Behavioral variability in brown howler monkeys (*Alouatta guariba*) at low density at the Reserva Particular do Patrimônio Natural – Feliciano Miguel Abdala

By

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Dedicated to my grandma, Betty Jean, for unconditional love during her lifetime,
and to too many others in my life who were called away before we were ready to say goodbye.

It gets easier, but it never gets easy.

Jason Isbell

Acknowledgments

I have been thinking a lot about resilience as I finish this work, both in my personal life and in the lives of the primates that I had the privilege to study. Resilience is not an inherent characteristic in any individual or any system – it is something that is built over time as we face trials and forge our identities. As a queer trans person and a scholar, I would not have been able to get to this point in my life without a tremendous degree of resilience – but I did not make it here through resilience alone. This work is the culmination of many years of training and collaboration and would not have been possible at all without the support of an international team of friends, colleagues, and advisors. Thank you, sincerely, to everyone who has helped me in any way throughout my academic career.

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My thesis is this

I want to believe to believe

to believe in

a universe willing

to understand

Chase Berggrun

Abstract

This dissertation provides a review of primate dietary flexibility under a variety of social and ecological circumstances and describes the impacts of extremely low population density on the behavior and distribution of a vulnerable primate, the brown howler monkey (*Alouatta guariba*), at the Reserva Particular do Patrimônio Natural – Feliciano Miguel Abdala (RPPN-FMA) in Caratinga, Brazil. Specifically, we (1) synthesized recent literature on behavioral and dietary flexibility across the Primate order and investigated (2) the impact of proximity to anthropogenic disturbances on the social behavior of adults in very small groups and (3) the ecological characteristics of group home ranges and areas with brown howler monkey sightings in comparison to areas without sightings.

Behavioral and ecological data for this project were collected between September 2018 and May 2019 at the RPPN-FMA. Behavioral data were collected from three groups of brown howlers, each with two adult females, one adult male, and associated offspring, with varying degrees of edge exposure in their home ranges. Due to prohibitively small sample sizes only behavioral data from September – November 2018 and April and May 2019 are presented here.

We predicted that variation in exposure to anthropogenic disturbances, as approximated by proportion of forest edge in home ranges ("edge density"), would correlate with variation in diet and social behavior. Specifically, we expected that groups with greater edge density would spend less time socializing than the group in the forest interior and more time feeding on leaves and less time feeding on fruits. We also predicted that, similar to other species of howler monkeys found in small groups, females would have stronger than expected social relationships with one another. We further predicted that, based on low population density and the ideal free model of group distribution, areas with brown howler monkey sightings would be higher quality than areas without sightings.

We found that the group in the forest interior had a consistently strong female-female dyad that associated and groomed more often than would be expected based on group composition, while the two groups with exposure to forest edges had higher intermonthly variation in social behavior and dyadic relationships. We did not find any statistical relationship between habitat quality or diet and proportion of forest edge in monthly home ranges. However, we did observe significant differences in the vegetation characteristics of areas with howler monkey sightings and without howler monkey sightings, suggesting that at low population density howler monkey groups are more likely to be found in higher quality areas of the RPPN-FMA.

These findings further reinforce the relativity of concepts like habitat quality, in that both areas which appear to be lower quality to observers may in fact be tolerable or preferred by our study species and that what is low quality for one species may be tolerable or even preferred habitat for another species.

Introduction

This dissertation provides a review of behavioral and dietary flexibility across the order Primates, evaluates the social relationships of small groups of brown howler monkeys (*Alouatta guariba*) living at low population density, and compares ecological characteristics of howler monkey habitats within the Reserva Particular do Patrimônio Natural – Feliciano Miguel Abdala (RPPN-FMA) in Caratinga, Brazil to provide additional information on a vulnerable species in the aftermath of a disease outbreak that reduced population size by approximately 86% (Possamai et al., 2022; Jerusalinsky et al., 2021).

Behavioral flexibility is a hallmark of the Primate order, and the degree to which primates can adjust their behavior in response to demographic, environmental, or other changes is one determining factor in their persistence in disturbed or degraded habitats (Strier, 2017). Flexibility provides a barrier to extinction in the wake of perturbations and is a critical part of both individual and species-level resilience to immediate and long-term stressors (Strier, 2021). With at least 65% of primate species vulnerable, endangered, or critically endangered and 93% estimated to have declining population sizes (Estrada and Garber, 2022), understanding how species respond to ecological or demographic changes is critical to conservation planning and wildlife management (Strier, 2021).

Chapter 1 of this work provides a review of dietary flexibility across the Primate order. Examples of dietary and behavioral adjustments are contextualized by an overview of theoretical perspectives on what drives primate food choices under different ecological and social scenarios. We highlight the morphological, behavioral, and ecological factors that constrain primates' ability to meet their minimum energetic needs and specifically address the dietary flexibility of species in marginal habitats with an eye to understanding the ways that primates may adapt in the face of extreme ecological shifts induced by anthropogenic climate change.

Chapters 2 and 3 describe patterns of behavioral variability and habitat quality among three small groups of brown howler monkeys at the RPPN-FMA. Compared to other members of the family Atelidae (woolly monkeys, *Lagothrix spp.*; spider monkeys, *Ateles spp.*; and muriquis, *Brachyteles spp.*), howler monkeys are more folivorous and distributed across a wider geographic range, from southern Mexico to northern Argentina (Strier, 1992; Di Fiore et al., 2011). Howler monkeys exhibit high levels of behavioral flexibility, especially dietary flexibility, that allow them to persist in habitats where other primates may not (Eisenberg, 1978; Rosenberger et al., 2011). Howler monkeys, with the exception of mantled howler monkeys (*Alouatta palliata*), tend to live in relatively small groups with 2-4 adult males and 2-4 adult females, spend 60-80% of their day resting, and have relatively small day ranges of less than 600m (Kowalewski et al., 2014). However, while able to tolerate life in degraded habitats, howler monkeys are still at risk of extinction across their range to due genetic isolation as a result of habitat loss and fragmentation, increasing exposure to anthropogenic disturbances, and disease outbreaks (Bicca-Marques et al., 2020).

Brown howler monkeys at our study site, the RPPN-FMA, are part of a diverse primate community that includes the critically endangered northern muriqui (*Brachyteles hypoxanthus*), near-threatened black capuchin (*Sapajus nigritus*), and endangered buffy-headed marmoset (*Callithrix flaviceps*). Brown howler monkey population density and median group sizes had been declining at the RPPN-FMA since the early 1980s when the first systematic study of this population took place (Table 1). Following an outbreak of yellow fever in 2016-2017 (Bicca-Marques et al., 2017), the population experienced a further and extreme decline, reducing density to between 0.04 and 0.07 ind./ha (Possamai et al., 2022). The data presented in chapters 2 and 3 were collected over one year after the peak of the 2016-2017 yellow fever outbreak. While these data were collected in the context of extremely low population density and small group sizes, behavioral observations are unlikely to be biased by reassortment of groups and territories as has been seen in other populations of howler monkeys following

population decline (e.g., Black howler monkeys in Belize after a hurricane; Pavelka & Chapman, 2006).

Chapter 2 describes variation in the social behavior of three small groups of brown howler monkeys with varying degrees of exposure to anthropogenic disturbance. Although social behavior makes up a comparatively small percent of howler monkeys' daily activity budgets (around 5% for many species), intragroup social relationships influence the degree to which females receive protection from possibly infanticidal extra-group males and can form coalitions to exclude extra-group females thereby reducing intragroup competition (Di Fiore et al., 2011). Each of the three study groups had one adult male and two adult females, facilitating direct comparisons. We found that the group in the forest interior (i.e., furthest from anthropogenic disturbances) had a consistently strong female-female dyadic relationship, while the two groups whose habitats had varying exposure to forest edges and anthropogenic disturbance showed greater intermonthly variation in dyadic social relationships. Relationship stability, especially among females, correlates with life-history variables like infant survival in highly social primate species like baboons (i.e., Silk et al. 2003). While our results were not statistically significant, our work contributes to the understanding of behavioral variation in a less-social primate species and points to promising directions for future research into howler monkey sociality.

In chapter 3, we test the ideal free model, which predicts that individuals should distribute themselves in the highest quality habitats available in order to maximize energy gain (Fretwell 1972; Fretwell & Lucas 1970). To test this prediction, we created vegetation plots in areas with howler monkey sightings ("sighted areas" defined by creating buffers around howler monkey sighting points from 2017 and 2018) and areas without howler monkey sightings ("control areas" that fell within the sampling area but outside of the sighted areas). We predicted that sighted areas would be higher quality than control areas, specifically having a more connected and continuous upper canopy, denser shrub layer, a higher number of canopy layers,

more emergent trees, greater median basal area, and taller median tree height (Jung et al., 2015; Ostro et al., 2001). In partial support of our prediction, we found that sighted areas had greater median diameter at breast height (DBH), greater median tree height, higher median basal area, and a greater number of canopy layers than control areas. We did not find significant variation in habitat quality or diet among the three groups despite differences in proportion of forest edge within their home ranges, suggesting that at such low density, remaining howler monkey groups have been able to distribute themselves in similarly high quality areas of the RPPN-FMA. Further, proximity to anthropogenic disturbance did not seem to preclude howler monkeys from selecting or using certain habitats, reinforcing the relativity of terms like high and low habitat quality.

A major limitation of the empirical chapters is the overall paucity of behavioral data from the study period. Only months in which there were at least two half-day (≥6 hour) follows for at least two of the three groups were used in behavioral analyses, thus behavioral data are presented from only five months (September – November 2018 and April and May 2019) of the 10-month study period due to prohibitively small sample sizes. Statistical power and sample size calculations were carried out using the University of California at San Francisco's online Sample Size Calculator (https://sample-size.net) to verify that minimum sample sizes necessary to avoid Type I (with $\alpha = 0.05$) and Type II (ß) statistical errors. All statistical analyses were carried out with these limitations in mind, however, our ability to extrapolate or generalize from these data is limited due to sample sizes.

Nonetheless, this work adds to our understanding of howler monkey behavior and ecology by contributing additional data from a population living at lower density and in smaller groups than is typically seen in this species or genus. Our findings that greater exposure to anthropogenic edges had no significant effect on social behavior and diet and that howler monkeys were distributed in similarly high quality areas of the RPPN-FMA demonstrate that areas which observers may deem lower quality are in fact tolerable or even preferred for study

species. This work further reinforces our understanding that habitat quality is relative and species persistence in any given area depends largely on the degree to which individuals can adjust diet and behavior in response to local ecology.

References

Aureli, F., Fraser, O. N., Schaffner, C. M., & Schino, G. (2012). The regulation of social relationships. In: *The Evolution of Primate Societies,* Mitani, J. C., Call, J., Kappeler, P. M., et al. (eds), University of Chicago Press, Chicago.

Bicca-Marques J. C., Chaves O. M., & Hass, G. P. (2020) Howler monkey habitat to tolerance shrinking: Lifetime warranty or death sentence? *American Journal of Primatology.* 84. https://doi.org/10.1002/ajp.23089

Bicca- Marques, J. C., Calegaro Marques, C., Rylands, A., Strier, K. B., Mittermeier, R., De Almeida, M. A., ... & Teixeira, D. S. (2017). Yellow fever threatens Atlantic Forest primates. *Science Advances* eLetter. https://www.doi.org/10.1126/sciadv.1600946

Di Fiore, A., Link, A., & Campbell, C. J. (2011). The Atelines: Behavior and socioecological diversity in a new world monkey radiation. In: *Primates in Perspective*, Campbell, C. J., Fuentes, A., MacKinnon, K. C., et al. (eds). Oxford University Press

Estrada, A., & Garber, P.A. (2022) Principal Drivers and Conservation Solutions to the Impending Primate Extinction Crisis: Introduction to the Special Issue. *International Journal of Primatology*. 43, 1–14. https://doi.org/10.1007/s10764-022-00283-1

Fretwell, S. D. (1972). *Populations in a seasonal environment.* Princeton, NJ: Princeton University Press.

Fretwell, S. D., & Lucas, H. L. (1970). On territorial behavior and other factors influencing habitat distribution in birds. *Acta biotheoretica*. 19(1), 16-36.

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

Jerusalinsky, L., Bicca-Marques, J. C., Neves, L. G., Alves, S. L., Ingberman, B., Buss, G., Fries, B. G., … de Melo, F. R., Mittermeier, R. A. & Cortes-Ortíz, L. (2021). *Alouatta guariba* (amended version of 2020 assessment). *The IUCN Red List of Threatened Species* https://dx.doi.org/10.2305/IUCN.UK.2021-1.RLTS.T39916A190417874.en

Jung, L., Mourthe, I., Grelle, C. E. V., Strier, K. B., & Boubli, J. P. (2015) Effects of local habitat variation on the behavioral ecology of two sympatric groups of brown howler monkey (*Alouatta clamitans*). *PLoS ONE.* https://doi.org/10.1371/journal.pone.0129789

Oklander, L.I., Buss, G., Bicca-Marques, J.C., Hirano, Z. B., Chaves, O. M., ... Jerusaliksky L. (2022) Brown Howler Monkey *In* Mittermeier, R. A., Reuter, K. E., Rylands, A. B., Jerusalinsku, L., Schwitzer, C., Strier, K. B., Ratsimbazafy, J., & Humle, T. *Primates in Peril: The World's 25 Most Endangered Primates 2022-2023*. IUCN SSC Primate Specialist Group, International Primatological Society, and Re:wild, Washington, D.C.

Ostro, L. E. T., Silver, S. C., Koontz, F. W., Horwich, R. H., & Brockett, R. (2001) Shifts in social structure of black howler (*Alouatta pigra*) groups associated with natural and experimental variation in population density. *International Journal of Primatology.* 22. https://doi.org/10.1023/A:1012013315920

Pavelka, M.S.M., & Chapman, C.A. (2006). Population Structure of Black Howlers (*Alouatta pigra*) in Southern Belize and Responses to Hurricane Iris. In: Estrada, A., Garber, P.A., Pavelka, M.S.M., Luecke, L. (eds) *New Perspectives in the Study of Mesoamerican Primates*. Springer, Boston, MA. https://doi.org/10.1007/0-387-25872-8_7

Possamai, C. B. P., de Melo, F. R., Mendes, S. L., & Strier, K. B. (2022) Demographic changes in an Atlantic Forest primate Community following a yellow fever outbreak. *American Journal of Primatology.* e23425. https://doi.org/10.1002/ajp.23425

Rosenberger, A. L., Halenar, L., & Cooke, S. B. (2011). The making of platyrrhine semifolivores: models for the evolution of folivory in primates. *The Anatomical Record.* 294(12), 2112-2130. https://doi.org/10.1002/ar.21510

Silk J. B., Alberts S. C., Altmann J. (2003) Social bonds of female baboons enhance infant survival. *Science.* 302(5648), 1231-4. https://doi.org/10.1126/science.1088580.

Strier, K. B. (1992). Atelinae adaptations: behavioral strategies and ecological constraints. *American Journal of Physical Anthropology.* 88(4), 515-524. https://doi.org/10.1002/ajpa.1330880407

Strier, K. B. (2017). What does variation in primate behavior mean? *American Journal of Physical Anthropology* 162(S63): 4-14. https://doi.org/10.1002/ajpa.23143

Strier, K. B., Lee, P. C., & Ives, A. R. 2014. Behavioral flexibility and the evolution of primate social states*. PLoS ONE*. https://doi.org/10.1371/journal.pone.0114099

Strier, K. B. (2021) The limits of resilience. *Primates.* 62**,** 861–868. https://doi.org/10.1007/s10329-021-00953-3

Tables and Figures

Study period	Population density (ind./ha)	Median group size (range)	Number of groups	Citation
April 1983 – May 1984	1.170	7 (3-12)	19	Mendes, 1989
June 1992 – Sept. 1993	1.493	NA	NA	Hirsch, 1995 (Observer A)
June 1992 – Sept. 1993	0.922	NA	NA	Hirsch, 1995 (Observer B)
August 1999	0.605 – 0.689	NA	NA	Strier et al., 1999
Oct. 1996 – Aug. 2000	NA	7 (3-11)	10	Strier et al., 2001
July – Aug. 2003	0.502	NA	NA	Almeida-Silva et al., 2005
Aug. – Nov. 2005	0.290	5.5 (5-6)	2	Jung et al., 2015
2015	0.544 – 0.633	4 (2-12)	71	Possamai et al., 2022
May 2017 – April 2018	0.040 – 0.073	NA (2-5)	7	Possamai et al., 2022
Sept. 2018 – May 2019	NA	5 (4-6)	3	This study

Table 1: Trends in howler monkey population density at the RPPN-FMA.

This table summarizes the historical trend of decreasing population density and decreasing median group size over the last 40 years at the RPPN-FMA. The 2016-2017 outbreak of yellow fever caused a significant drop of approximately 86% in the howler monkey population, reflected in the much lower population density of the 2018-2019 census (expanded from Possamai et al., 2022). Values listed as NA were not reported.

Chapter 1: Behavioral Flexibility and Diet

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Introduction

The ability to alter feeding, ranging, or social patterns in response to temporal variation in ecological or demographic conditions is an essential part of primate adaptation (Strier, 2017). One component of primate behavioral flexibility is the capacity that many primates exhibit to switch food types along different spatiotemporal scales (e.g., between feeding patches, between forest fragments, seasonally, inter-annually because of ENSO events or climate change). However, dietary flexibility is one of many behavioral strategies primates employ to cope with fluctuations in the availability of preferred foods.

In this chapter, we begin with a brief overview of theoretical models predicting primate behavior and food choice, as well as factors that impose limits on the extent to which primates can shift behavior and diet to cope with food scarcity. We next review the ways in which variation in the spatial and temporal distribution of primate foods affect primate distribution and behavior. We specifically consider the dietary and behavioral flexibility of primate populations living in marginal habitats, as the ability to survive extreme climatic, latitudinal, or altitudinal conditions can provide important insights into the potential of primates to adjust to anthropogenic pressures including global climate change. In our final section, we provide a schematic model for integrating the dynamic interactions among behavioral adjustments in feeding, ranging, and grouping patterns in wild primates.

Theoretical perspectives on drivers of food choice and behavioral flexibility

No perfect food exists for any primate, so individuals are faced with negotiating a series of trade-offs in order to effectively balance energy expended in obtaining food with the energy and nutrients gained from that food. The amount of food an individual can consume is limited by time available for foraging, body size, and intestinal morphology, among other factors. Thus, the

chemical composition and abundance of the foods an individual selects is one inherent limitation in the quest to obtain sufficient nutrients for maintenance, growth, and reproduction (Borries and Koenig this volume). Primate food choice is explained as a function of this balancing act between energy expenditure or gain, as well as between consumption of different macronutrients (i.e., carbohydrates, lipids, and protein) and micronutrients (i.e., vitamins and minerals) (Felton and Lambert this volume).

Models of foraging theory (FT) (e.g., the optimal diet model, Krebs, 1978; the patch depletion model, Krebs, 1978, Stephens & Krebs, 1986) predict foraging decisions based on the trade-offs between maximizing energy input and minimizing energy output such that energy is optimized in foraging choices (Stephens & Krebs, 1986). For example, according to the patch depletion model (or marginal value theorem) foragers should vacate patches when it becomes more profitable to expend energy searching for a new patch rather than remain in a patch with rapidly diminishing energetic returns (Krebs, 1978; Stephens & Krebs, 1986; Ydenberg, Brown, & Stephens, 2007). In most applications of FT, energy is considered the fundamental currency. Consistent with this focus on energy, primate species have previously been classified as energy maximizers or minimizers, a distinction based on whether they seek to maximize energy intake versus minimizing energy expenditure, respectively (Milton, 1980; Schoener, 1971). Among the Atelidae, for example, *Alouatta* are distinguished by following a behavioral and dietary strategy that minimizes energy expenditure (Milton, 1980; Strier, 1992), while *Ateles, Lagothrix,* and *Brachyteles* maximize energy intake by consuming a diet higher in easily digested, high-energy foods like fruits (Strier, 1992).

Protein is also thought to influence primate food choice. To acquire essential amino acids, frugivorous primates include some leaves, insects, or other proteinaceous source in their diets (Hawes et al. this volume). Therefore, protein is often talked about as a limiting factor in food choice for primates (Ganzhorn et al., 2016; Mattson, 1980). Protein intake is most frequently explored as a driver of food selection, and especially leaf selection in folivorous

primates (reviewed in Ganzhorn et al., 2016), but rarely included in maximization or optimization models as energy is (Felton, Felton, Lindenmayer, & Foley 2009). Indeed, part of the difficulty in considering protein is that it is often difficult to disentangle what drives protein consumption, especially in folivorous primates. This raises the question of whether high protein consumption is indicative of higher protein requirements, or merely a consequence of the consumption of protein-rich leaves in the quest to obtain sufficient energy (e.g., Evans, Foley, Chapman, & Rothman, 2021; Rothman, Raubenheimer, & Chapman, 2011; Thurau, Rahajanirina, & Irwin, 2021).

