competition avoidance strategy, thus minimizing their chances of being displaced by a larger howler monkey group and reducing their need to spend additional energy on travel and/or agonism. It is beneficial for all monkeys to both conserve energy and decrease the probability of receiving aggression, which can lead to stress and injury (Beehner, Bergman, Cheney, Seyfarth, & Whitten, 2005; Tennenhouse, 2016; Tennenhouse, Putman, Boisseau, & Brown, 2017). While we did not collect data on displacement of lone males from particular trees by howler monkey groups, we consistently observed lone males traveling away from localized forest areas whenever monkey groups approached (Bolt, personal observation), lending support to this idea.

While feeding, lone males consumed greater amounts of stems and vines and lesser amounts of leaves than expected, while group-living males displayed the opposite pattern. These findings support our prediction that lone males would consume a larger amount of low-quality food items, with vines (i.e., woody or herbaceous lianas) considered fallback foods for the mantled howler monkey (Dunn, Asensio, Arroyo-Rodríguez, Schnitzer, & Cristóbal-Azkarate, 2012), and stems (i.e., woody or herbaceous plant components including leaf petiole and pulvinus that serve as leaf attachment structures; Baum, 2005; Russell, 2018) also likely comprising nutrient-poor fallback foods. Fallback foods are poor-quality foods that are widely distributed throughout habitats and consumed at higher rates during times of reduced food availability (Marshall, Boyko, Feilen, Boyko, & Leighton, 2009). Vines occur at higher abundance in fragmented and disturbed forest environments (Arroyo-Rodríguez, Asensio, Dunn, Cristóbal-Azkarate, & Gonzalez-Zamora, 2015; Laurance, Ferreira, Rankin-De Merona, & Laurance, 1998), such as LSBRS, and mantled howlers living in environments with high population densities feed on vines at high rates (Asensio, Cristóbal-Azkarate, Dias, Veá, & Rodríguez-Luna, 2007; Rodríguez-Luna, Domínguez-Domínguez, Morales-Mávil, & Martínez-Morales, 2003). At a tropical rainforest

site in Los Tuxtlas, Mexico, monkeys consumed vines for increasing percentages of total feeding time, ranging from 8.8 to 33% as monkey population density increased over time (Asensio et al., 2007; Rodríguez-Luna et al., 2003). Although overall rate of vine consumption was much lower for both lone and group-living males at the densely-populated LSBRS site (4 vs. 0.6% of total food items consumed), differences in vine consumption attest to differences in feeding behavior between lone and group-living males. Stems were also consumed at low rates by howler monkeys in other tropical environments (Glander, 1981; Muñoz, Estrada, Naranjo, & Ochoa, 2006), likely because they contain high amounts of cellulose, few nutrients, and irritating features such as thorns (Gotsch et al., 2015; Milton, 1980). Lone males may have consumed more low-quality, fallback food resources than expected due to differences in localized habitat quality, with smaller feeding and resting trees containing fewer leaves and stems but comparable numbers of vines as in larger trees (Arroyo-Rodríguez et al., 2015; Laurance et al., 1998). This interpretation may also account for our finding that lone males consumed fewer leaves than expected, since their smaller feeding trees would also likely contain fewer leaves (Chapman et al., 1992; LaRose, 1996), requiring them to supplement with any lower-quality stems and vines available.

While our prediction assumed leaves to generally be a low-quality food source for mantled howler monkeys, we did not differentiate between young and mature leaves, which vary widely in nutritive quality (di Fiore et al., 2011; Milton, 1979). Compared to mature leaves, young leaves contain more protein, less cellulose, and fewer secondary compounds that may act as irritants to monkeys (di Fiore et al., 2011; Milton, 1979; Occhibove et al., 2015), and are preferred by mantled howler monkeys along with fruit and flowers (Estrada et al., 1999; LaRose, 1996). However, previous research on young versus mature leaf consumption at LSBRS found that howler monkeys consistently fed on mature leaves throughout the forest, and when nutritive contents were examined, both leaf types contained sufficient protein to meet howler monkey nutritional needs, with more sugars present in mature leaves (Occhibove et al., 2015). Lone male howler monkeys may therefore have consumed fewer leaves than expected due to both types of leaves being desirable resources at LSBRS, and group-living monkeys generally outcompeting solitary males for large trees containing more leaves. Since howlers here consistently range throughout the site (Bolt et al., 2018; Bolt, Schreier, et al., 2020) and do not change their activity budgets when in poorer habitats (Schreier et al., accepted), lone males may therefore not be able to spend more time traveling to new feeding trees when in such habitats to find preferred food items. This means that lone males must then compensate by consuming whatever food items are available in small trees, such as stems and vines but fewer leaves.