Models of primate food choice are most often expressed in economic terms of expenditure and gain. In many instances, these models discriminate between energy (primarily derived from carbohydrates, though also from fat) and protein as the explanatory variables driving primate food choice. The earliest models of foraging theory (e.g., Krebs, 1978; Stephens & Krebs, 1986) were most frequently based on one currency (i.e., energy *or* protein). Yet, despite their utility for formulating general hypotheses, models based on maximization or minimization of one particular currency such as energy or protein are difficult to apply to primates that have notably complex nutritional requirements (Felton et al., 2009).

Uni-dimensional frameworks have ceded primacy in primate nutritional and foraging ecology to multidimensional models (e.g., nutritional geometry: Simpson & Raubenheimer, 1993; Simpson & Raubenheimer, 2012; Raubenheimer this volume) that consider multiple nutritional components and biologically meaningful ratios between them to determine which nutritional components, and interactions among components, influence primate foraging behavior (Raubenheimer, Machovsky-Capuska, Chapman, & Rothman, 2015; Simpson & Raubenheimer, 2012). For example, the ratio of nonprotein energy (NPE, defined as intake of energy from nonstructural carbohydrates, digestible fiber, and fat) to protein (NPE:P) in animal diets has been found to be a predictor of fitness-related variables (Cui, Wang, Zhang, Wang, Lu, & Raubenheimer, 2020; Lee et al., 2008; Lodwick & Salmi, 2019; Ponton et al., 2011; Simpson

& Raubenheimer, 2009; Solon-Biet et al., 2014). Highly frugivorous spider monkeys (*Ateles chamek*) managed nutrients in their diet by maintaining a balance of NPE:P of 8:1 kcal; as preferred food availability varied, nonprotein energy fluctuated while protein was regulated (Felton et al., 2009). Similarly, frugivorous chimpanzees (*Pan troglodytes*) maintained an NPE:P of 7:1 kcal, prioritizing protein intake while NPE intake varied with daily diet (Uwimbabazi, Raubenheimer, Tweheyo, Basuta, Conklin-Brittain, Wrangham, & Rothman, 2021). Unlike spider monkeys and chimpanzees, folivorous gorillas prioritized nonprotein energy when constrained by food availability, overeating protein and maintaining nonprotein energy, indicating a different NPE:P strategy under environmental constraints (Rothman et al., 2011).

Another aspect of this multidimensional approach is consideration of micronutrients and the often related investigation of the importance of foods that may be eaten infrequently or in small quantities. For example, decaying wood eaten by mountain gorillas in Uganda was revealed to provide 95% of the gorillas' dietary sodium despite being only 3.9% of their wet food intake (Rothman, Van Soest, & Pell, 2006). Decaying wood is otherwise a very poor food source, low in protein and sugars, high in fiber, and containing higher amounts of digestion inhibiting compounds like lignin (Rothman et al., 2006b).

The complexity of the chemical and ecological factors that impact primate food choices further compound the challenges an individual must navigate to find and consume enough food to survive, grow, and reproduce. These challenges can be thought of as variables that can negatively impact an individual's ability to maintain a positive balance between energy intake and expenditure. When an individual fails to maintain a positive energy intake-expenditure balance, negative physiological consequences can seriously impact behavior, reproduction, and survival (Cui et al., 2020; Emery Thompson, 2016; Lambert & Rothman, 2015: Vogel et al., 2012). Not acquiring enough energy or protein for prolonged periods of time can have significant physiological consequences, such as decreased reproductive success; therefore, primates exhibit numerous behavioral and morphological adaptations to ensure that energy and/or

protein needs can be met during periods of food shortage (Emery Thompson, 2016; Simmen & Rasamimananal, 2018; Vogel et al., 2012).

Changes in foraging behavior can lead to different diets or result from an individual trying to maintain a similar diet despite variation in the availability and distribution of these foods. Shifts in both may reflect behavioral strategies to reduce energy expenditure in times of food shortage. Often, as primates increase time spent looking for food or processing difficult to access foods, time devoted to other behaviors such as grooming or resting may decrease (van Schaik & Brockman, 2005). Furthermore, spatiotemporal differences in food abundance have been used to explain the significant variation in primate social relationships (especially among female primates) and grouping systems (e.g., Wrangham, 1980). However, many other factors such as demography and phylogeny play a significant role in determining the range of behavioral responses available for a species (Chapman & Rothman, 2009; Kamilar & Baden, 2012; Koenig, Scarry, Wheeler, & Borries, 2013).

Constraints on behavioral flexibility and diet

How animals meet their energetic and nutritional demands varies depending on evolutionary history, life history stage, and behavior. While foraging theory predicts that individuals should behave in such a way to maximize intake while minimizing expenditure, there are numerous constraints on an individual's ability to obtain the ideal mix of nutrients they need to fuel maintenance and growth. Exogenous and endogenous constraints on an individual's ability to alter behavior or diet interact with spatiotemporal variation in food abundance to influence which behavioral strategies (e.g., changing ranging or grouping patterns, increasing foraging time during periods of food shortage, increasing reliance on lower-quality food items, etc.) a species may adopt. The degree to which animals can alter their behavior in response to

the decreased availability of preferred foods is dynamic, influenced by phylogeny, demography, physiology, and morphology.

Behavioral shifts, such as changes in group size or day range length, can occur within feeding bouts, between seasons, or inter-annually as food availability varies (Chapman, Rothman, & Lambert, 2012; Lambert & Rothman, 2015; Strier, 2017; van Schaik, Terborgh, & Wright, 1993). Dietary shifts, which are both a component and outcome of behavioral flexibility, also occur on variable time scales and are often short-term strategies of expedience for primates faced with nutritional challenges (Strier, 2017). Spatiotemporal variation in food abundance (e.g., seasonal shifts, or variation in habitat quality between feeding patches) will result in behavioral changes that reflect a species' adaptations and ability to adjust behavior in response to external stimuli.

Constraints on behavioral flexibility and diet: competition

Resource scarcity, whether the result of periods of food shortage or decreased food abundance in low-quality habitats, can lead to increased inter- and intra-specific competition. Demographic factors, such as the population densities and group sizes of both conspecifics and sympatric species with overlapping diets, vary over individual lifetimes as well as across and within populations. Competitive abilities, dominance rank (for these species in which it occurs), and cooperative alliances that affect access to food can also change during a lifetime, with consequences for diets at both individual and interspecific levels.

Levels of interspecific feeding competition depends upon the degree of dietary overlap between sympatric species and how that overlap varies in accordance with spatio-temporal shifts in food availability (Campera, Balestri, Besnard, Phelps, Rakotoarimanana, et al., 2021; Neha, Khatun, & Ul Hasan, 2021; Ruslin, Matsuda, & Md-Zain, 2019). Strategies by which primates partition dietary niches include varying feeding strata, food type, or food species.

Extreme cases of one or more of these kinds of niche divergence can be seen in polyspecific associations. For example, differing rates of association between Diana monkeys (*Cercopithecus diana*) and other guenon species in the Taï forest in Côte d'Ivoire did not influence the food type consumed; indeed, food type consumed during polyspecific associations overlapped by 90.8 to 98.1% between guenons (Kane & McGraw, 2017). However, the proportion of different food species consumed varied between Diana monkey groups. These results indicate that, while guenons maintained a similar level of frugivory, the species consumed varied in such a way that competition was effectively reduced between groups.

Comparisons of closely related species of sympatric Atelidae help to illustrate how variation in local ecological conditions, such as rainfall and food availability, may shape both intra- and interspecific competition in diets (Figure 1). In general, atelins are more frugivorous than *Alouatta* though the proportion of fruits in their respective diets varies due to ecological factors like seasonality. Specifically, both *Brachyteles* and *Alouatta* are less frugivorous in the most seasonal fragmented forests than in continuous forests, but *Brachyteles* is more frugivorous relative to sympatric *Alouatta* (expanded from Strier, 1992). These comparisons highlight the role of dietary niche partitioning within primate communities and its importance for understanding both dietary competition and variation within and among species. They also illustrate the importance of intraspecific comparisons for understanding the degree to which primates can shift their diets to mitigate the impacts of interspecific competition.

Niche partitioning or differentiation is not always evident among sympatric species. For example, black-and-gold howler monkeys (*Alouatta caraya*) and brown howler monkeys (*Alouatta guariba clamitans*) in northern Argentina exhibited different behavioral responses to seasonal changes in fruit availability yet had largely similar diets (Agostini, Holzmann, & Di Bitetti, 2010, 2012). Black-and-gold howlers, which lived in larger groups than brown howlers, adopted a clear energy minimization strategy during periods of decreased fruit availability by

spending significantly less time traveling and moving, while brown howlers did not significantly alter their behavior in relation to food availability (Agostini et al., 2010, 2012).

Constraints on behavioral flexibility and diet: physiology and morphology

The ability to change behavior or switch between different food types in response to resource scarcity is further constrained by physiology and morphology. The nutritional requirements of an individual depend on activity, body size, age, and reproductive state. Thus, responses to food abundance can change at many points throughout an individual's life concurrent with life history stages. Body mass typically accounts for most variation in absolute nutrient intake, but scaling for body mass (i.e., $m^{0.75)}$ reveals that females have higher relative nutritional demands than males (as a result of reproduction and lactation) and that juveniles have high relative nutritional demands to fuel growth and development (Key & Ross, 1999; Oftedal, 1991). For example, despite having similar absolute energy and macronutrient intake patterns across age-sex classes, when intake was scaled to body mass, age and sex were found to influence energy and macronutrient intake in Bornean orangutans (*Pongo pygmaeus wurmbii*) (Vogel et al., 2016).

Digestive morphology and food passage rates play significant roles in an individual's ability to switch between food types. For the most part, protein digestion occurs in the stomach, lipid digestion occurs in the small intestine, and digestion of carbohydrates occurs in the stomach and large intestine; as a result, most digestive specializations seen in primates are seen in the stomach and large intestine (Lambert, 1998). Foods like leaves require more time in the gut to maximize nutrient absorption, while foods like fruits can pass through relatively quickly because they are more easily broken down.

For primarily folivorous species like howler monkeys (*Alouatta spp.*), enlarged hindguts (the caecum and colon) combined with slow food passage rates enable them to extract a

significant proportion of the nutrients available in leaves (Lambert, 1998; Liu, Amato, Hou, Gomez, Dunn, et al., 2022; McGrosky, Meloro, Navarrete, Heldstab, Kitchener, Isler, & Claus 2019; Milton, 1986; Milton, 1997). The intestinal morphology of howler monkeys is a significant component of their ability to switch between numerous food types and species, allowing significant dietary flexibility within and between species in the genus (Carneiro, Moreno, Fernandes, Souza, Bastos, Félix, & da Rocha, 2021; Espinosa-Gómez, Gómez-Rosales, Wallis, Canales-Espinosa, & Hernández-Salazar, 2013; Garber, Righini, & Kowalewski, 2015). However, the same mechanisms that facilitate food processing and nutrient absorption can impose limits on digestive efficiency: an individual needs to balance the amount of food consumed (volume) with nutrient extraction (time) in the gut (Milton, 1986). Digestive capabilities can impose limits on diet selection and thus constrain an individual's capacity for diet switching in the face of preferred-food shortages (Penry, 1993).

Additional processing before digestion may address some of the limitations imposed by intestinal morphology. Many primates exhibit dental morphology (e.g., molar enamel thickness, occlusal surface complexity or topography) associated with processing fallback foods, indicating a critical function of this morphology in breaking down foods that are more difficult to access or process (McGraw & Daegling, 2020; Rosenberger & Kinzey, 1976; Rosenberger & Strier, 1989; Vogel, Haag, Mitri-Setia, van Schaik, & Dominy, 2009). For example, primarily frugivorous Bornean orangutans possess molars with thick enamel and crenulations on the occlusal surface that are adaptations for processing tough foods, such as bark (Ungar, 2007; Vogel et al., 2009). The interaction of morphology and body size imposes limits on the speed and efficiency with which an individual can digest and absorb nutrients (Chapman et al., 2012; Lambert, 1998; Strier, 1992). For instance, leaves require more time to be fully digested compared with fruit pulp or insects because most of the energy contained in leaves is in the form of structural carbohydrates (i.e., cellulose and hemicellulose) that can only be broken down via microbial action in the gut (Kay, 1984; Karasov & Martinez del Rio, 2007). Thus, below approximately

700g, a folivorous diet is difficult to maintain because of the imbalance between energy required to digest leaves and energy obtained from leaf material (Kay, 1984).

Smaller primates that require more energy per unit of body mass are restricted to energy-dense foods like insects. Small-bodied primates are able to obtain sufficient energy from insects due to highly specialized morphology and, for some species, endogenous production of the enzyme chitinase that breaks down the structural carbohydrate chitin, which forms a large part of insect exoskeletons (Janiak, Chaney, & Tosi, 2017). For the most part, larger primates cannot subsist on insect-based diets due to the energy that must be expended in obtaining a sufficient volume of food. However, social insects such as ants or termites are important food resources for large-bodied primates like chimpanzees (*Pan troglodytes spp.*), though usually extractive foraging aided by tools is necessary to exploit these resources (Isbell, 1998; Raubenheimer & Rothman, 2013). Body size, morphology, and physiology interact to inform an individual's nutritional requirements. How an animal meets those requirements is in turn limited by competition with conspecifics and sympatric species. The limits that these variables impose integrate with evolutionary history (i.e., phylogeny) to form the basis for responses to food scarcity.

Habitat heterogeneity, resource distribution, and social behavior

Derived from foraging theory, the ideal free model posits that, given certain assumptions about movement and resource distribution, foragers should be distributed in such a way that energy gain is highest – they should occupy the feeding patches where food quality or potential energy gain is highest (Fretwell 1972; Fretwell & Lucas 1970). However, interpretations of the ideal free model are complicated by the significant role that competition plays in shaping foraging decisions for most primates and by the complexity of primate diets.

High heterogeneity, typically reflecting local legacies of human occupation or use, causes significant variation in forest type and habitat quality (e.g., nutrient content of food items, tree species diversity, density of top food species, etc.) within forest fragments (Chapman, Chapman, Rode, Hauck, & McDowell, 2003; Jung, Mourthe, Grelle, Strier, & Boubli, 2015; Chapman et al. this volume). Ecological variation within mosaic habitats often leads to increased use of areas with high plant species diversity, or a higher density of food species (Sha et al., 2017). Density of top food species, in particular, were correlated with habitat use in both mantled howler monkeys (*Alouatta palliata*) in Costa Rica (Stoner, 1996) and black howler monkeys (*Alouatta pigra*) in Belize (Ostro, Silver, Koontz, & Young, 2000). However, at higher population densities in highly heterogeneous habitats, groups may occupy lower quality areas compared to conspecifics and be faced with additional nutritional or energetic costs. Within the Reserva Particular do Patrimônio Natural-Feliciano Miguel Abdala in Minas Gerais, Brazil, two groups of brown howler monkeys were shown to have significantly different diets and behavioral patterns that correlated with local ecology (Jung et al., 2015). A group in a higher quality area (valley with evergreen forest) spent less time traveling and had a smaller home range, in addition to a diet higher in fruits and lower in mature leaves, when compared to a group in a lower quality area (hillside with secondary mostly deciduous forest previously a coffee plantation) of the forest fragment (Jung et al., 2015).

In some instances, it may be the case that primate distribution and/or abundance is not shaped by energy gain, but rather by characteristics of plant foods like the protein-to-fiber ratio of leaves (but see Wallis et al., 2012; Chapman et al. this volume) or macro- and micro-nutrient content of available foods. Furthermore, food types (i.e., flower, fruit, leaf) vary naturally according to plant species characteristics and developmental stage. It is generally accepted that foods like fruits are more patchily distributed than items like leaves. While all leaves are certainly not equal, their abundance in relation to fruits generally means that even if they occur in discrete patches, those patches are still more abundant or contain more food items. Yet,

leaves can vary significantly in quality based on phenophase, plant species, soil composition, or sun exposure, among other factors and folivorous primates often choose leaves that have higher protein and lower fiber contents, and fewer secondary metabolites or toxins (Chapman et al., 2003; Ganzhorn, 1995; Glander, 1978) and this variation can impact primate behavior and distribution. Population density of redtail monkeys (*Cercopithecus ascanius*) was significantly related to the amount of copper consumed per calorie of food, but not basal area of food trees or density of food trees per hectare (ha), suggesting that copper may be limiting for this primate (Rode, Chapman, McDowell, & Stickler 2006), though further information is needed on copper availability in the environment to better assess this.

Feeding patch size can impose an upper limit on the number of individuals that can feed in one location at any time (Strier, 2016). Intragroup competition increases with the number of animals foraging within a finite patch and, to compensate for increased intragroup feeding competition, animals must either move more frequently to find feeding patches (thus expending more energy) or adjust feeding group size (Aureli et al., 2008; Koenig et al., 2013; Strier 2016). Perhaps the most well-known examples of this strategy are chimpanzees (*Pan troglodytes spp.*) and spider monkeys (*Ateles spp.*) that routinely fission into smaller feeding parties when preferred fruit patches are small and form larger parties when these patches can accommodate more individuals (Aguilar-Melo, Calmé, Pinacho-Guendulain, Smith-Aguilar, & Ramos-Fernández, 2020; Chapman, Chapman, & Wrangham, 1995; Hartwell, Notman, Kalbitzer, Chapman, & Pavelka, 2018). For female spider monkeys (*Ateles geoffroyi*) in Costa Rica, decreased fruit abundance was correlated with smaller subgroup sizes but not with fecal glucocorticoids, suggesting that smaller subgroups provide an effective buffer against physiological stress caused by fluctuations in food abundance (Rodrigues, 2017). Muriquis (*Brachyteles spp.*) are also known to adjust party sizes in response to fruit availability, though the same pattern does not hold for abundance of leaves (Moraes, Carvalho, & Strier, 1998; Strier, 1989).

The separation of a larger group into smaller subgroups – that persist for several hours, several days, or longer – is a strategy seen to differing degrees in many primate taxa as a mechanism for coping with changes in resource abundance (Aureli et al., 2008). The emergence of these fission-fusion dynamics is often attributed to changes in fruit abundance, as is seen in chimpanzees and spider monkeys (e.g., Chapman et al., 1995). However, many other taxa exhibit flexible social systems in response to resource scarcity. For instance, red-capped mangabeys (*Cercocebus torquatus*) in Gabon were observed to forage in decreased party sizes when fruit availability increased (Dolado, Cooke, & Beltran, 2016) whereas black capuchin monkeys (*Sapajus nigritus*) increased group spread when feeding on fruit, adjusting cohesion dynamically in accordance with activity (Luccas & Izar, 2021). Other taxa, such as ruffed lemurs (*Varecia spp.*) exhibit significant degrees of intra-specific variation in degree of social flexibility ranging from cohesive to highly fluid (Vasey, 2006). One population of black-and-white ruffed lemurs (*Varecia variegata*) at Ranomafana National Park, Madagascar exhibited a high degree of fission-fusion dynamics, with subgroup transitions occurring every 90 minutes, on average (Baden, Webster, & Kamilar, 2016). Furthermore, smaller and less cohesive subgroups were observed during cooler and wetter months when fruit availability was lower, indicating that flexible social dynamics in black-and-white ruffed lemurs serve to reduce intragroup feeding competition (Baden et al., 2016). The degree to which primates can adjust group size is contingent upon phylogenetic constraints and local ecology and the complex interplay of spatial and temporal changes in food abundance.

Habitat disturbance, diet, and behavior

Variation in habitat quality, especially forest contiguity and floristic structure, can have significant impacts on food availability. Habitat quality is often measured using variables like tree species diversity or observation of anthropogenic disturbances such as logging (Vogel &

Dominy, 2011). In general, habitats that are considered to be of higher quality have greater tree species diversity, higher densities of top food species, and lower levels of disturbance, though many of these ecological variables are site specific. Primates living in lower quality habitats often have reduced home range sizes, decreased dietary diversity, and increased competition both with conspecifics and sympatric species (Strier, 2009).

Residency in lower quality habitats can result in significant changes to primate behavior and physiology. For instance, Sulawesi macaques (*Macaca tonkeana*) living in lower quality habitats relied more heavily on alternative food items (e.g., insects or fungi), spent more time foraging, less time moving, and more time resting when compared to a group in a higher quality habitat (Riley et al., 2007). In addition, Ménard et al. (2013, 2014) documented significant differences in dietary composition and behavior between Barbary macaques (*Macaca sylvanus*) living in habitats with differing degrees of anthropogenic disturbance. Macaques in lower quality habitats where livestock grazing was more common fed more on underground resources, shrubs, and acorns and also had increased day range lengths and spent more time foraging and moving compared to conspecifics in higher quality habitats (Ménard et al., 2013, 2014). Life in lower quality habitats often results in increased energy expenditure and reduced diet quality, both of which are associated with reduced fitness, though the effects of anthropogenic disturbance on diet are varied and complex (Chapman et al. this volume).

Degradation can alter the floristic composition of primate habitats, in turn causing changes to diet and behavior. In some instances, fragmentation or degradation decreases the availability of preferred foods and increases reliance on fallback foods (Onderdonk & Chapman 2000). Geladas (*Theropithecus gelada*) are graminivorous throughout the year but rely on underground storage organs in the dry season when green grasses are less abundant and may, in fact, rely more on underground foods like corms or rhizomes in anthropogenically altered landscapes (Jarvey, Low, Pappano, Bergman, & Beehner, 2018; Kifle & Bekele 2021). Other primates, like spider monkeys, that may alter group size or cohesion to cope with fluctuations in

preferred food availability may also rely on fallback foods in degraded habitats. For example, brown spider monkeys (*Ateles hybridus*) living in a 65-ha forest fragment in northern Colombia consumed significantly more leaves and decaying wood than expected (de Luna et al., 2017). Thus, habitat degradation imposes additional significant constraints on dietary and behavioral flexibility.

Habitat degradation and fragmentation can also push primates to use novel or exotic food resources, including invasive species or cultivated crops. Crop feeding has been reported across the order Primates, and dietary changes in response to the introduction of cultivated foods have been recorded in many taxa. For example, brown howler monkeys in Rio Grande do Sul state, Brazil were observed feeding from 6 species of cultivated fruits, accounting for <1 to 18% of annual feeding (Chaves & Bicca-Marques, 2017). Consumption of cultivated fruits was in proportion to their availability; however, cultivated fruit feeding was unrelated to the availability of wild fruits in the area (Chaves & Bicca-Marques, 2017). Similar exploitation of nutrient and energy dense cultivated fruits outside of periods of decreased fruit availability has been observed in great apes (Hockings & McLennan, 2012; Naughton-Treves, 1998; Seiler & Robbins, 2016). Of course, increased reliance on cultivated crops also increases the likelihood of negative human-nonhuman primate interactions, which can have significant conservation implications (Hill, 2015).

Investigations of dietary diversity for primates in disturbed habitats indicate the inclusion of exotic or novel plant species as an additional strategy for coping with decreased food availability. The diet of colobus monkeys (*Colobus angolensis palliatus*) in Kenya's Diani Forest consisted of up to 40.3% exotic (non-indigenous) plant species across home ranges with varying levels of disturbance (Dunham, 2017). The inclusion of novel food sources is seen in lemuroids, as well: folivorous southern bamboo lemurs (*Hapalemur meridionalis*) included a higher proportion of exotic and pioneer species in their diets when compared to sympatric, frugivorous collared brown lemurs (*Eulemur collaris*) (Eppley et al., 2017). Folivorous primates

such as southern bamboo lemurs or brown howler monkeys may be less severely impacted by habitat degradation due to higher levels of dietary flexibility when compared to frugivorous primates.

Temporal shifts in food availability, behavioral flexibility, and diet

Variation in the size and distribution of food patches can occur over time as well as across space. There are often trade-offs between behavioral responses that result in flexible, fission-fusion grouping patterns, and the inclusion of abundant food sources where patchy foods are scarce. Female-bonded species, such as baboons and macaques, are more likely to shift their diets, while male-bonded species, such as chimpanzees and spider monkeys, are more likely to adjust their party sizes (Wrangham, 1980).

Food availability varies along multiple time scales in response to shifting ecological conditions. The tropical forests where nearly all primate species are found do not typically experience high degrees of seasonality in temperature or day length; however, many tropical forests are characterized by significant rainfall seasonality (van Schaik et al., 1993). Seasonal patterns of rainfall vary inter-annually and can be impacted by climatic events such as the El Niño-Southern Oscillation (ENSO)—with resulting interannual changes in, for example, fruit availability (Chapman et al. 2018)—and global climate change (Rothman et al., 2015). Additionally, in some regions, changes in climate and weather patterns contribute to peaks in fruit production known as masting events that occur every 2-10 years (Ashton, 1988; Knott, 1998). The abundance of preferred foods shifts weekly based on phenophase, seasonally with rainfall, and inter-annually with larger climatic patterns, yet because responses to ecological variation may be constrained by physiology or morphology, behavioral responses to ecological shifts are highly variable (van Schaik & Brockman, 2005).

For species that live in highly seasonal habitats, behavioral flexibility provides a key advantage in adapting to fluctuations in food abundance. Indeed, most primates living in highly seasonal habitats cope with intra-annual shifts in resource availability by altering dietary or behavioral patterns throughout the year (Hemingway & Bynum, 2005). Seasonal shifts in behavior are often the result of increased competition over scarce resources or adjustments to cope with reduced energy intake. Typical behavioral responses to decreases in the availability of preferred foods include changing ranging patterns or altering activity patterns to conserve energy (Lambert & Rothman, 2015; van Schaik et al., 1993). However, it is important to note that the rainy season and dry season may have different meanings in different habitats. For example, in Kibale National Park, Uganda, fruiting peaks tend to occur between the end of the first rainy season and the beginning of the dry season (Chapman, Wrangham, Chapman, Kennard, & Zanne, 1999), whereas in Caratinga, Minas Gerais, Brazil, fruiting peaks during the rainy season (Strier, 1991; Strier & Boubli, 2006).

Howler monkeys are often characterized as behavioral or facultative folivores because they typically consume fruit in proportion to its spatiotemporal availability (Rosenberger, Halenar, & Cooke, 2011; Strier, 1992). Black-and-gold howlers and brown howlers in highly seasonal habitats at the southernmost edge of the genus' distribution (southern Brazil and northern Argentina) generally consume a more folivorous diet than Central American species (Garber et al., 2015). Across study sites, brown howlers consume at least 60% leaves throughout the year, but consume fruit in proportion to its availability in their habitats (Aguiar, dos Reis, Ludwig, & Rocha, 2003; Chaves & Bicca-Marques, 2016; Mendes, 1989; Strier, 1992; but see Santos, Bianchini, & dos Reis, 2013). For instance, Mendes (1989) found that, during the wet season (a period of increased fruit abundance), brown howler monkeys at the Reserva Particular do Patrimônio-Feliciano Miguel Abdala (RPPN-FMA) in Minas Gerais, Brazil spent 14.5% less time feeding on leaves but 28.4% more time feeding on fruits. Additional studies with brown howler monkeys report high year-round consumption of leaves with fruit consumption

typically varying seasonally and with local ecological characteristics (Agostini et al., 2010; Aguiar et al., 2003; Chiarello, 1993, 1994; Miranda & Passos, 2004). Brown howler monkeys can be thought of as shifting diets along a folivory-frugivory spectrum as resource availability shifts in their habitats (Mendes, 1989; Strier, 1992).

Dietary flexibility in brown howler monkeys is associated with spatial and temporal fluctuations in abundance of high quality foods like fruits; however, relationships between diet and behavior are more difficult to discern. Both Mendes (1989) and Agostini et al. (2012) reported that resting time did not change between rainy and dry seasons in southeastern Brazil and northeastern Argentina, respectively. However, Chiarello (1993) reported that, in a population of brown howler monkeys in São Paulo state, resting time was significantly higher in the summer (rainy season) than the winter (dry season). Increased resting time among howler monkeys compared to other primates is generally attributed to their highly folivorous diet because leaves are more difficult to digest than fruits (Milton, 1980). Resting time, it seems, should be significantly related to the degree of leaves consumed yet the conflicting findings from multiple studies with brown howlers indicate that additional factors beyond diet may influence the amount of time spent resting.

Furthermore, results of the few year-long studies conducted with brown howler monkeys indicate that the proportion of time dedicated to socializing, traveling, and feeding also show differential patterns of shifting between rainy and dry seasons. Brown howler monkeys at RPPN-FMA increased time spent traveling and decreased time spent feeding during the rainy season (Mendes, 1989). Brown howlers in São Paulo state also spent significantly less time feeding during the rainy season and less time in social interactions, but did not shift time spent traveling between the rainy and dry seasons (Chiarello, 1993, 1995). Similarly to Chiarello (1993, 1995), Agostini and colleagues (2012) found that brown howlers in northeastern Argentina did not significantly shift ranging patterns between the rainy and dry season; however, Agostini et al. (2012) observed significantly more social interactions during the rainy season.

Indeed, for howler monkeys, their high degree of behavioral flexibility appears to enable multiple behavioral adjustments to cope with seasonal shifts in the availability of high quality foods.

Supra-annual changes in fruit availability, such as fruit masting in Southeast Asian forests, also have significant impacts on behavior and diet. During fruit masting events, the diet of orangutans in Gunung Palung National Park, Borneo, consisted of up to 100% fruits, yet during periods of low fruit availability orangutans consumed a diet consisting of as little as 21% fruit and up to 37% tree bark (Knott, 1998). The presence of ketones in orangutan urine analyzed from the low fruit period indicates that these orangutans were under energetic and nutritional stress during severe food scarcity, despite spending the same amount of time foraging, and relied, in part, on catabolization of body fat for survival (Knott, 1998). Leaf monkeys (*Presbytis rubicunda rubida)* and gibbons (*Hylobates albibarbis*), also in Gunung Palung National Park, show differing responses to fruit masting and periods of low fruit availability (Clink, Dillis, Feilen, Beaudrot, & Marshall, 2017). Leaf monkeys had higher dietary diversity and richness when compared to gibbons (likely due to higher consumption of non-fruit items), but both species increased their fruit and seed consumption when fruits became more abundant and increased the amount of leaves and figs in their diets during periods of decreased fruit abundance (Clink et al., 2017).

In the short-term, seasonal changes in the availability of preferred foods or high-quality foods can put significant energetic or nutritional stress on primates, which must be addressed via changes in behavior. Prolonged periods of nutritional or energetic limitation can have significant physiological consequences for primates (e.g., Knott, 1998). Behavioral flexibility is one of the principal mechanisms for primates coping with temporal variation in food abundance. Conserving energy by reducing costly behaviors such as traveling, while increasing behaviors such as resting, can have a significant impact on an individual’s ability to maintain positive or neutral energy balance.

Behavior and diet in marginal habitats

Most primates live in tropical regions. A limited number of species occupy latitudes significantly farther north or south of the equator, and life at the extremes can create considerable challenges for these animals. Distance from the equator is positively correlated with increased seasonality and greater changes in day length (hours of sunlight) between seasons. Seasonal fluctuations in temperature and rainfall have significant effects on primate behavior, imposing constraints via fluctuations in the availability of preferred foods that can impact an individual's ability obtain sufficient energy (reviewed above). Seasonal shifts in day length can impose additional constraints by limiting the amount of time individuals can allocate to various behaviors such as foraging (Coleman, Setchell, & Hill, 2021; Hill et al., 2003; Van Doorn, O'riain, & Swedell, 2010).

Primates that live at high altitudes on Madagascar, in Asia, Africa, and Central and South America exhibit a wide range of adaptations to cope with the unique physiological challenges that altitude can bring (Grow, Gursky-Doyen, & Krzton, 2014; Hou, Chapman, Jay, Guo, & Raubenheimer, 2020). A comparison of macaques and colobines in temperate Asian forests revealed that both species adjusted diet as latitude and altitude increased; however, the effect of altitude on diet was stronger for colobines, which live as high as 4500 m above sea level in China (Kirkpatrick & Grueter, 2010; Tsuji, Hanya, & Greuter, 2013). Asian colobines (e.g., *Rhinopithecus* spp.) typically exhibit pronounced seasonal variation in diet and rely on lichen as a principal component of diet for up to 10 months of the year at some sites (Grueter et al., 2010; Hou, He, Wu, Chapman, Pan, et al., 2018). For snub-nosed monkeys in particular, altitude and temperature are correlated with increased time spent feeding (Kraus & Strier, 2022). Indeed, altitude and latitude better predicted feeding effort of black-and-white snub-nosed monkeys (*Rhinopithecus bieti*) in Yunnan Province, China than forest area, home range, group size, or population density (Huang et al., 2017).

Extreme weather and deviation from average climate conditions also impact primate diet and behavior. There are numerous examples of phenomena like hurricanes or cyclones impacting primate populations. Analysis of hair cortisol concentrations and body weight in a population of ring-tailed lemurs (*Lemur catta*) at Beza Mahafaly Special Reserve in Madagascar revealed significant variation associated with drought and cyclonic activity (Fardi, Sauther, Cuozzo, Jacky, & Bernstein, 2017). Both hair cortisol concentration and body weight responses to drought and a cyclone varied by age-sex class, indicating that an individual's sex and life-stage can significantly influence their ability to adjust behavior in response to extreme weather events. In general, female ring-tailed lemurs had higher hair cortisol concentration as a result of drought while males exhibited higher hair cortisol concentration during the post-cyclone period (both of which were periods of reduced food availability) (Fardi et al., 2017). The impact of events such as cyclones likely extend many months past the initial occurrence due to defoliation and tree damage reducing the availability or diversity of foods, but behavioral and dietary flexibility may lessen the impacts of these events on some primate populations (Dinsmore, Strier, & Lewis, 2021).

Semi-regular weather patterns such as ENSO can cause significantly different weather conditions in primate habitats, which in turn can impact food availability and behavior. For instance, during an extreme drought that occurred in an El Niño year, gray-cheeked mangabeys (*Lophocebus albigena*) frequently fed on bark, a very low-quality food resource (Lambert, Chapman, Wrangham, & Conklin-Brittain, 2004). ENSO events have also been associated with reduced fecundity in Milne Edward's sifaka, likely as a result of decreased rainfall and food abundance (*Propithecus edwardsi*) (Dunham, Erhart, Overdorff, & Wright, 2008). Similarly, ENSO conditions in three years preceding population censuses were associated with decreased reproductive output and increased offspring mortality in white-faced capuchins (*Cebus capucinus*) in Costa Rica (Campos, Jack, & Fedigan, 2015). ENSO events can increase or decrease rainfall and/or temperature based on geography; therefore, the effects of ENSO on

primate behavior and diet can vary significantly within and between species and geographic regions.

There is emerging evidence that over longer time scales (i.e., decades), global climate change is also having a significant impact on plant species and thus primate food availability. A short-term comparison of leaf chemistry at Kibale National Park revealed that variation among individual trees was greater than variation over the study periods of August 1998 - June 1999 and July 1999 - May 2000 (Chapman et al., 2003). However, analysis of long-term data on leaf chemistry also conducted at Kibale revealed that leaf quality declined significantly when the same trees were reassessed after 15 and 30 years (Rothman et al., 2015). Specifically, fiber content of leaves from the same trees increased over 15 and 30 years, while protein content declined over 15 years (Rothman et al., 2015). Indeed, greenhouse experiments support the conclusion that global climate change may have a significant negative impact on leaf quality: in multiple experiments, nitrogen (a common proxy for protein) declined as greenhouse gas levels were artificially increased (Stiling & Cornelissen, 2007; Zvereva & Kozlov, 2006). For numerous folivorous species, leaf quality, especially protein-to-fiber ratio, is positively correlated with habitat use and group distribution (Ganzhorn, 1992; but see Wallis et al. 2012). Declining leaf quality could have significant impacts on primate communities as the planet's climate continues to change.

The effects of climate change can compound as increasingly extreme weather patterns impact the phenology and productivity of forests (Butt et al., 2015), thus reducing food availability for consumers at different trophic levels. While it can be difficult to assess the impacts of climatic variation on primate communities without long-term studies, data from several projects of at least 20 years are beginning to show the potential impact of large-scale climatic variation on primate behavior, ecology, and demography (Campos et al., 2017). For instance, in their analysis of seven primate species for which long-term data are available, Campos and colleagues (2017) found that for seasonally breeding species (the northern

muriqui, *Brachyteles hypoxanthus*; Milne Edward's sifaka, *Propithecus edwardsi*; and blue monkeys, *Cercopithecus mitis stuhlmanni*), there was strong evidence of decreased fertility as a result of climatic variables such as warmer temperatures. In many cases, primates are also at a heightened risk of extinction due to the compounding effects of global climate change and anthropogenic habitat alteration, hunting, and disease (Estrada et al., 2017).

Dynamic trade-offs between dietary and behavioral flexibility

The concept of flexibility has become increasingly important in comparative models of primate behavior as our knowledge of behavioral variation within and among species has grown (Chapman & Rothman, 2009; Strier, 2009, 2017). Dietary flexibility, which represents a subset of behavioral flexibility, has long been associated with dietary shifts documented to occur in response to fluctuations in food supplies due to seasonality and extreme climatic events such as extended droughts (e.g., van Schaik & Brockman, 2005). The dichotomy between the ability to shift to alternative foods versus shifting other aspects of behavior, such as ranging and grouping patterns, has also been a key distinguishing feature among some of the early predictive models of primate socio-ecology (e.g., Isbell, 1991; Sterck, Watts, & van Schaik, 1997; van Schaik, 1989; Wrangham, 1980). Indeed, it appears that the tendency of a species to respond to scarcities in the availability of preferred foods may be related, at least in part, to its dispersal regime and corresponding social systems (Figure 2). Thus, female-bonded primates living in cohesive groups are more likely to shift their diet and ranging patterns in response to declines in preferred food availability, whereas primates living in fission-fusion societies with male philopatry are more likely to shift their grouping and ranging patterns. However, extreme conditions related to strong seasonality, habitat fragmentation, perturbations, and saturation, can force increasingly greater shifts toward folivory that may be beyond the physiological limits for some species (e.g., Korstjens et al., 2010).

Because of their relatively high energy requirements, extended exposure to extreme conditions that decrease the availability of energy-rich foods can result in fitness consequences such as decreased fecundity and increased mortality. Constraints on adjusting dispersal regimes, which are phylogenetically constrained (Strier, Lee, & Ives, 2014), require behavioral and dietary flexibility that may negatively impact the resilience of primate population over time (Bicca-Marques et al., 2020, Strier, 2021b).

Summary and Conclusions

Despite its relatively advanced empirical and theoretical foundation, there are still many gaps in our understanding of primate dietary and behavioral flexibility. For example, the relatively short duration of many studies makes it difficult to distinguish behavioral and dietary variation from flexibility (Strier, 2017). These distinctions are confounded by the challenges of obtaining reliable data on physiological regulating mechanisms, that underlie, for example, nutrient balancing, or the relative trade-offs between energy stress and protein stress in wild primates (e.g., Vogel et al., 2012). Nonetheless, major advances have occurred in the development of noninvasive, affordable assessments of primate physiology, including fecal steroid assays to measure levels of glucocorticoids and urinary C-peptide assays, which now make it possible to evaluate levels of social and energetic stress in wild primates (e.g., Chen, Yao, Yang, Xiang, Ostner, & Cristóbal-Azkarate, 2021; Emery Thompson, 2016; Sacco, Granatosky, Laird, & Milich, 2021). Ongoing refinements, including species-specific validations of these assays, will permit their application across a wider diversity of species, generating the comparative data necessary to detect patterns in physiological mechanisms that may underlie species differences in behavioral flexibility.

- Physiology (e.g., nutritional requirements) and morphology (e.g., dentition or body size) impose significant constraints on dietary and behavioral flexibility in primates. These limitations are compounded by ecological, demographic, and behavioral characteristics that may change significantly within individual lifetimes.
- The abundance of high quality (energy-dense) foods fluctuates across numerous spatial and temporal time scales. Assessments considering scale (i.e., within one forest fragment, Jung et al., 2015; seasonal, Agostini et al., 2012; inter-annual, Campos et al., 2017) are necessary to fully understanding the degree to which behavior can vary within and among species.
- Understanding behavioral and dietary flexibility is increasingly important to conservation and management programs on behalf of populations of endangered species that persist in severely altered habitats on suboptimal diets (Korstjens et al., 2010; Meyer & Pie, 2022; McLennan et al., 2017; Strier, 2021b). Incorporating the variation in primate behavioral flexibility into the assessments of their conservation status can provide additional insights into their ecological resilience and adaptive potential.

References

Agostini, I., Holzmann, I., & Di Bitetti, M. S. (2012). Influence of seasonality, group size, and presence of a congener on activity patterns of howler monkeys. *Journal of Mammalogy, 93*(3), 645-657.

Aguiar, L., dos Reis, N. R., Ludwig, G., & Rocha, V. J. (2003). Dieta, área de vida, vocalizações e estimativas populacionais de *Alouatta guariba* em um remanescente florestal no norte do estado do Paraná. *Neotropical Primates 11*(2), 78.