Interestingly, both lone and group-living males consumed high-value food items such as fruit and flowers in the same proportion as expected based on chance. With more fruit and flowers generally available in larger trees (Leighton & Leighton, 1982) and group-living males feeding from larger trees than lone males (this study), our findings suggest that intragroup feeding competition may be diminishing

the amount of high-value food items that individual group-living males can obtain, making it approximately equal to those obtained by lone males from smaller trees. Group-living males face feeding competition from females and juveniles in one-male groups, and additionally from other males in multi-male groups (Glander, 1992). In multi-male mantled howler monkey groups, there are male dominance hierarchies which reflect individual differences in competitive ability (Jones, 1980), suggesting that higher-ranking males may consume a greater proportion of high-value food items than lower-ranking males within the same social group. We collected data on primarily multi-male groups at LSBRS (Table 1), but could not assess the impact of dominance rank on feeding behavior due to our inability to consistently identify individuals in this population. Future research should address how dominance rank affects intragroup feeding competition at LSBRS.

Future research should also examine the impact of seasonal differences on male feeding behavior. Our investigation did not take into account any potential seasonal differences in resource availability (Glander, 1981); for example, fruit and flowers produced by both vines and trees may be available at different times of year, and have been found to be seasonally variable at other tropical rainforest sites (e.g., Estrada et al., 1999). We did not collect vegetation data at LSBRS during any dry season (i.e., December–January) sampling periods (Bolt et al., 2018, 2019; Bolt, Schreier, et al., 2020), but found that all males consumed a greater proportion of leaves during dry season sampling compared to during the wet season (i.e., May–August) sampling (Schreier & Bolt, unpublished data). However, only group-living males consumed a greater proportion of fruit during wet season sampling compared to dry season sampling (Schreier & Bolt, unpublished data), suggesting that group-living males may be consistently outcompeting lone males for this high-quality resource at certain times of year. Across seasons, lone males consumed more stems and vines and fewer leaves than group-living males (Schreier & Bolt, unpublished data). Male feeding and resting tree DBH also varied seasonally, with all males consistently using larger feeding and resting trees during wet season sampling and smaller trees during dry season sampling (Schreier & Bolt, unpublished data). However, group-living males consistently used larger trees than lone males across seasons. Future study should more fully investigate these seasonal variables.

In addition to tree use and feeding differences between lone and group-living males, we also found differences in howling behavior. Lone males howled at lower rates than group-living males, although howling bouts were longer when they did occur. Previous research has shown that howling rate may relate to group size in mantled howler monkeys, with larger groups howling at higher rates than smaller groups (Schreier & Bolt, 2020). Howling rate may therefore relate to mate defense for group-living males, with males howling to advertise the number of sexually mature males already present in a group, and to therefore deter new males from joining and gaining sexual access to females (Bolt, 2013a; Schreier & Bolt, 2020). While this interpretation is plausible for males already in social groups, lone males do not have any females to defend. Both lone and group-living males may additionally howl to attract mates. The mate attraction

hypothesis (e.g., Bolt, 2013a; Delgado, 2006) suggests that males howl as a courtship display to females, potentially as an honest indicator of individual male quality (Zahavi, 1975). Males may therefore howl to attract extra-group females, potentially allowing solitary males to form social groups by having solitary females join them (Glander, 1992). This may explain why lone males had longer howling bouts than group-living males at LSBRS.