Ashton, P. S. (1988). Dipterocarp biology as a window to the understanding of tropical forest structure. *Annual Review of Ecology and Systematics, 19*, 347-370. DOI:10.1146/annurev.es.19.110188.002023

Aureli, F., Schaffner, C. M., Boesch, C., Bearder, S. K., Call, J., Chapman, C. A., . . . Van Schaik, C. P. (2008). Fission-Fusion Dynamics New Research Frameworks. *Current Anthropology, 49*(4), 627-654. DOI:10.1086/586708

Barboza, P. S., Parker, K. L., & Hume, I. D. (2009). *Integrative wildlife nutrition*. Springer.

Bicca-Marques, Chaves, & Hass (2020) Howler monkey habitat to tolerance shrinking: Lifetime warranty or death sentence? *American Journal of Primatology* 84. https://doi.org/10.1002/ajp.23089

Campera, M., Balestri, M., Besnard, F., Phelps, M., Rakotoarimanana, F., Nijman, V., ... & Donati, G. (2021). The Influence of Seasonal Availability of Young Leaves on Dietary Niche Separation in Two Ecologically Similar Folivorous Lemurs. *Folia Primatologica*, *92*(3), 139-150. https://doi.org/10.1159/000517297

Campos, F. A., Morris, W. F., Alberts, S. C., Altmann, J., Brockman, D. B., … Fedigan, L. M. (2017). Does climate variability influence the demography of wild primates? Evidence from long-term life-history data in seven species. *Global Change Biology.* 1-15.

Carneiro, L.A, Moreno, T. B., Fernandes, B. D., Souza, C. M., Bastos, T. S., Félix, A. P., & da Rocha, C. (2021). Effects of two dietary fiber levels on nutrient digestibility and intestinal fermentation products in captive brown howler monkeys (*Alouatta guariba*). *American Journal of Primatology*, *83*(3), https://doi.org/10.1002/ajp.23238e23238

Chapman, C. A., & Rothman, J. M. (2009). Within-species differences in primate social structure: evolution of plasticity and phylogenetic constraints. *Primates*. *50*, 12-22. DOI:10.1007/s10329-008-0123-0.

Chapman, C. A., Rothman, J. M., Lambert, J. E. (2012). Food as a selective force in primates *In* Mitani, J. C., Call, J., Kappeler, P. M., Palombit, R. A., Silk, J. B. (Eds.) *The Evolution of Primate Societies*. University of Chicago Press.

Chapman, C. A., Schoof, V. A. M., Bonnell, T. R., Gogarten, J. F., & Calme, S. (2015). Competing pressures on populations: long-term dynamics of food availability, food quality, disease, stress and animal abundance. *Philosophical Transactions of the Royal Society B-Biological Sciences, 370*(1669). DOI:10.1098/rstb.2014.0112

Chapman, C., Wrangham, R., Chapman, L., Kennard, D., & Zanne, A. (1999). Fruit and flower phenology at two sites in Kibale National Park, Uganda. *Journal of Tropical Ecology,* 15(2), 189-211.

Chapman, C.A. (1987). Flexibility in diets of three species of Costa Rican primates. *Folia Primatologica 49*:90-105.

Chaves, Ó. M., & Bicca-Marques, J. C. (2016). Feeding strategies of brown howler monkeys in response to variations in food availability. *PloS one, 11*(2), e0145819.

Chen, H., Yao, H., Yang, W. *et al.* Validation of a Fecal T3 Metabolite Assay for Measuring Energetics in Wild Golden Snub-Nosed Monkeys (*Rhinopithecus roxellana*). *Int J PrimatolInternational Journal of Primatology* 42, 759–763 (2021). https://doi.org/10.1007/s10764-021-00236-0

Chiarello, A. G. (1993). Activity pattern of the brown howler monkey *Alouatta fusca*, Geoffroy 1812, in a forest fragment of southeastern Brazil. *Primates, 34*(3), 289-293.

Chiarello, A. G. (1995). Grooming in brown howler monkeys, *Alouatta fusca*. *American Journal of Primatology, 35*(1), 73-81.

Coleman, B.T., Setchell, J.M. & Hill, R.A. (2021) Seasonal variation in the behavioural ecology of samango monkeys (*Cercopithecus albogularis schwarzi*) in a southern latitude montane environment. *Primates* 62**,** 1005–1018 (2021). https://doi.org/10.1007/s10329-021-00939-1

Cui, Z., Wang, Z., Zhang, S., Wang, B., Lu, J., & Raubenheimer, D. (2020). Living near the limits: Effects of interannual variation in food availability on diet and reproduction in a temperate primate, the Taihangshan macaque (*Macaca mulatta tcheliensis*). *American Journal of Primatology*, *82*(1), https://doi.org/10.1002/ajp.23080e23080.

de Moraes, P. L. R., de Carvalho, O., & Strier, K. B. (1998). Population variation in patch and party size in muriquis (*Brachyteles arachnoides*). *International Journal of Primatology, 19*(2), 325-337. DOI:10.1023/a:1020339817762

Di Fiore, A. (2004). Diet and feeding ecology of woolly monkeys in a western Amazonian rain forest. *International Journal of Primatology*. *25*(4), 767-801.

Dinsmore, M. P., Strier, K. B., & Louis Jr, E. E. (2021). The influence of seasonality, anthropogenic disturbances, and cyclonic activity on the behavior of northern sportive lemurs (*Lepilemur septentrionalis*) at Montagne des Français, Madagascar. *American journal of primatology*, *83*(12), https://doi.org/10.1002/ajp.23333

Dunham, A. E., Erhart, E. M., Overdorff, D. J., & Wright, P. C. (2008). Evaluating effects of deforestation, hunting, and El Niño events on a threatened lemur. *Biological Conservation, 141*(1), 287-297. DOI:10.1016/j.biocon.2007.10.006

Emery Thompson, M., (2016) Energetics of feeding, social behavior, and life history in non-human primates. *Hormones and Behavior*. DOI:10.1016/j.yhbeh.2016.08.009

Estrada, A., Garber, P. A., Rylands, A. B., Roos, C., Fernandez-Duque, E., Di Fiore, A., . . . Li, B. G. (2017). Impending extinction crisis of the world's primates: Why primates matter. *Science Advances, 3*(1). DOI:10.1126/sciadv.1600946

Evans, K.D., Foley, W.J., Chapman, C.A. et al. (2021) Deconstructing Protein in the Diet and Biomass of Colobine Primates. *Int J PrimatolInternational Journal of Primatology* 42, 283–300 (2021). https://doi.org/10.1007/s10764-021-00203-9

Felton, A. M., Felton, A., Lindenmayer, D. B., & Foley, W. J. (2009a). Nutritional goals of wild primates. *Functional Ecology, 23*(1), 70-78. DOI:10.1111/j.1365-2435.2008.01526.x

Felton, A. M., Felton, A., Wood, J. T., Foley, W. J., Raubenheimer, D., … Lindenmayer, D. B., (2009b). Nutritional ecology of *Ateles chamek* in lowland Bolivia: How macronutrient balancing influences food choices. *International Journal of Primatology*. 30, 675-696.

Ganzhorn, J. U. (1992). Leaf chemistry and the biomass of folivorous primates in tropical forests – test of a hypothesis. *Oecologia, 91*(4), 540-547. DOI:10.1007/bf00650329

Garber, P. A., Righini, N., & Kowalewski, M. M. (2015). Evidence of alternative dietary syndromes and nutritional goals in the genus *Alouatta*. *In* Kowalewski, M., Garber, P., A., Cortés-Ortiz, L., Urbani, B., & Youlatos, D. (Eds.) *Howler Monkeys: Behavior, Ecology, and Conservation*, Springer.

Glander, K. E. (1978). Howling monkey feeding behavior and plant secondary compounds: a study of strategies. *In* Montgomery, C. G. (Ed.) *The ecology of arboreal folivores*. Smithsonian Institution Press.

Hartwell, K.S., Notman, H., Kalbitzer, U. *et al.* Fruit availability has a complex relationship with fission–fusion dynamics in spider monkeys. *Primates* 62**,** 165–175 (2021). https://doi.org/10.1007/s10329-020-00862-x

Hemingway, C. A., & Bynum, N. (2005). The influence of seasonality on primate diet and ranging. *In* Brockman, D. B., & van Schaik, C. P. (Eds.) *Seasonality in Primates: Studies of Living and Extinct Human and Non-Human Primates.* DOI:10.1017/cbo9780511542343.004

Hladik, C. M., & Simmen, B., (1996). Taste perception and feeding behavior in non-human primates and human populations. *Evolutionary Anthropology*, 5, 58-71.

Hou, R., Chapman, C. A., Jay, O., Guo, S., Li, B., & Raubenheimer, D. (2020). Cold and hungry: combined effects of low temperature and resource scarcity on an edge-of-range temperate primate, the golden snub-nose monkey. *Ecography*, *43*(11), 1672-1682. https://doi.org/10.1111/ecog.05295

Hou, R., He, S., Wu, F., Chapman, C. A., Pan, R., Garber, P. A., ... & Li, B. (2018). Seasonal variation in diet and nutrition of the northern-most population of *Rhinopithecus roxellana*. *American Journal of Primatology*, *80*(4), e22755. https://doi.org/10.1002/ajp.22755

Irwin, M. T., Raharison, J., Chapman, C. A., Junge, R. E., & Rothman, J. M., (2017). Minerals in the foods and diet of diademed sifakas: Are they nutritional challenges? *American Journal of Primatology*, 79:e22623, 1-14. DOI:10.1002/ajp.22623

Isbell, L. A. (1991). Contest and scramble competition: patterns of female aggression and ranging behavior among primates. *Behavioral Ecology*. 2(2), 143-155.

Janson, C. H. & Chapman, C. A. (1999). Resources and primate community structure *In* Fleagle, J. G., Janson, C. H., & Reed, K. *Primate Communities*. Cambridge University Press.

Jarvey, J.C., Low, B.S., Pappano, D.J. *et al.* Graminivory and Fallback Foods: Annual Diet Profile of Geladas (*Theropithecus gelada*) Living in the Simien Mountains National Park, Ethiopia. *International Journal of Primatology* 39, 105–126 (2018). https://doi.org/10.1007/s10764-018-0018-x

Jung, L., Mourthe, I., Grelle, C. E. V., Strier, K. B., & Boubli, J. P. (2015). Effects of Local Habitat Variation on the Behavioral Ecology of Two Sympatric Groups of Brown Howler Monkey (*Alouatta clamitans*). *Plos One, 10*(7). DOI:10.1371/journal.pone.0129789

Karasov, W. H. & Martinez del Rio, C. (2007). *Physiological Ecology: How animals process energy, nutrients, and toxins.* Princeton University Press.

Kay, R. F. (1984). On the use of anatomical features to infer foraging behavior in extinct primates *In* Cant, J. & Rodman, P. *Adaptations for Foraging in Nonhuman Primates*. Columbia University Press. 21-53.

Kifle, Z., & Bekele, A. (2021). Feeding ecology and diet of the southern geladas (*Theropithecus gelada obscurus*) in human-modified landscape, Wollo, Ethiopia. *Ecology and Evolution*, *11*(16), 11373-11386. https://doi.org/10.1002/ece3.7927

Knott, C. D. (1998). Changes in orangutan caloric intake, energy balance, and ketones in response to fluctuating fruit availability. *International Journal of Primatology, 19*(6), 1061-1079. DOI:10.1023/a:1020330404983

Koenig, A., Scarry, C. J., Wheeler, B. C., & Borries, C. (2013). Variation in grouping patterns, mating systems and social structure: what socio-ecological models attempt to explain. *Philosophical Transactions of the Royal Society B-Biological Sciences, 368*(1618). DOI:10.1098/rstb.2012.0348

Korstjens, A. M., Lehmann, J. & Dunbar, R. I. M. (2010). Resting time as an ecological constraint on primate biogeography. *Animal Behaviour*, *79*(2), 361-374.

Kraus JB, Strier KB. (2022) Geographic, climatic, and phylogenetic drivers of variation in colobine activity budgets. *Primates*. https://doi: 10.1007/s10329-022-01015-y

Lambert, J. E., & Rothman, J. M. (2015). Fallback Foods, Optimal Diets, and Nutritional Targets: Primate Responses to Varying Food Availability and Quality. *In* D. Brenneis & K. B. Strier (Eds.), *Annual Review of Anthropology, 44*, 493-512. Annual Reviews: Palo Alto.

Lambert, J. E., Chapman, C. A., Wrangham, R. W., & Conklin-Brittain, N. L. (2004). Hardness of cercopithecine foods: Implications for the critical function of enamel thickness in exploiting fallback foods. *American Journal of Physical Anthropology, 125*(4), 363-368. DOI:10.1002/ajpa.10403

Liu, R., Amato, K., Hou, R., Gomez, A., Dunn, D. W., Zhang, J., ... & Guo, S. (2022). Specialised digestive adaptations within the hindgut of a colobine monkey. *The Innovation*, 100207. https://doi.org/10.1016/j.xinn.2022.100207

Lodwick, J. L., & Salmi, R. (2019). Nutritional composition of the diet of the western gorilla (*Gorilla gorilla*): Interspecific variation in diet quality. *American journal of primatology*, *81*(9), https://doi.org/10.1002/ajp.23044.

Luccas, V., Izar, P. (2021) Black capuchin monkeys dynamically adjust group spread throughout the day. *Primates* 62, 789–799 (2021). https://doi.org/10.1007/s10329-021-00926-6

McGraw, W. S., & Daegling, D. J. (2020). Diet, feeding behavior, and jaw architecture of Taï monkeys: Congruence and chaos in the realm of functional morphology. *Evolutionary Anthropology: Issues, News, and Reviews*, *29*(1), 14-28. https://doi.org/10.1002/evan.21799

McGrosky, A., Meloro, C., Navarrete, A., Heldstab, S. A., Kitchener, A. C., Isler, K., & Clauss, M. (2019). Gross intestinal morphometry and allometry in primates. *American Journal of Primatology*, *81*(8), https://doi.org/10.1002/ajp.23035e23035.

Ménard, N., Motsch, P., Delahaye, A., Saintvanne, A., Le Flohic, G., Dupé, S., . . . Pierre, J.-S. (2013). Effect of habitat quality on the ecological behaviour of a temperate-living primate: time-budget adjustments. *Primates, 54*(3), 217-228.

Ménard, N., Motsch, P., Delahaye, A., Saintvanne, A., Le Flohic, G., Dupé, S., . . . Pierre, J. S. (2014). Effect of habitat quality on diet flexibility in Barbary macaques. *American journal of primatology, 76*(7), 679-693.

Mendes, S. L. (1989). Estudo ecológico de *Alouatta fusca* (Primates: Cebidae) na Estação Biológica de Caratinga, MG. *Revista Nordestina de Biologia, 6*(2), 71-104.

Meyer, A.L.S., Pie, M.R. Climate Change Estimates Surpass Rates of Climatic Niche Evolution in Primates. *Int J PrimatolInternational Journal of Primatology* 43, 40–56 (2022). https://doi.org/10.1007/s10764-021-00253-z

Milton, K. (1980). *The foraging strategy of howler monkeys: a study in primate economics*: Columbia University Press.

Milton, K. (1981). Food choice and digestive strategies of two sympatric primate species. *The American Naturalist*. 117(4), 496-505.

Milton, K. (1984). Habitat, diet, and activity patterns of free-ranging woolly spider monkeys (*Brachyteles arachnoides* E. Geoffroy 1806). *International Journal of Primatology*. 5(5), 491-514.

Milton, K. (1986). Digestive physiology in primates. *Physiology*, 1(2), 76-79.

Milton, K. (1997). Physiological ecology of howler (*Alouatta*): Energetic and digestive considerations and comparison with the Colobinae. *International Journal of Primatology*. 19(3), 513-548.

Neha, S.A., Khatun, U.H. & Ul Hasan, M.A. (2021) Resource partitioning and niche overlap between hoolock gibbon (*Hoolock hoolock*) and other frugivorous vertebrates in a tropical semi-evergreen forest. *Primates* 62, 331–342 (2021). https://doi.org/10.1007/s10329-021-00888-9

Ostro, L. E. T., Silver, S. C., Koontz, F. W., & Young, T. P. (2000). Habitat selection by translocated black howler monkeys in Belize. *Animal Conservation, 3*, 175-181. DOI:10.1111/j.1469-1795.2000.tb00242.x

Penry, D.L. 1993. Digestive constraints on diet selection *In* Hughes, R. *Diet selection: an interdisciplinary approach to foraging behaviour*, Blackwell Scientific Publications: Cambridge, MA.

Riley, E. P. (2007). Flexibility in diet and activity patterns of *Macaca tonkeana* in response to anthropogenic habitat alteration. *International Journal of Primatology, 28*(1), 107-133.

Rode, K. D., Chapman, C. A., McDowell, L. R., & Stickler, C. (2006). Nutritional correlates of population density across habitats and logging intensities in redtail monkeys (*Cercopithecus ascanius*). *Biotropica, 38*(5), 625-634. DOI:10.1111/j.1744-7429.2006.00183.x

Rosenberger, A. L., Halenar, L., & Cooke, S. B. (2011). The making of platyrrhine semifolivores: models for the evolution of folivory in primates. *The Anatomical Record, 294*(12), 2112-2130.

Rothman, J. M., Chapman, C. A., Struhsaker, T. T., Raubenheimer, D., Twinomugisha, D., & Waterman, P. G. (2015). Long-term declines in nutritional quality of tropical leaves. *Ecology, 96*(3), 873-878. DOI:10.1890/14-0391.1

Rothman, J. M., Raubenheimer, D., Chapman, C. A., (2011). Nutritional geometry: Gorillas prioritize non-protein energy while consuming surplus protein. *Biology Letters*. DOI:10.1098/rsbl.2011.0321

Rothman, J. M., Van Soest, P. J., & Pell, A. N. (2006). Decaying wood is a sodium source for mountain gorillas. *Biology Letters, 2*(3), 321-324. DOI:10.1098/rsbl.2006.0480

Ruslin, F., Matsuda, I. & Md-Zain, B.M. (2019) The feeding ecology and dietary overlap in two sympatric primate species, the long-tailed macaque (*Macaca fascicularis*) and dusky langur (*Trachypithecus obscurus obscurus*), in Malaysia. *Primates* 60**,** 41–500 (2019). https://doi.org/10.1007/s10329-018-00705-w

Russo, S.E., Campbell, C.J., Dew, J.L. et al. (2005) A Multi-Forest Comparison of Dietary Preferences and Seed Dispersal by *Ateles spp. International Journal of Primatology* 26, 1017–1037 (2005). https://doi.org/10.1007/s10764-005-6456-2

Sacco, A. J., Granatosky, M. C., Laird, M. F., & Milich, K. M. (2021). Validation of a method for quantifying urinary C-peptide in platyrrhine monkeys. *General and Comparative Endocrinology*, *300*, https://doi.org/10.1016/j.ygcen.2020.113644113644.

Santos, G. A. d. S. D., Bianchini, E., & Reis, N. R. d. (2013). Seasonal variation of consumption of the species used as fruit source by brown howler monkeys (Alouatta clamitans) in southern Brazil. *Biota Neotropica, 13*(3), 148-153.

Simmen, B., & Rasamimanana, H. (2018). Energy (im-) balance in frugivorous lemurs in southern Madagascar: a preliminary study in *Lemur catta* and *Eulemur rufifrons*× *collaris*. *Folia Primatologica*, 89(6), 382-396. https://doi.org/10.1159/000492570

Simpson, S.J. and Raubenheimer, D. (2012). *The nature of nutrition: a unifying framework from animal adaptation to human obesity*. Princeton University Press.

Sterck, E. H. M., Watts, D. P., & van Schaik, C. P. (1997). The evolution of female social relationships in nonhuman primates*. Behavioral Ecology and Sociobiology* 41, 291-309.

Stevenson, P., Quiñones, M. J., & Ahumada, J. A. (2000). Influence of fruit availability on ecological overlap among four neotropical primates at Tinigua National Park, Colombia. *Biotropica*. 32(3), 533-544.

Stiling, P., & Cornelissen, T. (2007). How does elevated carbon dioxide (CO2) affect plant-herbivore interactions? A field experiment and meta-analysis of CO2-mediated changes on plant chemistry and herbivore performance. *Global Change Biology, 13*(9), 1823-1842. DOI:10.1111/j.1365-2486.2007.01392.x

Stoner, K. E. (1996). Habitat selection and seasonal patterns of activity and foraging of mantled howling monkeys (Alouatta palliata) in northeastern Costa Rica. *International Journal of Primatology, 17*(1), 1-30. DOI:10.1007/bf02696156

Strier KB, Lee PC, & Ives AR. (2014) Behavioral flexibility and the evolution of primate social states*. PLoS One*. Dec 3;9(12):e114099. Doi: 10.1371/journal.pone.0114099.

Strier, K. B. (1989). Effects of patch size on feeding associations in muriquis (*Brachyteles arachnoides*). *Folia Primatologica, 52*(1-2), 70-77. DOI:10.1159/000156383

Strier, K. B. (1991). Diet in one group of woolly spider monkeys, or muriquis (*Brachyteles arachnoides*). *American Journal of Primatology* 23, 113-126.

Strier, K. B. (1992). Atelinae adaptations: behavioral strategies and ecological constraints. *American Journal of Physical Anthropology, 88*(4), 515-524.

Strier, K. B. (2009). Seeing the forest through the seeds: mechanisms of primate behavioral diversity from individuals to populations and beyond. *Current Anthropology 50*(2), 213-228. DOI: 10.1086/592026

Strier, K. B. (2016). *Primate Behavioral Ecology*, *5th edition*, Routledge (Taylor & Francis)

Strier, K. B. (2017). What does variation in primate behavior mean? *American Journal of Physical Anthropology 162*:S63, 4-14.

Strier, K.B. (2021a) *Primate Behavioral Ecology*. Routledge. Companion website: https://routledgetextbooks.com/textbooks/9780367222888/

Strier, K.B. (2021b) The limits of resilience. *Primates* 62**,** 861–868. (2021). https://doi.org/10.1007/s10329-021-00953-3

Strier, K. B., & Boubli, J. P. (2006). A history of long-term research and conservation of northern muriquis (*Brachyteles hypoxanthus*) at the Estação Biológica de Caratinga/RPPN-FMA. *Primate Conservation*. *20*, 53-63. DOI:10.1896/0898-6207.20.1.53

Tabeli, M., Bastos, A., & Lee, P. C. (2005). Diet of southern muriquis in continuous Brazilian Atlantic Forest. *International Journal of Primatology*. *26*(5), 1175-1187

Thurau, E. G., Rahajanirina, A. N., & Irwin, M. T. (2021). Condensed tannins in the diet of folivorous diademed sifakas and the gap between crude and available protein. *American Journal of Primatology*, 83(3), https://doi.org/10.1002/ajp.23239e23239.

Uwimbabazi, M., Raubenheimer, D., Tweheyo, M., Basuta, G. I., Conklin-Brittain, N. L., Wrangham, R. W., & Rothman, J. M. (2021). Nutritional geometry of female chimpanzees (*Pan troglodytes). American Journal of Primatology*, *83*(7), https://doi.org/10.1002/ajp.23269e23269.

van Schaik, C. P. (1989). The ecology of social relationships amongst female primates *In* Standen, V., & Foley, R. A. (eds.) *Comparative socioecology: the behavioral ecology of humans and other mammals*. Blackwell: Oxford.

van Schaik, C. P. & Brockman, D. B. (2005). Seasonality in primate ecology, reproduction, and life history: an overview *In* Brockman, D. B. & van Schaik, C. P. (Eds.) *Seasonality in Primates*. Cambridge University Press.

van Schaik, C. P., Terborgh, J. W., & Wright, S. J. (1993). The phenology of tropical forests: adaptive significance and consequences for primary consumers. *Annual Review of ecology and Systematics, 24*(1), 353-377.

Vogel, E. & Dominy, N. (2011). Ecological methods *In* Campbell, C. J., Fuentes, A., MacKinnon, K. C., Bearder, S. K., Stumpf, R. M., (Eds.) *Primates in Perspective*. Oxford University Press.

Vogel, E. R., Knott, C. D., Crowley, B. E., Blakely, M. D., Larsen, M. D., & Dominy, N.J. (2012). Bornean orangutans on the brink of protein bankruptcy. *Biology Letters 8*(3), 333-336.

Wrangham, R. W. (1980) An ecological model of female-bonded primate groups. *Behaviour*. *75*(3/4), 262-300.

Zvereva, E. L., & Kozlov, M. V. (2006). Consequences of simultaneous elevation of carbon dioxide and temperature for plant-herbivore interactions: a meta analysis. *Global Change Biology, 12*(1), 27-41. DOI:10.1111/j.1365-2486.2005.01086.x

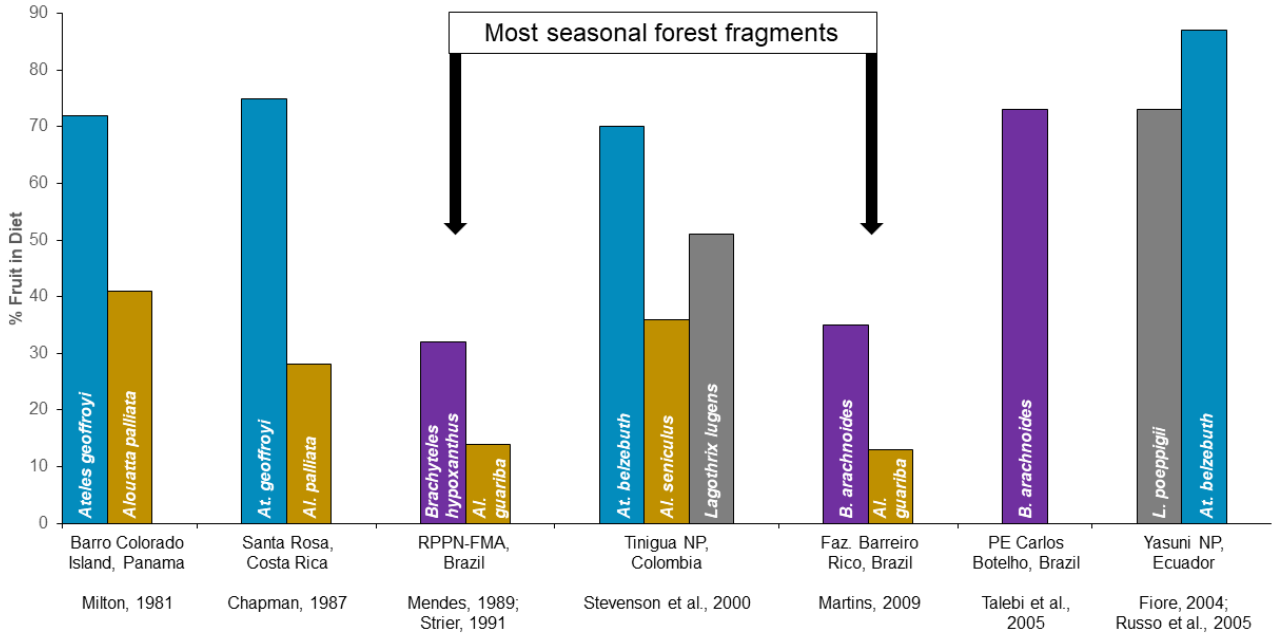

Figure 1. Sympatric and intergeneric comparisons of Atelidae diet. Both *Brachyteles* and *Alouatta* are less frugivorous in the most seasonal, fragmented forests. Nonetheless, where dietary data are available for both genera (RPPN-FMA), *Brachyteles* resembles *Ateles* elsewhere in being proportionately more frugivorous relative to sympatric *Alouatta*. (updated from Strier, 2021a online supplement).

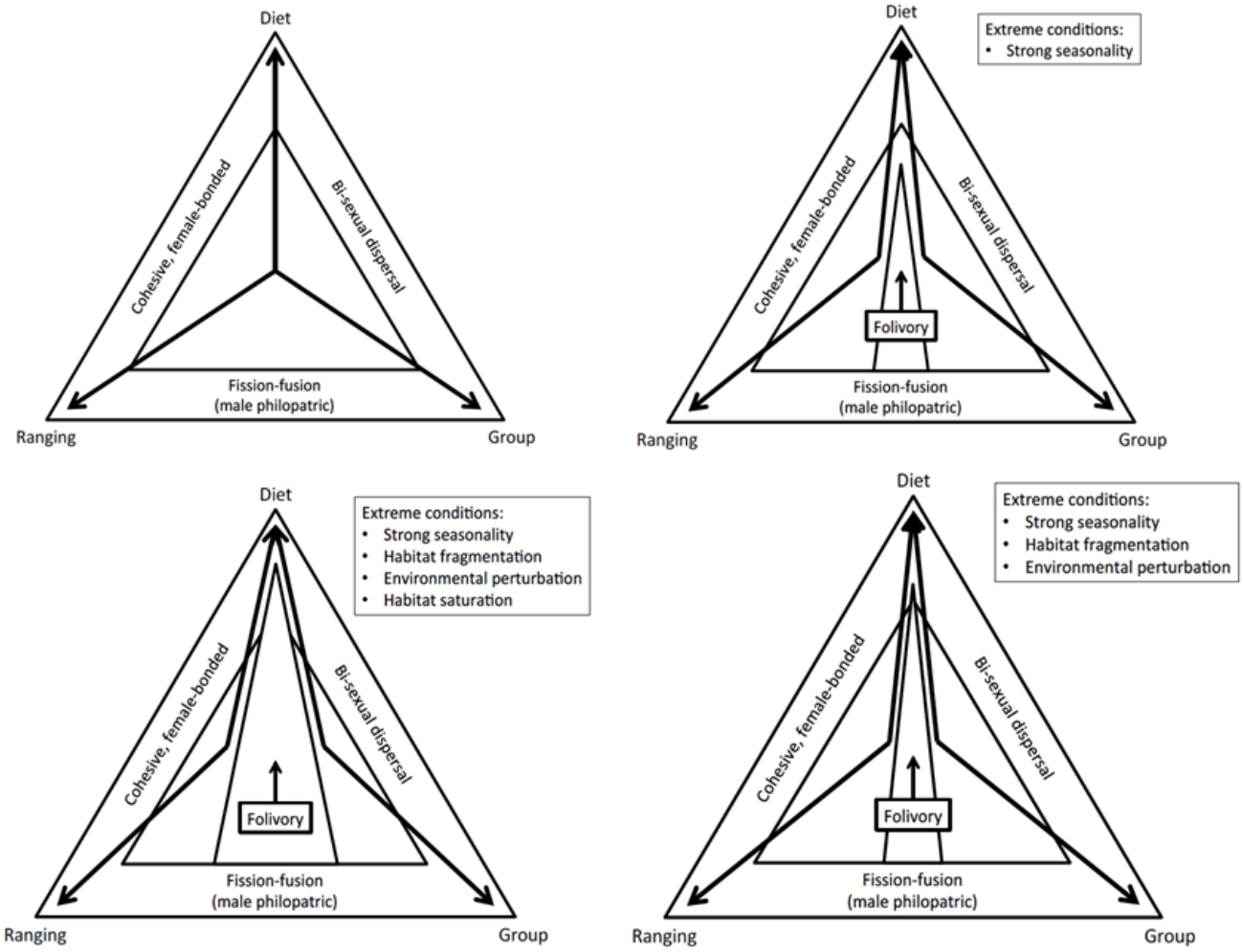

Figure 2. Schematic model of behavioral responses to food availability. Behavioral adjustments to changes in food availability include changes in diet, grouping, and ranging patterns (upper left). The way that primates respond to changes in food availability also reflect patterns of dispersal and social systems, following Strier (2009). Female bonded species are most likely to change ranging and diet; fission-fusion (male philopatric) species (see Strier, Possamai, & Mendes, 2015) are most likely to change ranging and grouping; and species with bisexual dispersal regimes are most likely to change grouping patterns and diet, as originally described by Strier (2009). Extreme ecological conditions, such as those shown in sequential panels (clockwise from upper right), can impact the ability of a species to respond to food availability,

which can in turn interact with constraints on a species' ability to subsist on leaves and other low quality foods (Strier, 2021a).

Chapter 2: Social Behavior in Small Groups of Brown Howler Monkeys (*Alouatta guariba*) in an Atlantic Forest Fragment

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Abstract

Anthropogenic habitat disturbance and demographic variables such as group size are known to impact primate behavior. We present 5 months of data collected on the social relationships of three small groups of brown howler monkeys (*Alouatta guariba*) with varying degrees of exposure to human activity to evaluate intraspecific behavioral variation. Observations were made at the Reserva Particular do Patrimônio Natural - Feliciano Miguel Abdala in Caratinga, Brazil, between September 2018 and May 2019. Group sizes ranged from 4-6 individuals, with one adult male and two adult females whose membership remained constant in each group. We found that in a group in the forest interior, the female-female dyad associated and groomed more often than expected and was never seen in agonistic behavior, similar to what has been reported in other howler monkeys found in similarly small groups in other areas (e.g., *Alouatta pigra*, *Alouatta seniculus*). By contrast, in the two groups with exposure to high forest edge densities, there was greater intermonthly variation in dyadic spatial associations, grooming rates, and agonistic interactions, suggesting potential responses to anthropogenic disturbances.

Introduction

Primate social dynamics are sensitive to changes in competition within and between groups, and thus are influenced by ecology, demography, and population density (Aureli et al., 2012; Strier et al., 2014). In addition to phylogenetically constrained behaviors like dispersal, group size influences the number and quality of relationships that an individual may form throughout their lifetime (Strier et al., 2014). Howler monkey (*Alouatta* spp.) social groups range from male-female pairs to large multi-male, multi-female groups of up to 40 individuals (Di Fiore et al., 2011). Bisexual dispersal should preclude adult howler monkeys from living in groups with their extended kin (Glander, 1980, 1992; Clarke and Glander, 1984; Rumiz, 1990; Strier, 2008;

but see Pope, 1998, 2000; Van Belle et al., 2014). Indeed, in large groups of mantled howler monkeys (*A. palliata*), females are thought to form relationships with adult males that can offer resources and protection from infanticidal extra-group males (Crockett and Janson, 2000). Correspondingly, their intrasexual relationships have been characterized as relatively weak (Zucker and Clarke, 1998; Wang and Milton, 2003; Milton et al., 2016).

Howler species that typically live in smaller groups (i.e., fewer than 15 individuals) show more variation in social relationships (*A. seniculus*, Sánchez-Villagra et al., 1998; Pope, 2000; *A. pigra*, Corewyn and Pavelka, 2007; Van Belle et al., 2011). For example, female black howler monkeys in Palenque, Mexico, frequently associated and affiliated with other females in their social groups regardless of kinship (Van Belle et al., 2014). Similarly, female red howler monkeys in the western Llanos of Venezuela formed coalitions with unrelated females that aided in establishing territory and in excluding other females from feeding and mating opportunities (Pope, 2000). Thus, it seems that strong female-female relationships may be common in some small howler monkey groups.

In addition, in small group-living howler monkeys, female-male social relationships can fluctuate with male group membership. Black howler monkey males did not form strong associations with females in their groups during periods of instability in adult male group membership, yet when male membership remained stable, their strong associations with females likely led to higher mating success (Van Belle et al., 2008). Similarly, in one group of brown howler monkeys (*A. guariba*) at the Reserva Particular do Patrimônio Natural – Feliciano Miguel Abdala (RPPN-FMA; site of this study) female-male associations weakened during a temporary take-over by a non-resident male and strengthened when the original resident male returned to the group (Mendes, 1989).

While social associations are variable depending on group size, allo-grooming in howler monkeys is also exclusively carried out by females (Chiarello, 1995; Miranda et al., 2004). At the Santa Genebra Reserve near Campinas, São Paulo, Brazil, female brown howler monkeys

initiated 91% of grooming bouts and the male of the study group received the majority (37%) of allo-grooming; however, while grooming was primarily done by females and directed at the adult male, one female groomed the male twice as much as the other female in the group (Chiarello, 1995). At the RPPN-FMA, female brown howler monkeys were responsible for 96% of allo-grooming among adults, but the female-female dyad groomed more often than either of the two female-male dyads (Mendes, 1989). This suggests that while females initiate most of the grooming observed in this species, males are not always the primary recipient.

In addition to group size and composition, variation in habitat quality and levels of anthropogenic disturbance sometimes, but not always, affects the frequency and diversity of social behaviors in howler monkeys (Jung et al., 2015; Negrín et al., 2016). At the RPPN-FMA, a group of brown howler monkeys occupying a high quality valley habitat spent more time socializing than the group occupying a lower quality hilltop habitat (Jung et al., 2015). Additionally, at one site in Costa Rica (the Curú Wildlife Refuge), mantled howler groups in closer proximity to anthropogenic disturbance were less cohesive and had larger home ranges than sympatric groups in higher quality areas (McKinney, 2019) while at the La Suerte Biological Research Station, where mantled howlers occur at high density (0.73 ind./ha; Schreier and Bolt, 2020), groups did not alter behavior or ranging in edges versus interior habitats (Schreier et al., 2021).

Brown howler monkeys in the small (*ca* 1,000 ha) forest fragment at the RPPN-FMA in southeastern Brazil occupy habitats with varying exposure to human activities and have experienced major demographic changes over the past 35 years. Historically they occurred at high densities (1.17 ind./ha; (Mendes, 1989) with a median group size of 7 individuals (range = 3-12). By 2003, the population of howlers at the RPPN-FMA had declined by roughly 50% (0.502 ind./ha; Almeida-Silva et al., 2005) corresponding with a decrease in population density and median group size to 4 individuals, though the range in group sizes remained constant. A

further and much more drastic population decrease of 80% occurred in the wake of a yellow fever outbreak in late 2016-early 2017 (Possamai et al., 2019; Possamai et al., 2022).

While prior work at the RPPN-FMA has demonstrated variation in brown howler monkey behavior in response to habitat quality, as measured by ecological variables such as number of emergent trees, number of canopy layers, canopy connectivity, and canopy continuity (Jung et al. 2015), nothing yet has been done comparing groups with different levels of exposure to human activities. Here, we capitalize on the population decline and expand on Jung et al. (2015) by including groups with different exposure to human activities to compare social behavior and responses to anthropogenic disturbance in three groups of similarly small size.

Specifically, based on similar group size and composition, we predicted: i-a) if the strongest social relationships in brown howler monkey groups are opposite sex (Chiarello, 1995; Zucker and Clarke, 1998; Wang and Milton, 2003; Milton et al., 2016), then female-male dyads should be observed in proximity more often, have a higher number of social bouts, and spend more time grooming when compared to female-female dyads. Alternatively, i-b) if females form a “stable core” in brown howler monkey groups similar to those of black howler monkeys (Corewyn and Pavelka, 2007; Van Belle et al., 2011), then female-female dyads should be observed in proximity more often, have a greater number of social bouts, and spend more time grooming than female-male dyads. Further, ii-a) if variation in proximity to human activity influences social behavior, we predicted that groups with higher a proportion of forest edge, meters of edge per hectares in their home range (“edge density,” Hargis et al., 1998), would spend less time socializing than the group in the forest interior assuming edges imply lower habitat quality (Jung et al., 2015; McKinney, 2019). Alternatively, ii-b) if brown howler monkeys at the RPPN-FMA are able to persist in more disturbed areas without altering spatial or social behavior (Schreier et al., 2021), then there would be no significant differences in behavior between the three study groups.

Methods

Study site and groups

This study was carried out between August 2018 and May 2019 at the RPPN-FMA (19º50'S, 41º50'N) a roughly 1,000 ha fragment of the Brazilian Atlantic Forest, one of the most biodiverse and threatened ecosystems in the world. The RPPN-FMA varies in altitude between 400 and 680 m and is characterized by extensive variation in composition and quality due to historical extraction and land-use patterns (e.g., selective logging, coffee cultivation, etc.) (Boubli et al., 2011; Jung et al., 2015). Rainfall and temperature are highly seasonal at this site, with the rainiest months typically occurring between November and April (Strier et al., 2001).

We collected data for this study from three groups (CM, CR, and RB) of brown howler monkeys living in the Matão region of the RPPN-FMA. We selected groups based on proximity to the research station and habitat type (i.e., edge/roadside habitats (groups CM and CR) or interior habitat (group RB)). Each group had three adults (one male, "M," and two females, "FA" and "FB") and associated offspring (N = 2-3 (CM); 1 (CR); 1-2 (RB)). Two births occurred during the study period: FB in group RB gave birth to an infant between 16 April 2019 and 10 May 2019; FA in group CM gave birth to an infant between successive days of observation on 4 and 5 May 2019.

Data collection

Data collection began in September 2018 (groups CM and CR) or October 2018 (group RB) and continued through May 2019. One week per month was allocated to finding and following each group. Behavioral data were collected on all group members using instantaneous scan samples conducted at 30-minute intervals and the first behavior of each individual lasting

longer than 5 seconds was recorded (Altmann, 1974). Continuous behavioral data were collected from adults during 15-minute periods in the interval between scan samples. Focal sample collection began with the most-visible individual each morning and then rotated through all adults in the group (N=3 in each group) in a consistent pattern to avoid sampling bias. During focal samples, social behaviors such as grooming were recorded to the nearest second, with social partners and directionality also recorded. Focal subjects were considered out of sight if they were not visible for more than 3 minutes and all focal samples of less than 12 minutes were discarded (proportions derived from Wang and Milton, 2003; Van Belle et al., 2011). Intergroup encounters, vocalization (e.g., “long call”) bouts, agonistic encounters (e.g., barking, lunging, chasing), or copulations were recorded *ad libitum*.