Previous howling research at LSBRS also found support for the ecological resource defense hypothesis, with males producing longer howling bouts when in forest zones with generally richer vegetation (Bolt et al., 2019; Bolt, Russell, et al., 2020). Lone males may therefore howl for longer durations of time when occasionally in areas with rich ecological resources, such as when in larger trees. However, lone and group-living males did not differ in general distribution or activity budget across lower-quality anthropogenic edge and higher-quality forest interior zones at LSBRS, and preliminary investigation of tree usage while howling did not uncover any relationship between tree size and howling behavior (Bolt & Schreier, unpublished data). Alternately, since lone males are not likely to be superior competitors for contested resources when faced with a group, they may howl for longer durations of time when they perceive that another individual or group is in close proximity to facilitate spatial distancing and avoid direct confrontation (Kitchen et al., 2015). While we did not collect systematic data on the distance between groups, they varied widely with overlap among groups (Bolt, personal observation), and it is possible that increased proximity to other individuals or groups may increase howl bout length. If producing longer howling bouts helps lone males avoid competition with groups and thus increase their chances of survival (Chiarello, 1995; Sekulic, 1982b), then howling enhances the fitness of lone males more than group-living males.

It is also possible that lone males may howl for longer durations of time to reduce predation risk, using howls to confuse and drive away potential predators (Bolt, 2016b). However, when howl triggers were examined, lone males did not howl in response to interspecies encounters—including those involving potential predators at LSBRS—any more than would be expected based on chance. Instead, lone males howled in response to anthropogenic noise more often than expected, but not to any other potential triggers. Mantled howler monkeys are known to respond to high-amplitude acoustic disturbances such as planes, vehicles, and chainsaws (Baldwin & Baldwin, 1976; Carpenter, 1934), and likely do so because of heightened arousal levels after being startled (Kitchen et al., 2015). At LSBRS, anthropogenic noise is audible throughout the site (Bolt, personal observation) and monkeys are equally likely to howl in response to anthropogenic noise across different forest regions (Bolt et al., 2019; Bolt, Russell, et al., 2020). It is unclear why lone males howl in response to anthropogenic noise at LSBRS more often than expected compared to other triggers, but this may be due to a misperception that anthropogenic noise reflects the presence of another howler group nearby, or be an artifact of the small number of lone male howling bouts in our dataset. Alternately, howling triggers may have varied due to differences in male age and experience with hearing anthropogenic noise. The lone males sampled are liable

to be younger than group-living males, with lone male age estimated to range from 1.5 to 5.2 years old and group-living males older than 5.2 years in mantled howler monkeys (Glander, 1992). It is unknown whether males may change their howling behavior in response to greater exposure to and understanding of their environments, but this phenomenon is present in other primate species (e.g., vervet monkey [*Chlorocebus pygerythrus*], Seyfarth & Cheney, 1990). If so, lone males may not yet have learned how to gauge the level of threat from anthropogenic noise, which unlike other howling triggers, is a stimulus that was not present during their evolutionary past. Young males may be overreacting to anthropogenic noise because they have not yet learned to appropriately calibrate their response to potential threats, unlike older group males. We did not consistently estimate or collect data on lone male age during sampling, but did notice variation in body and scrotal size between lone male individuals, suggesting that the lone males observed at LSBRS likely represented a range of ages, but appeared to be generally younger than group-living males. Further research on the relationship between male howler monkey age and howling behavior is needed.

Overall, our results demonstrate that lone male mantled howler monkeys at LSBRS differ in their behavioral ecology from group-living males, with lone males using smaller feeding and resting trees, consuming more fallback foods, and howling less often but for longer durations of time. While the amount of data we collected on lone male behavioral ecology was relatively small, the difficulty of finding and following "secretive solitaries" (Glander, 1992) for any consistent duration of time has likely prevented similar studies from being undertaken at other research sites. The dearth of quantitative information available about the solitary life stage for male primates suggests that our data, while limited, represent an important resource for better understanding the behavioral ecology of lone males in a folivorous-fruitivorous monkey species. Through examining how the solitary life stage is manifested in an energy-minimizing platyrrhine species, we gain valuable insight into this little-understood time of life for male primates.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

AUTHOR CONTRIBUTIONS

Laura M. Bolt: Conceptualization; data curation; formal analysis; investigation; methodology; project administration; supervision; visualization; writing-original draft; writing-review and editing. **Maeve N. Cavanaugh:** Software; visualization; writing-review and editing. **Amy L. Schreier:** Conceptualization; data curation; formal analysis; funding acquisition; investigation; methodology; project administration; supervision; writing-review and editing.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available in figshare at 10.6084/m9.figshare.12844391.

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