Sample sizes and limitations

Due to prohibitively small sample sizes, only data from September-November 2018 and April-May 2019 are presented here (Table 1). Small sample sizes limit the statistical power of any analysis and can lead to increased likelihood of false-positive or false-negative findings (Forstmeier et al., 2017). Due to the small sample sizes of the current study, all data were analyzed using non-parametric tests. Extrapolation from these data is also limited because 91.36% of all observations (N=752) were made between 8:00 and 16:00, and thus activity data are likely to be biased against resting time in the early and late hours of the day.

Behavioral data analysis

We analyzed all data in R version 3.5.1 (R Core Team 2021). To assess whether time of day had a significant relationship to behavior, we calculated hourly medians for each behavior within each group and compared hourly behavior within each month using Kruskal-Wallis tests,

calculating effect sizes for significant results. We further tested these data using additional Kruskal-Wallis tests to determine whether the observed behaviors at each hour of the day differed between groups. We conducted post hoc pairwise Dunn tests when group behaviors differed based on time of day, with Bonferroni adjusted p-values. We performed these time of day analyses to determine whether social behavior was more likely to occur at certain hours of the day, and account for the potential bias against social behavior observations in the data set.

The first set of social behavior analyses was carried out using a simple ratio index (SRI) as a descriptive metric. The SRI quantifies the proportion of time that individuals are observed in spatial associations, here defined as 0-1 m (Cairns and Schwager, 1987; Farine and Whitehead, 2015). Following convention, the SRI was calculated as $SRI = N_{AB}/(N_{AB} + N_A + N_B)$, where N_{AB} = the number of scan samples of individuals A and B together, N_A= the number of scan samples of individual A without individual B as nearest neighbor, and N_B = the number of scan samples of individual B without individual A as nearest neighbor. SRI scores range between 0-1, with 0 showing that the dyad was never seen together and 1 indicating that the dyad was always seen together.

To statistically compare spatial associations, we used chi-square goodness-of-fit tests (following Van Belle et al., 2011) or exact multinomial tests when expected values were less than 5. Expected values were calculated as the sum of all observations with a dyad in proximity divided by the number of scan samples with each member of the dyad present. Because only scans with all adult group members present were used in these analyses, the expected proportion for each of the three dyads was always 0.33. When testing yielded significant results, we calculated standardized residuals to determine the dyads with the largest differences between observed and expected values.

The second set of social behavior analyses was based on the number of social bouts observed between each dyad during continuous focal sampling. Following Van Belle et al. (2011) a social bout was defined as any social interaction in the same category (e.g., grooming,

agonistic behavior) lasting greater than 30 seconds and separated from other social behaviors by >5 minutes. The observed number of social bouts was compared to the expected numbers obtained by dividing the hours of observation for each dyad by the total hours of observation for all dyads. Grooming rates (minutes of grooming per hours of observation) were compared across dyads within each group for using Kruskal-Wallis tests with post hoc pairwise testing and Bonferroni adjusted *p* values when significant differences were observed.

Spatial data analysis

To evaluate the effects of habitat edge density on behavior across groups, we analyzed spatial data in R using the package 'adehabitatHR' (Calenge, 2006) and imported data into QGIS 2.18 (QGIS Development Team) for mapping and further analysis. We used all scans with GPS data to calculate monthly home ranges for each of the 5 months of the study period, even if individual behaviors were not visible. The total number of location sightings ranged from 225-278; Table 1).

Following the most recent study of howler monkey behavior and ecology at the RPPN-FMA (Jung et al., 2015), we calculated monthly home ranges using the 100% minimum convex polygon method (MCP). The 100% MCP method creates the smallest possible polygon covering all GPS locations for the groups. Polygons were adjusted to subtract areas of the Reserve (such as pasture remnants) with unsuitable habitat (Grueter et al., 2009). Home range size estimates can vary significantly based on the method of estimation (e.g., Grueter et al., 2009), thus while the MCP method may produce overly conservative estimates we used this calculation to facilitate comparisons with prior research. We calculated percent overlap of home ranges, where appropriate, in QGIS using adjusted MCP monthly home ranges.

For a preliminary assessment of habitat quality and proximity to human activity we calculated edge density for each monthly home range by dividing the home range (ha) by

meters of edge, defined as either cleared area or area along a dirt road used by vehicles and people on foot or bikes (Hargis et al., 1998). This resulted in edge densities representing m/ha for each of the groups during each month of the 5-mo study period.

Results

Spatial associations and social interactions

We found no effect of time of day on social behavior that could bias our comparisons (Table 2). SRI values ranged from 0.00 (group RB, FB-M dyad in April) to 0.85 (also group RB, FA-FB), with consistently higher SRI values for one of the female-male dyads in two of the three groups (group CM, FA-M > FB-M dyad; group CR, FB-M > FA-M dyad across all months). SRI values in the FA-M and FB-M dyads in group RB did not show a clear pattern across months (Table 3).

In all three groups, the female-female dyads usually associated as often as expected based on group composition, but in at least one month in each group the female-female dyad associated significantly more than expected (Figure 1). Female-male spatial associations were more variable but usually occurred less than expected based on group composition, with the exception of one female-male dyad in group CM, which associated more often than expected in April and May 2019 and one female-male dyad in group CR, which associated more often than expected in November 2018.

The frequency of social bouts observed per dyad and month across groups ranged from 0 to 6, corresponding to 0.00-1.7143 bouts per hour of observation (Table 3). Exact multinomial tests showed only one month in one group where the number of social bouts was significantly different than expected (group RB, April: p value = 0.0210), likely driven by the absence of

social bouts involving either female-male dyad. In groups CM and CR, the female-female dyads did not socialize significantly more than the female-male dyads.

Median total grooming rates across groups ranged from 0.00 for the FA-M dyad in group CR to 1.26 minutes grooming/hour of observation for the FA-FB dyad in group RB (Table 3). There were no significant differences in grooming rates between dyads in group CM and CR, however in group RB grooming rates differed significantly between the dyads (Kruskal-Wallis test, H=8.8578, *p* value = 0.01193; Figure 2). Post hoc pairwise testing with Bonferroni adjusted p-values showed that the female-female dyad groomed significantly more than either female-male dyad (FA-FB to FA-M adjusted *p* value = 0.043; FA-FB to FB-M adjusted *p* value = 0.043) while there was no significant difference between grooming time for the two female-male dyads (FA-M to FB-M adjusted *p* value = 0.124). As expected from prior studies (Mendes, 1989), females were responsible for the majority of grooming, with responsibility ranging from 70% (group RB in October) to 100% (in all groups in at least one month) (Table 3). The adult male was the recipient of the majority of grooming in group CM during September and October and in group CR during October and May. In group RB, the resident male was infrequently groomed, with his time as recipient ranging from 0% in April to 20% in May.

Rates of agonism ranged from 0.00 to 0.4362 events per hour of observation and were concentrated in 18 events across all groups (Table 3). The highest rate of agonistic interactions occurred between FA-FB in group CM in October, when female B repeatedly chased and lunged at female A. No instances of female-female agonism were seen in groups CR or RB. Hitting, chasing, and supplants were the most observed agonistic behaviors (each witnessed five times).

Only two copulations were witnessed during this study, both in group CM. Female A and the resident male copulated once on October 9, and female B and the resident male copulated once on May 5 (the day after female A gave birth to an infant).

Home range size and anthropogenic disturbance

Monthly home range size varied from 0.81-6.49 ha across groups. Group CM used the largest home range of 6.49 ha in October 2018, while group RB used the smallest home range of 0.81 ha in May 2019 (Table 4). Of the two groups with edge exposure, edge density ranged from 0.00 to 152.44 m/ha in group CR and 47.07 to 183.09 m/ha in group CM. Edge density does not appear to be related to habitat size, though there are too few groups and months to assess this statistically. The median proportion of time spent in social activity was too low (e.g., 0.00) in all but one month for one group and cannot therefore be evaluated (Table 4).

Discussion

Our results suggest that levels of anthropogenic disturbance, as measured by edge density, may affect brown howler monkey social dynamics in our study. The group with no edge exposure (RB) was similar to other small group-living species like red howler monkeys and black howler monkeys in having stronger than expected relationships between females (Pope, 2000; Corewyn and Pavelka, 2007; Van Belle et al. 2011). Specifically, the female-female dyad in group RB consistently associated more than expected, spent more time spent grooming than either female-male dyad, and was never observed in agonistic interactions.

While the female-female dyad in each of the three study groups associated more than expected in at least some months, in the two groups with edge exposure (CM and CR) dyadic spatial associations were more variable and were not reflected in grooming rates. In both edge groups, one female-male dyad associated more often than the other, and in some months, they associated significantly more than expected. The weakest female-male dyad in both groups was one in which the female was also carrying a dependent offspring. However, we do not know which individuals were responsible for maintaining or avoiding the associations.

Female primates of many species express significant interest in infants and will often associate more with new mothers than other group members (Dunayer and Berman, 2018). Infant births influence dyadic relationships in other howler monkey species (e.g., *A. palliata,* Zucker and Clarke, 1998; *A. pigra*, Van Belle et al., 2011), often leading females to spend more time in the company of females with young infants. In one of the edge groups (CM), the birth of an infant between 4-5 May 2019 coincided with an increase in the spatial associations between the mother (FA) and the other female (FB). However, in the non-edge group (RB), the birth of an infant between 16 April-10 May 2019 did not alter the consistently strong female-female associations, suggesting that factors other than the presence of an infant underlie their social preferences.

While we were not able to compare social behavior across the three groups, it is possible that proximity to human activity has some influence on the stability or predictability of social relationships. Despite identical group sizes and sex ratios, the two groups (CM and CR) with edge exposure had greater variation in dyadic social relationships throughout the study period compared to the more consistent relationships in the group with no edge exposure. However, these differences could also reflect other factors, such as differences in group histories or kinship among group members, instead of or in addition to potential anthropogenic disturbance.

Howler monkeys are often characterized as being extraordinarily adaptable and able to survive in a variety of habitats, however, responses to habitat fragmentation and degradation are highly variable in this genus (Bicca-Marques et al., 2003; Bicca-Marques et al., 2020). Given brown howlers' heightened risk of extinction due to a succession of yellow fever outbreaks in 2008-2009 and 2016-2017 (Bicca-Marques et al., 2017; Buss et al., 2019) further research assessing intraspecific behavioral variation in fragments like the RPPN-FMA is needed.

References

Almeida-Silva, B., Cunha, A. A., Boubli, J. P., et al. 2005. Population density and vertical stratification of four primate species at the Estação Biológica de Caratinga/RPPN-FMA, Minas Gerais, Brazil. *Neotrop Prim* (13).

Altmann, J. 1974. Observational Study of Behavior: Sampling Methods. *Behaviour*. (49)3/4, 227-267.

Aureli, F., Fraser, O. N., Schaffner, C. M., & Schino, G. 2012. The regulation of social relationships. In: *The Evolution of Primate Societies,* Mitani, J. C., Call, J., Kappeler, P. M., et al. (eds), University of Chicago Press, Chicago.

Bicca-Marques, J.C. How do Howler Monkeys Cope with Habitat Fragmentation? In: *Primates in Fragments: Ecology and Conservation,* Marsh, L. K. (eds). Springer, Boston, MA.

Bicca-Marques, J. C., Calegaro-Marques, C., Rylands, A. B., et al. 2017. Yellow fever threatens Atlantic Forest primates. *Science Advances* eLetters. https://www.science.org/do/10.1126/comment.195875/full/

Bicca-Marques, J. C., Chaves, Ó. M., Hass, G. P. 2020. Howler monkey tolerance to habitat shrinking: Lifetime warranty or death sentence? *Am J Primatol*. (82)4, e23089. https://doi.org/10.1002/ajp.23089

Boubli, J. P., Couto-Santos, F. R., Strier, K. B. 2011. Structure and floristic composition of one of the last forest fragments containing the critically endangered Northern Muriqui (*Brachyteles hypoxanthus*, Primates). *Ecotropica* 17:53-69.

Buss, G., Oklander, L. I., Bicca-Marques, J. C., et al. 2019. Brown Howler Monkey. In: *Primates in Peril: The World's 25 Most Endangered Primates 2018–2020,* Schwitzer, C., Mittermeier, R. A., Rylands, A. B., et al. (eds) IUCN SSC Primate Specialist Group, International Primatological Society, Global Wildlife Conservation, and Bristol Zoological Society, Washington, DC

Cairns, S. J., and Schwager, S. J. 1987. A comparison of association indices. *Anim Behav*. https://doi.org/10.1016/S0003-3472(87)80018-0

Calenge, C. 2006. The package "adehabitat" for the R software: A tool for the analysis of space and habitat use by animals. *Ecol Modell*. https://doi.org/10.1016/j.ecolmodel.2006.03.017

Chiarello, A. G. 1995. Grooming in brown howler monkeys, *Alouatta fusca*. *Am J Primatol.* https://doi.org/10.1002/ajp.1350350107

Clarke, M. R., and Glander, K. E. 1984. Female reproductive success in a group of free-ranging howling monkeys (*Alouatta palliata*) in Costa Rica. In: *Female Primates: Studies by Women Primatologists*, Small, M. F. (ed). Liss, New York

Corewyn, L. C., and Pavelka, M. S. M. 2007.) A preliminary study of proximity patterns among age-sex classes in a population of Central American black howlers (*Alouatta pigra*). *Neotrop Prim* 14:130–134

Crockett, C. M., and Janson, C. H. 2000. Infanticide in red howlers: Female group size, male membership, and a possible link to folivory. In: *Infanticide by Males and Its Implications*, van Schaik CP, Janson CH (eds). Cambridge University Press, Cambridge

Di Fiore, A., Link, A., Campbell, C. J. 2011. The Atelines: Behavior and socioecological diversity in a new world monkey radiation. In: *Primates in Perspective*, Campbell, C. J., Fuentes, A., MacKinnon, K. C., et al. (eds). Oxford University Press

Dunayer, E. S., and Berman, C. M. 2018. Infant Handling Among Primates. *Int J Comp Psychol*, 31. https://doi.org/10.46867/ijcp.2018.31.02.06

Farine, D. R., and Whitehead, H. 2015. Constructing, conducting, and interpreting animal social network analysis. *J Anim Ecol*. https://doi.org/10.1111/1365-2656.12418

Forstmeier, W., Wagenmakers, E. J., Parker, T. H. 2017. Detecting and avoiding likely false-positive findings – a practical guide*. Biol Rev.* https://doi.org/10.1111/brv.12315

Glander, K. E. 1980. Reproduction and population growth in free-ranging mantled howling monkeys. *Am J Phys Anthropol.* https://doi.org/10.1002/ajpa.1330530106

Glander, K. E. 1992. Dispersal patterns in Costa Rican mantled howling monkeys*. Int J of Primatol*. (13), 415-436.

Grueter, C. C., Li, D., Ren, B., Wei, F. 2009. Choice of analytical method can have dramatic effects on primate home range estimates. *Primates*. https://doi.org/10.1007/s10329-008-0113-2

Hargis, C. D., Bissonette, J. A., David, J. L. 1998. The behavior of landscape metrics commonly used in the study of habitat fragmentation. *Landsc Ecol* 13:167–186. https://doi.org/10.1023/A:1007965018633

Jung, L., Mourthe, I., Grelle, C. E. V., et al. 2015. Effects of local habitat variation on the behavioral ecology of two sympatric groups of brown howler monkey (*Alouatta clamitans*). *PLoS ONE* https://doi.org/10.1371/journal.pone.0129789

McKinney, T. 2019. Ecological and Behavioural Flexibility of Mantled Howlers (*Alouatta palliata*) in Response to Anthropogenic Habitat Disturbance. *Folia Primatol* https://doi.org/10.1159/000499825

Mendes, S. L. 1989. Estudo ecológico de *Alouatta fusca* (Primates: Cebidae) na Estação Biológica de Caratinga, MG. *Revista Nordestina de Biologia* 6:71–104

Milton, K., Nolin, D.A., Ellis, K., et al. 2016. Genetic, spatial, and social relationships among adults in a group of howler monkeys (*Alouatta palliata*) from Barro Colorado Island, Panama. *Primates* https://doi.org/10.1007/s10329-016-0523-5

Miranda, J. M. D., Bernardi, I. P., Moro-Rios, R.F., et al. 2004. Social Structure of *Alouatta guariba clamitans*: A Group with a Dominant Female. *Neotrop Prim* 12 https://doi.org/10.1896/1413-4705.12.3.135

Negrín, A. R., Fuentes, A. C., Espinosa, D. C., Dias, P. A. D. 2016. The loss of behavioral diversity as a consequence of anthropogenic habitat disturbance: the social interactions of black howler monkeys. *Primates*. https://doi.org/10.1007/s10329-015-0503-1

Pope, T. R. 1998. Effects of Demographic Change on Group Kin Structure and Gene Dynamics of Populations of Red Howling Monkeys. *J Mammal* 79:692. https://doi.org/10.2307/1383081

Pope, T. R. 2000. Reproductive success increases with degree of kinship in cooperative coalitions of female red howler monkeys (*Alouatta seniculus*). *Behav Ecol and Sociobiol* 48:253–267 https://doi.org/10.1007/s002650000236

Possamai, C. B. P., Mendes, S. L., Strier, K. B. 2019. Decline of a primate community following a yellow fever outbreak in the Brazilian Atlantic Forest. Forty-second meeting of the American Society of Primatologists. Madison, WI

Possamai C. B. P., de Melo F. R., Mendes S. L., Strier K. B. (2022) Demographic changes in an Atlantic Forest primate Community following a yellow fever outbreak. *American Journal of Primatology* e23425 https://doi.org/10.1002/ajp.23425

R Core Team 2021. R: A language and environment for statistical computing.

Rumiz, D. I. 1990. *Alouatta caraya*: Population density and demography in Northern Argentina. *Am J Primatol* 21. https://doi.org/10.1002/ajp.1350210404

Sánchez-Villagra, M. R., Pope, T. R., Salas, V. 1998. Relation of intergroup variation in allogrooming to group social structure and ectoparasite loads in red howlers (*Alouatta seniculus*). *Int J Primatol* 19. https://doi.org/10.1023/A:1020360422305

Schreier, A. L., and Bolt, L. M. 2020. Howling for food and females: A cross-site comparison of mantled howler monkey (*Alouatta palliata*) howling behavior in Costa Rica. 89th Annual Meeting of the American Association of Physical Anthropologists. Los Angeles, California.

Schreier, A. L., Bolt, L. M., Russell, D. G., et al. 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. https://doi.org/10.1159/000511974

Strier, K. B, 2008. The Effects of Kin on Primate Life Histories. *Annu Rev Anthropol* 37:21–36. https://doi.org/10.1146/annurev.anthro.37.081407.085218

Strier, K. B., Lee, P. C., Ives, A. R. 2014. Behavioral flexibility and the evolution of primate social states*. PLoS ONE* 9. https://doi.org/10.1371/journal.pone.0114099

Strier, K. B., Mendes, S. L., Santos, R. R. 2001. Timing of births in sympatric brown howler monkeys (*Alouatta fusca clamitans*) and Northern Muriquis (*Brachyteles arachnoides hypoxanthus*). *Am J Primatol* 55. https://doi.org/10.1002/ajp.1042

Van Belle, S., Estrada, A., Di Fiore, A. 2014. Kin-biased spatial associations and social interactions in male and female black howler monkeys (*Alouatta pigra*). *Behaviour* 151:2029–2057. https://doi.org/10.1163/1568539X-00003229

Van Belle, S., Estrada, A., Strier, K. B. 2011. Insights into social relationships among female black howler monkeys *Alouatta pigra* at Palenque National Park, Mexico. *Curr Zool* 57. https://doi.org/10.1093/czoolo/57.1.1

Van Belle, S., Estrada, A., Strier, K. B. 2008. Social Relationships Among Male *Alouatta pigra. Int J Primatol* 29:1481–1498. https://doi.org/10.1007/s10764-008-9309-y

Wang, E., and Milton, K. 2003. Intragroup Social Relationships of Male *Alouatta palliata* on Barro Colorado Island, Republic of Panama. *Int J Primatol* 24. https://doi.org/10.1023/B:IJOP.0000005989.29238.ce

Zucker, E. L., and Clarke, M. R. 1998. Agonistic and affiliative relationships of adult female howlers (*Alouatta palliata*) in Costa Rica over a 4-year period. *Int J Primatol* 19. https://doi.org/10.1023/A:1020356321396

QGIS Development Team 2021. QGIS Geographic Information System. QGIS Association. http://www.qgis.org

	Group	Number of complete scan samples (focal hours, h)					Total
		Sep-18	Oct-18	Nov-18	Apr-19	May-19	
All adults with nearest neighbor data	CM	63 (13.57h)	36 (9.17h)	0 (0.00)	89 (26.00h)	49 (13.25h)	237 (61.98h)
	CR	51 (11.53h)	23 (5.25h)	28 (6.50h)	74 (18.90h)	58 (16.50h)	234 (58.68h)
	RB	NA (NA)	73 (18.25h)	61 (14.75h)	24 (8.83h)	35 (8.75h)	193 (50.58h)
All adults	CM	63	38	0	96	56	253
	CR	51	24	28	78	69	250
	RB	NA	77	63	33	36	209
Whole/partial group with behavior	CM	68	40	0	106	57	271
	CR	54	24	29	81	70	258
	RB	NA	81	63	37	37	218
Whole/partial group with location	CM	68	40	0	113	57	278
	CR	54	24	29	83	70	260
	RB	NA	81	63	44	37	225

Table 1: Sample sizes for all groups across different observation categories. For scan samples, the N for each group is shown for group scans with all adults present and nearest neighbor recorded for each adult, for all scans with adults present (but with incomplete nearest neighbor data), for all scans where the whole or partial group was present and behavioral data were recorded, and for all scans where the whole or partial group was present and location data were recorded (sometimes without behavioral data due to visibility).

Time of Day	Group	Median	Min	Max	IQR	N	KW χ2	df	*P*
8:00	CM	0.00	0.00	0.40	0.00	21	0.7144	2	0.6996
	CR	0.00	0.00	0.50	0.00	26			
	RB	0.00	0.00	0.00	0.00	16			
9:00	CM	0.00	0.00	0.25	0.00	33	0.8348	2	0.6588
	CR	0.00	0.00	0.67	0.00	30			
	RB	0.00	0.00	0.50	0.00	26			
10:00	CM	0.00	0.00	0.75	0.00	36	0.0873	2	0.9573
	CR	0.00	0.00	0.67	0.00	32			
	RB	0.00	0.00	0.67	0.00	28			
11:00	CM	0.00	0.00	0.25	0.00	34	2.0850	2	0.3526
	CR	0.00	0.00	1.00	0.00	42			
	RB	0.00	0.00	0.00	0.00	32			
12:00	CM	0.00	0.00	0.40	0.00	41	0.2113	2	0.8997
	CR	0.00	0.00	0.67	0.00	43			
	RB	0.00	0.00	0.33	0.00	34			
13:00	CM	0.00	0.00	0.67	0.00	46	2.6200	2	0.2698
	CR	0.00	0.00	0.67	0.00	37			
	RB	0.00	0.00	0.00	0.00	31			
14:00	CM	0.00	0.00	0.40	0.00	44	1.1730	2	0.5563
	CR	0.00	0.00	0.67	0.00	34			
	RB	0.00	0.00	0.00	0.00	26			
15:00	CM	0.00	0.00	0.40	0.00	41	2.8092	2	0.2455
	CR	0.00	0.00	0.00	0.00	35			
	RB	0.00	0.00	0.00	0.00	22			
16:00	CM	0.00	0.00	0.67	0.00	24	2.2950	2	0.3174
	CR	0.00	0.00	0.00	0.00	27			
	RB	0.00	0.00	0.67	0.00	26			

Table 2: Results of Kruskal-Wallis tests comparing social behavior across groups during each hour of observation for which sufficient data were collected. Time of day (h), group ID, hourly median percentage of scans in social behavior, minimum, maximum, interquartile range, and number of scan samples from that hour (N) are given. Results of Kruskal-Wallis tests including Kruskal-Wallis χ2, degrees of freedom (df), and *P* value are also shown.

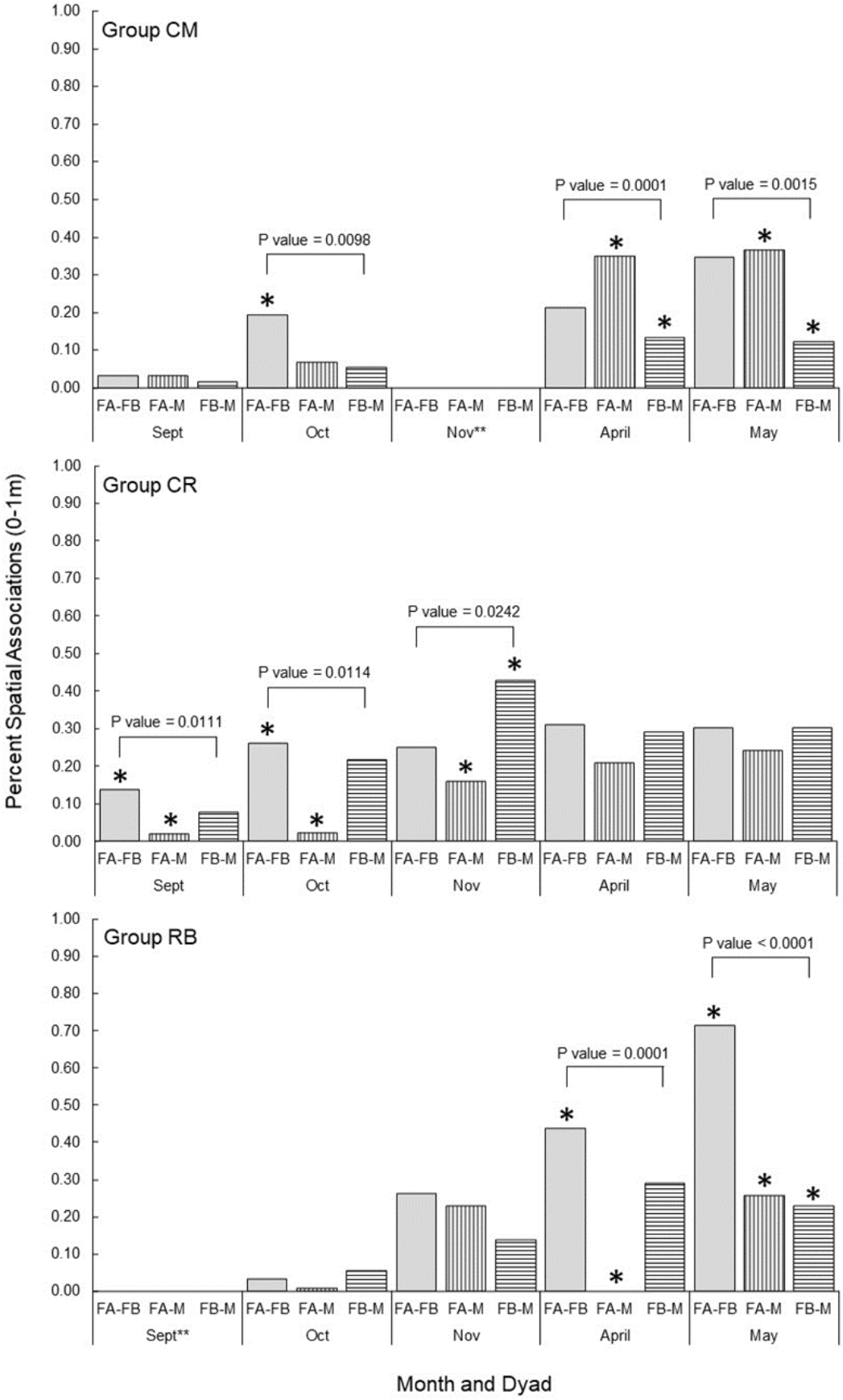
Group CM
P value = 0.0098
P value = 0.0001
P value = 0.0015
Group CR
P value = 0.0111
P value = 0.0114
P value = 0.0242
Group RB
P value = 0.0001
P value < 0.0001
Percent Spatial Associations (0-1m)
1.00
0.90
0.80
0.70
0.60
0.50
0.40
0.30
0.20
0.10
0.00
FA-FB FA-M FB-M
Sept
Sept**
Oct
Nov
Nov**
April
May
Month and Dyad

Figure 1: Percentages of spatial associations (scan samples within 0-1m) by group and dyad. Female-female (FA-FB) dyads are shown in solid gray, female A-male (FA-M) dyads are shown in vertical stripes and female B-male (FB-M) dyads are shown in horizontal stripes. Chi square goodness-of-fit tests were used to compare observed values to expected values based on the frequency with which each dyad was observed. *P* values are shown for significant results and residuals indicating large contributions to significance are indicated with an asterisk.

				Social bouts				Grooming		Agonism	
Group	Month	Dyad	SRI	Social bout rate	N obs. social bouts	N exp. social bouts	*P* value	Groom rate (mins/h)	% Groom initiated by females	N agonism	Agonism rate (N/h)
CM	Sept	FA-FB	0.24	0.4348	4	3.38	0.7868	0.7065	94.44	0	0.0000
		FA-M	0.24	0.2194	2	3.35		0.4113		2	0.1474
		FB-M	0.13	0.4486	4	3.27		0.7009		0	0.0000
	Oct	FA-FB	0.78	0.8000	5	2.73	0.7868	0.6133	100.00	4	0.4362
		FA-M	0.38	0.3243	2	2.69		0.8514		0	0.0000
		FB-M	0.27	0.1690	1	2.58		0.1127		0	0.0000
	Nov[a]	FA-FB									
		FA-M									
		FB-M									
	April	FA-FB	0.46	0.1785	3	3.56	0.3574	0.7636	91.60	1	0.0385
		FA-M	0.67	0.3386	6	3.75		0.0376		0	0.0000
		FB-M	0.32	0.1148	2	3.69		0.4785		0	0.0000
	May	FA-FB	0.62	0.0000	0	3.63	NA	0.0000	NA	0	0.0000
		FA-M	0.62	0.0000	0	3.63		0.0000		0	0.0000
		FB-M	0.24	0.0000	0	3.74		0.0000		0	0.0000
CR	Sept	FA-FB	0.74	0.7500	6	4.52	0.4693	1.1875	87.60	0	0.0000
		FA-M	0.15	0.2667	2	4.24		0.7444		0	0.0000
		FB-M	0.50	0.6667	5	4.24		0.7667		3	0.1735
	Oct	FA-FB	0.71	0.8571	3	3.00	0.0504	1.6905	100.00	0	0.0000
		FA-M	0.08	0.0000	1	3.00		0.0000		1	0.1905
		FB-M	0.59	1.7143	6	3.00		1.9286		1	0.1905
	Nov	FA-FB	0.48	0.6667	3	1.38	0.3335	1.8333	100.00	0	0.0000
		FA-M	0.32	0.0000	0	1.31		0.0000		0	0.0000
		FB-M	0.65	0.2353	2	1.31		0.0000		2	0.3077
	April	FA-FB	0.43	0.2338	3	1.68	0.3268	0.4156	73.56	0	0.0000
		FA-M	0.47	0.0000	0	1.64		0.0000		0	0.0000
		FB-M	0.59	0.1558	2	1.68		0.1494		0	0.0000
	May	FA-FB	0.55	0.0000	0	1.02	0.3834	0.0000	100.00	0	0.0000
		FA-M	0.42	0.1860	2	0.98		0.4496		0	0.0000

		FB-M	**0.53**	**0.0909**	**1**	**1.00**		**0.1970**		**0**	**0.0000**
RB	Sept[b]	FA-FB									
		FA-M									
		FB-M									
	Oct	FA-FB	0.31	0.1633	2	1.34	0.5561	0.3673	70.41	0	0.0000
		FA-M	0.07	0.0000	0	1.32		0.0000		0	0.0000
		FB-M	0.44	0.1633	2	1.34		0.2993		0	0.0000
	Nov	FA-FB	0.60	0.4103	4	2.31	0.3243	1.0342	100.00	0	0.0000
		FA-M	0.51	0.1000	1	2.37		0.0500		1	0.0678
		FB-M	0.37	0.2051	3	2.31		0.0684		3	0.2034
	April	FA-FB	0.78	0.6957	4	1.28	*0.0210	2.0145	100.00	0	0.0000
		FA-M	0.00	0.0000	0	1.44		0.0000		0	0.0000
		FB-M	0.58	0.0000	0	1.28		0.0000		0	0.0000
	May	FA-FB	0.85	0.3636	2	0.94	0.4126	1.4848	100.00	0	0.0000
		FA-M	0.33	0.0000	0	0.99		0.0000		0	0.0000
		FB-M	0.30	0.1600	1	1.07		0.3333		0	0.0000

Table 3: Group, study month, dyad, SRI value, social bout rate (number of bouts per hour of observation), observed number of social bouts, expected number of social bouts based on hours of observation for each dyad, P values with * indicating significant results, monthly grooming rate (minutes of grooming per hours of observation for each dyad), percent of grooming each month initiated by either female in a group, number of agonistic interactions observed each month for each dyad, and rate of agonistic interactions (number of agonistic interactions per hour of observation).

[a] No data were collected for group CM during November 2018.

[b] Data collection for group RB did not begin until October 2018.

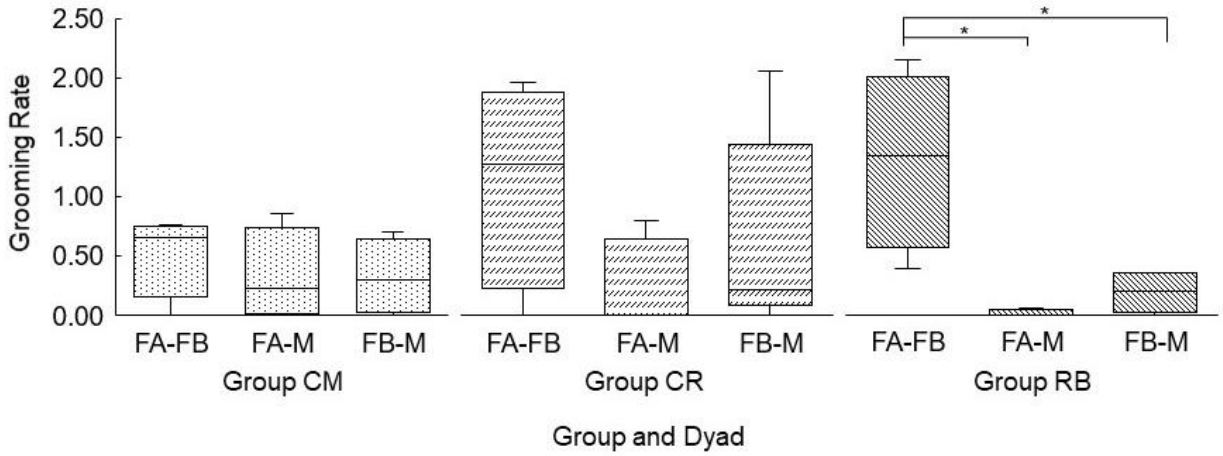

Figure 2: Grooming rates (minutes of grooming per hour of observation) for each dyad in each group summed across the 5-mo study period are shown in this plot. Group CM is shown in light gray dots, group CR is in light gray horizontal bars and group RB in dark gray diagonal bars. Significant differences as indicated by *post hoc* pairwise tests with Bonferroni adjusted *p* values are indicated with an asterisk (*p* values reported in text).

Group	Month	Adj MCP (ha)	Edge density (m/ha)	Median % social behavior	Range % social behavior
CM	Sept	5.98	91.55	0.00	0.00-0.11
	Oct	6.49	62.99	0.00	0.00-0.14
	Nov	NA	NA	NA	NA
	April	2.60	47.07	0.00	0.00-0.08
	May	1.17	183.09	0.00	0.00-0.00
CR	Sept	3.19	152.44	0.00	0.00-0.29
	Oct	1.49	22.83	0.06	0.00-0.40
	Nov	0.94	0.00	0.00	0.00-0.00
	April	4.26	42.53	0.00	0.00-0.00
	May	3.92	27.18	0.00	0.00-0.06
RB	Sept	NA	NA	NA	NA
	Oct	3.66	0.00	0.00	0.00-0.13
	Nov	3.00	0.00	0.00	0.00-0.04
	April	1.39	0.00	0.00	0.00-0.00
	May	0.81	0.00	0.00	0.00-0.00

Table 4: Group, month of study, adjusted MCP home range size in hectares, edge density (m/ha) and median and range percent scan samples observed in social behavior.

Chapter 3: Ecological Correlates of Brown Howler Monkey (*Alouatta guariba*) Habitat Use and Diet in an Atlantic Forest Fragment

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Abstract

Small scale variation in vegetation structure and food availability can significantly influence habitat use and diet in primates. Here we compared forest structure and phenological differences among study group home ranges and areas with and without sightings of brown howler monkeys (*Alouatta guariba*) from May 2017 to April 2018. We evaluated the effects of these differences on variation in home range size and diet among three groups at the Reserva Particular do Patrimônio Natural – Feliciano Miguel Abdala in Minas Gerais, Brazil across five months (September-November 2018; April-May 2019). Based on low howler monkey population density and the ideal free model of group distribution, we predicted that areas with howler monkey sightings would be of higher quality than control areas. We also predicted that howler monkey groups in home ranges with more forest edges and more anthropogenic disturbances would have lower quality home ranges and devote more of their feeding time to leaves and less time to fruits. Consistent with our prediction, areas in which howler monkeys were sighted had greater median diameter at breast height (DBH), greater median tree height, higher median basal area, and a greater number of canopy layers compared to areas without howler monkey sightings. Although the three study groups used areas that differed in their proportion of forest edge, there were no significant differences in habitat quality among the groups. Further, our prediction that time spent feeding on leaves and fruits would be lower in the groups with more forest edge in their home ranges was only true in May 2019. Thus, at low population densities, howler monkey groups appear to distribute themselves across higher quality habitats relative to availability and neither habitat quality nor diet differed with the proportion of forest edge in the monthly home ranges.

Introduction

Variation in local ecology is known to impact primate habitat use and diet. Many factors, such as elevation or past or present anthropogenic activity contribute to heterogeneity within and between forest patches (Chapman et al. 2003; Jung et al. 2015; Galán-Acedo et al. 2021). In heterogenous habitats, primates often prefer higher quality areas that have a greater number or density of different canopy layers, greater mean diameter at breast height (DBH), (*Microcebus rufus*, Ramananjato and Razafindratsima, 2021), a more connected canopy (*Symphalangus syndactylus*, *Hylobates lar*, Hankinson et al., 2021; *Alouatta guariba,* Jung et al., 2015), and a greater number of tall trees (*A. pigra*, Ostro et al., 2001; *Ateles geoffroyi,* Shedden et al., 2022). Many primate species have also been shown to prefer areas with greater food availability (*Alouatta guariba,* Camaratta et al., 2017; *Alouatta palliata*, Stoner 1996), higher plant species diversity and high diversity of top food species (Jung et al., 2015; *Macaca fascicularis*, Sha et al. 2018; *Lagothrix flavicauda*, Almeyda Zambrano et al. 2019), or greater primary plant productivity (*Cercopithecus albogularis schwarzi,* Parker et al. 2021; *Cercopithecus aethiops,* Willems and Hill 2009).

Preferred habitat types are often resource rich and thus occupancy of these areas can lead to significant energetic benefits for individuals, expressed by decreased effort obtaining food and/or increased nutritional quality of available foods (Hanya and Chapman 2013; Lambert and Rothman 2015). The ideal free model posits that individuals or groups in a heterogenous environment should distribute themselves in the highest quality areas within potential habitats because those living in higher quality areas receive tangible fitness benefits in terms of food abundance or quality (Fretwell 1972; Fretwell and Lucas 1970).

Howler monkeys (*Alouatta* spp.) are well known for their ability to persist in highly disturbed habitats, which is in part derived from their ability to digest large quantities of leaves (Bicca-Marques 2003). Folivorous primates can forage in forest edges that would be more challenging for frugivores because forest edges are generally less likely to have large fruiting trees (Lehman et al. 2006). Additionally, folivores in forest edges may benefit from the higher

protein content of leaves (Ganzhorn 1995). Indeed, the higher density of Guyanan red howler monkeys (*Alouata macconnelli)* in forest edge habitats compared to the forest interior at the Biological Dynamics of Forest Fragments Project site in Amazonas, Brazil was attributed to the properties described above (Lenz et al. 2014). However, while folivores can persist in forest edges and even benefit from the vegetation characteristics therein, life at forest edges can increase exposure to mistreatment from humans and, if arboreal primates are forced to descend to the ground to cross gaps in the forest, increase risk of vehicle collision or dog attacks (Chaves et al. 2022).

Folivory is a key dietary strategy of howler monkeys, reducing interspecific competition with other, more frugivorous monkeys and providing them a key source of nutrients throughout the year. However, while howler monkeys are broadly described as folivores due to the high volume of leaves in their diets, they are most accurately described as folivore-frugivores, consuming fruits in proportion to their spatio-temporal availability (Strier 1992; Garber et al. 2015). Thus, fruit distribution and availability also impact howler monkey distribution within habitats. Even for brown howler monkeys, which are one of the most folivorous species in the genus (Garber et al. 2015), fruit availability appears related to distribution within a habitat. At Morro São Pedro in southern Brazil, ripe and unripe fruit availability were twice as high in transects where brown howler monkeys were sighted compared to control transects without sightings of the monkeys, but neither leaf availability nor overall diversity of food species differed between areas (Camaratta et al. 2017).

While food availability is a key driver of individual or group distribution within potential habitats, high population density can preclude howler monkeys from living in higher quality areas. Those individuals or groups that live in lower quality habitats must often compensate by altering ranging behavior, grouping strategies, or feeding behavior (Strier 2009). For example, at the La Suerte Biological Research Station in Costa Rica where mantled howler monkeys (*A. palliata)* occur at high density (0.74 ind./ha.), groups living in lower quality edge habitats fed

from a greater number of tree species and from smaller trees compared to those in the higher quality forest interior (Bolt et al. 2021). Similarly, at the Reserva Particular do Patrimônio Natural – Feliciano Miguel Abdala (RPPN-FMA; site of this study), a group of brown howler monkeys in a lower quality area consumed fewer fruits and more mature leaves, spent more time traveling, and had a larger home range than a group in a higher quality area (Jung et al. 2015). When Jung et al. (2015) carried out their research in 2005, the population density of brown howler monkeys at the RPPN-FMA was estimated to be 0.29 ind./ha, which was much higher than the 0.04-0.07 ind./ha estimated following a 2016-2017 outbreak of yellow fever (Possamai et al. 2022). At this more recent low population density, remaining howler monkey groups might be expected to have experienced some degree of competitive release and therefore have been able to occupy more consistently high quality areas of the forest.

To assess this prediction, we compared forest structure and phenological differences among areas with and without brown howler monkey sightings at the RPPN-FMA and evaluated the effects of these differences on variation in home range size and diet among three study groups. Based on the ideal free model (Fretwell 1972; Fretwell and Lucas 1970), we hypothesized that areas where howler monkeys were observed (sighted areas) would be of higher quality than areas where they were not observed (control areas). Prior research at the RPPN-FMA demonstrated that the RPPN-FMA has higher plant species diversity (Shannon-Wiener index, *H'*) and higher plant species evenness (Pielou's evenness index, *J*) compared to other forest fragments in this region (Boubli et al., 2011). Using the ecological variables distinguished by Jung et al. (2015), we expected that sighted areas would have a more connected and continuous upper canopy, denser shrub layer, a higher number of canopy layers, more emergent trees when compared to control areas and that sighted areas would have greater basal area and taller trees than control areas (Ostro et al. 2001).

Because roadside habitats include a higher percentage of forest edges and are likely to have fewer big trees and fewer fruit trees, we expected there to be dietary differences between

howler monkey groups that occupied these areas versus those that occupied habitats in the interior of the forest. Howler monkeys in edge habitats at other sites have been observed feeding more on leaves and less on fruit than conspecifics in the forest interior (Bolt et al. 2021; McKinney 2019), thus we predicted that at our site, howler monkey groups with home ranges with a higher proportion of forest edge would similarly feed more on leaves and less on fruit than a group in the forest interior. However, the low population density of brown howler monkeys during this study could have permitted groups to occupy uniformly high quality habitats: if this alternative were true, then we would expect to find no significant differences in diet among the three study groups.

Methods

Study site

We collected data for this project between August 2018 and May 2019 at the RPPN-FMA (19º50'S, 41º50'N), a ~1000 ha fragment of the Brazilian Atlantic Forest near Caratinga, Minas Gerais. The RPPN-FMA exhibits high habitat heterogeneity due to historical extraction (i.e., selective logging) and agricultural use (i.e., cattle grazing, coffee cultivation) (Boubli et al. 2011; Jung et al. 2015). The peak of rainfall at this site usually occurs between November and April, with a drier and cooler season between May and October (Strier et al. 2001). Flower production typically peaks between March and June and again between September and December, while fruit production typically peaks between May and August and again between December and March (Strier 1991; Strier and Boubli 2006).

Data collection

Vegetation data collection

We distinguished sighted areas as those where howler monkeys had been observed from three sources: prior to the present study period, between May 2017 and April 2018, during six censuses conducted by CBP (N=62 sightings) and opportunistically during monitoring of the muriquis by team members on the Muriqui Project of Caratinga (N=64 sightings), and from Sep-Oct 2018 during sightings of three howler monkey study groups by AJH (N=242 sightings). GPS points were taken for all sightings, and a maximum buffer radius of 556 m around each point was derived by averaging the reported dry season day ranges (Jung et al. 2015, Aug-Nov 2005: mean=465.5 m; Mendes 1989, Nov 1983-April 1984: mean=364 m) and wet season day range (Mendes 1989, May-Oct 1983; mean=682 m) of brown howler monkeys at this site. Control areas were defined as those where no howler monkey sightings were obtained.

AJH placed twenty 20x10m plots in sighted and control areas throughout the study area, known as the Matão region of the RPPN-FMA, representing an area of 0.40 ha (Fig. 1). The number of plots placed in sighted and control areas was based on the proportion of sampled area where sightings (plus calculated buffer area) occurred (70%) versus those with no sightings occurred (30%) (Fig. 1). The 14 plots associated with sighted areas included nine plots, with three plots positioned within each of the three study group home ranges to allow for comparisons and five plots placed across the remaining sighted areas. The six control plots were placed in areas with no sightings. Plots were only placed in areas that were accessible (i.e., slope $\leq$ 0.5 degree elevation change) for safe and accurate sampling (*sensu* Boubli et al. 2011) and a minimum of 10m from trails or roads and with at least 10m between plot locations (following Boubli et al. 2011; Jung et al. 2015). Within the sampled areas meeting these criteria, the location of plots was selected using the “random points inside polygons (fixed)” function in QGIS 2.18 (QGIS Development Team 2021). Edge effects such as increased wind disturbance or greater tree mortality, among others, have been shown to frequently penetrate between 50-

100m into forest interiors, with some effects detectable 300-400m within a forest (Laurance et al. 2002; Pfeifer et al. 2017; Razafindrastima et al. 2017; Schreier et al. 2022). Therefore, our decision to place plots in roadside habitats at least 10m from the forest edge is unlikely to homogenize or bias results.

We marked plot corners with biodegradable flagging tape and recorded GPS coordinates for each plot. Within each plot, all trees with DBH > 5 cm were marked with biodegradable flagging tape (removed at the end of the study period) for phenological monitoring. To avoid resampling, each tree was given a unique ID number that was written on the flagging tape used to mark the trees. Structural measurements were carried out once in each plot and all structural measurements were completed by January 2019. Phenological data were collected in all 14 sighted plots in 8 consecutive months of study from October 2018 through May 2019. Phenological data were collected in all six control plots from November 2018 through February 2019, and April and May 2019.

Following Jung et al. (2015), we directly estimated the number of emergent trees, number of canopy layers, and canopy height in meters within each plot. Additionally, we estimated canopy density, connectivity, and continuity as well as liana density using a subjective a scale of 0-4 for each variable (0 = absent, 1 = 1-25%, 2 = 26-50%, 3 = 51-75%, 4 = 75-100%; following Jung et al., 2015; Boubli et al., 2011). Using the same 0-4 scale, percentage of crown cover for each phenophase (i.e., flowers, ripe fruit, unripe fruit, young leaves, mature leaves) was scored every month for each marked tree.

Dietary data collection

AJH collected behavioral data from three groups of brown howlers that were selected based on their distance from the research station and use of edge habitats along the dirt road that bisects the Reserve (groups CM and CR) or forest interior (group RB). Each group had one

male, two females, and associated offspring (N = 2-3 (CM); 1 (CR); 1-2 (RB)). Data collection for the two edge groups began in September 2018 while data collection for the interior group began in October 2018. Each month, one week per month was allocated to finding and following each of the three groups, with the fourth week spent collecting ecological data in the plots. The GPS location of the group and behavioral data on all group members were recorded using instantaneous scan samples at 30-minute intervals, noting the first behavior of each individual lasting longer than 5 seconds (Altmann 1974). Behaviors recorded were resting, feeding (including plant part), traveling, and socializing (Hardie et al. Chapter 1).

Data analyses

Vegetation analyses

From 24-113 GPS points were collected per group per month (see Table S1). GIS data and ecological variables were analyzed in QGIS 3.16 (QGIS Development Team) and R (R Core Team 2021) using the package 'adehabitatHR' (Calenge 2006). Ecological characteristics were compared across plots in the three groups' home ranges (n=3 plots per group), other sighted areas (n=5), and control areas (n=6) using Kruskal-Wallis tests with *post-hoc* Dunn's tests. A total of 433 trees were measured across 20 plots (mean = 21.65 ± 5.20 trees per plot). The total number of trees within the nine home range plots was 196 (mean±SD = 21.78±4.37 per plot), within the five sighted but not home range plots was 116 (mean±SD = 23.20±4.83) and within the six control plots was 121 (mean±SD = 20.17±6.15).

Home ranges were estimated using the adjusted minimum convex polygon (MCP) method, which creates the smallest polygon containing all GPS points in a given dataset and is then clipped to exclude unsuitable areas such as pastures (Grueter et al. 2009). While the MCP method can be sensitive to outliers or areas of infrequent use, we found that KDE estimates

with reference or *ad hoc* smoothing parameters produced overestimates of home range sizes (i.e., three to six times larger than MCP estimates, Table S1). Home range estimates are sensitive to sample size and habitat characteristics such as fragmentation or inclusion of agricultural matrices (Vieira et al. 2019), thus we elected to use a more conservative estimate to reduce the likelihood of overrepresenting the area used by each group.

We compared phenological availability of different plant parts among home range, sighted plots, and control plots using the Food Availability Index (FAI), where phenological scores for each tree were multiplied by basal area achieve a weighted index of plant part availability in each plot for each month (Agostini et al. 2010). Median FAI values for each plot were then compared using Kruskal Wallis tests with *post-hoc* Dunn's tests and Bonferroni adjusted *P*-values in each month with complete sampling of all plots (Dec. and Nov. 2018 and Jan., Feb, April, and May 2019).

Dietary data analyses

Monthly behavioral data were included in our analyses if there were two or more days with at least 6 group scans with all adults present each day. This resulted in including only September, October, and November of 2018 and April and May of 2019. Group RB was excluded from dietary analyses for April because feeding was too infrequently observed to be compared statistically (Table 1). The remaining behavioral data were analyzed in R (R Core Team 2021), using non-parametric tests to compare diet and activity among the three study groups. We used Kruskal-Wallis tests or Wilcoxon rank sum tests where appropriate based on the number of groups in each monthly comparison. When Kruskal-Wallis tests yielded significant results, we used *post hoc* Dunn's tests with a Bonferroni adjusted *P* value. Most of these observations (91.36% of N=752 scan samples) were made between 8:00 and 16:00h.

Results

Vegetation

Consistent with the ideal free model, sighted areas were higher quality than control areas based on their greater median DBH, higher median tree height, greater basal area, and greater number of canopy layers (Table 3). Sighted, but not home range plots, had a significantly higher density of lianas when compared to control plots. There were no differences across all categories of sighted and control plots for median canopy height, number of emergent trees, densities of different canopy layers, or canopy continuity (Table 3). Canopy connectivity differed significantly among the three categories but post-hoc pairwise comparisons were not significant.

Adjusted MCP monthly home ranges varied across the three groups (0.81 ha to 6.49 ha per month; Fig. 2). Despite the differences in monthly HR size, and in contrast to our predictions, we found no significant differences in forest structure among the home ranges of the three study groups (Table 2).

As with prior phenological studies at this site (Strier, 1991; Strier and Boubli, 2006), the availability of different plant parts varied across months in the present study period (Fig. 3). Mature leaf availability was significantly higher in both home range and other sighted plots when compared to control plots across all months of study

(Table S2). Young leaf availability was significantly higher in home range plots compared to control plots but not sighted plots in Dec. 2018, and flower availability was significantly higher in home range plots compared to sighted plots but not control plots in April 2019. Flower availability also differed significantly among plots in May 2019, however none of the *post hoc* pairwise comparisons were significant (Table S2).

Diet

Monthly differences in phenology as measured in the home range plots did not predict monthly differences in diet. However, this must be interpreted with extreme caution due to the low number of plots within each home range and the overall paucity of data.

We found significant differences in diet composition but not time spent feeding among the three study groups and only partial support for our prediction that groups with forest edge in their home ranges would spend more time feeding on leaves and less time feeding on fruits than the group in the forest interior. Results of a two-way comparison in September 2018 found no difference in the diet composition of groups CM and CR, but in April group CR ate significantly more flowers and less fruit than group CM (Table 3). Three-way comparisons revealed significant differences in diet composition in October 2018 and May 2019, but not November 2018. *Post hoc* testing showed that in October group CM consumed significantly more flowers than group RB (W = 2.73, adjusted $P = 0.009$) but not group CR (W = 2.13, adjusted $P = 0.493$). In May, and in support of our prediction, the groups with forest edge (CM and CR) consumed significantly more leaves than group RB in the forest interior (CM-RB, W = 3.24, adjusted $P = 0.002$; CR-RB, W = 3.62, adjusted $P < 0.001$) and significantly less fruit than group RB (CM-RB, W = -3.27, adjusted $P = 0.002$; CR-RB, W = -3.27, adjusted $P = 0.002$).

Discussion

We found that areas where howler monkeys were sighted at the RPPN-FMA in 2017-2018 were of uniformly higher quality than areas without howler monkey sightings in the same time period. In particular, vegetation plots in sighted areas (including study group home ranges) had greater median DBH, greater median basal area (i.e., tree density), a greater number of canopy layers, and higher median tree height. Although Jung et al. (2015) also found a

significantly greater number of canopy layers in higher quality areas, we did not find a greater number of emergent trees, higher canopy connectivity or continuity, or a denser shrub layer in higher quality areas as Jung et al. did. Our findings of greater median DBH, greater basal area, and higher median tree height are similar to findings from other species of howler monkeys at other where they show a preference for areas with more large trees (i.e., *A. pigra*, Ostro et al. 2001). We also found that sighted areas outside of group home ranges had a higher density of lianas, and while lianas are characteristic of secondary growth or more disturbed areas within forests, they can also serve as an important food source for brown howler monkeys (Martins 2009).

Each of the three groups in this study used monthly home ranges that varied in size from 0.81 ha to 6.49 ha. These monthly home ranges overlap with the home ranges obtained in this population over 13 months (Mendes 1989) and 3 months (Jung et al. 2015) in years when howler population densities were 1.17 ind./ha and 0.29 ind./ha, respectively. Nonetheless, our small sample size limits our ability to interpret these results relative to the established inverse relationship between population density and home range size within *Alouatta* (Fortes et al. 2015).

While we could not quantitatively evaluate whether the group in the forest interior (RB) had a higher quality habitat than the two groups along the dirt road (CM and CR), their home range was characterized by taller trees and a higher basal area indicating a higher density of big trees, which are known to provide more feeding opportunities for groups of howler monkeys (Ostro et al. 2001). RB also used the smallest overall home range and smallest monthly home range of any of the study groups, though monthly home ranges were highly variable and extrapolation from these data is complicated by our small sample sizes.

Despite some differences in habitat quality and proximity to anthropogenic disturbance, we did not find significant differences in time spent feeding among the three study groups. Moreover, our prediction that groups in home ranges with more edge exposure would spend

more time feeding on leaves and less time feeding on fruits than the group in the forest interior was only true in May 2019. This could indicate that even though home ranges are structurally similar, edge effects (i.e., increased die-off of large fruiting trees) might still impact food availability within the home ranges of our study groups, as has been reported for multiple lemur species (Lehman et al. 2006).

Nonetheless, our finding are consistent with the prediction that forest edges may not be inferior habitats to howler monkeys because of the higher protein content of leaves or the prevalence of pioneer tree species at forest edges that howler monkeys can exploit for fruits and leaves (Ganzhorn 1995). Indeed, the group with the highest proportion of forest edge in their home range (CM) was observed to rely almost entirely on fruit and leaves from embaúba (*Cecropia glaziovii*) trees along the roadside during the month of April, suggesting that these trees are a key resource for some brown howler monkeys at the RPPN-FMA, as they are for other howler monkey species throughout Central and South America (Estrada et al. 1999; Bolt et al. 2021).

Our study suggests that the ideal free model has some explanatory power for the distribution of this howler monkey population because all three study groups had higher quality habitats relative to other parts of the forest. Our data also suggest that edge habitats, despite their proximity to anthropogenic disturbances, may be comparable to interior habitats for howler monkeys living at low densities.

Future research with this population of brown howler monkeys should expand on the impacts of highly seasonal variation in vegetation and food availability on group distribution and diet over a complete annual cycle at this site (Mendes, 1989). Is could also investigate the distribution of howler monkeys relative to other sympatric primates, especially northern muriquis (*Brachyteles hypoxanthus*), whose diets overlap with those of howler monkeys (Strier, 1991). Seasonal changes in resource availability, interspecific competition, and other factors like predation risk limit the utility of the ideal free model in other species (Kennedy and Gray 1993;

Sirovnik et al. 2021) and thus may also impact its predictive power for howler monkey distribution.

References

Agostini I, Holzmann I, Di Bitetti MS (2010) Are howler monkey species ecologically equivalent? Trophic niche overlap in syntopic *Alouatta guariba clamitans* and *Alouatta caraya*. Am J Primatol 72:173-186. https://doi.org/10.1002/ajp.20775

Almeyda Zambrano SL, Broadbent EN, Shanee S, et al (2019) Habitat preference in the critically endangered yellow-tailed woolly monkey (*Lagothrix flavicauda*) at La Esperanza, Peru. Am J Primatol. https://doi.org/10.1002/ajp.23032

Altmann J (1974) Observational Study of Behavior: Sampling Methods. Behav 49. https://doi.org/10.1163/156853974X00534

Bicca-Marques JC (2003) How do Howler Monkeys Cope with Habitat Fragmentation? In: Primates in Fragments. Springer US, Boston, MA, pp 283–303

Bicca-Marques JC, Chaves ÓM, Hass GP (2020) Howler monkey tolerance to habitat shrinking: Lifetime warranty or death sentence? Am J Primatol 82. https://doi.org/10.1002/ajp.23089

Bolt LM, Russell DG, Schreier AL (2021) Anthropogenic edges impact howler monkey (Alouatta palliata) feeding behaviour in a Costa Rican rainforest. Primates 62:647–657. https://doi.org/10.1007/s10329-021-00904-y

Boubli JP, Couto-Santos FR, Strier KB (2011) Structure and floristic composition of one of the last forest fragments containing the critically endangered Northern Muriqui (Brachyteles Hypoxanthus, Primates). Ecotropica 17:

Calenge C (2006) The package “adehabitat” for the R software: A tool for the analysis of space and habitat use by animals. Ecol Modelling 197. https://doi.org/10.1016/j.ecolmodel.2006.03.017

Camaratta D, Chaves ÓM, Bicca-Marques JC (2017) Fruit availability drives the distribution of a folivorous-frugivorous primate within a large forest remnant. Am J Primatol 79:e22626. https://doi.org/10.1002/ajp.22626

Chapman CA, Lawes MJ, Naughton-Treves L, Gillespie T (2003) Primate Survival in Community-Owned Forest Fragments: Are Metapopulation Models Useful Amidst Intensive use? In: Primates in Fragments. Springer US, Boston, MA, pp 63–78

Chaves OM, Souza Junior JC, Buss G, et al (2022) Wildlife is imperiled in peri-urban landscapes: threats to arboreal mammals. Sci Total Environ 821. https://doi.org/10.1016/j.scitotenv.2021.152883

Vogel E, Dominy N (2011) Ecological methods. In: Campbell C, Fuentes A, MacKinnon K, et al. (eds) Primates in Perspective, 2nd edn. Oxford University Press, New York

Estrada A, Garber PA (2022) Principal Drivers and Conservation Solutions to the Impending Primate Extinction Crisis: Introduction to the Special Issue. Int J Primatol 43:1–14. https://doi.org/10.1007/s10764-022-00283-1

Fortes VB, Bicca-Marques JC, Urbani B, et al (2015) Ranging behavior and spatial cognition of howler monkeys. In: Kowalewski M, Garber P, Cortes-Ortiz L, et al. (eds) Howler Monkeys: Behavior, Ecology, and Conservation. Springer, New York, pp 219–255

Fretwell, SD (1972). Populations in a seasonal environment. Princeton, NJ: Princeton University Press.

Fretwell, SD, and Lucas, HL (1970). On territorial behavior and other factors influencing habitat distribution in birds. Acta biotheoretica, 19(1), 16-36.

Galán-Acedo C, Arroyo-Rodríguez V, Chapman CA (2021) Beyond patch size: The impact of regional context and habitat quality on three endangered primates. Perspect Ecol Conserv 19:207–215. https://doi.org/10.1016/j.pecon.2021.02.004

Ganzhorn JU (1995) Low-level forest disturbance effects on primary production, leaf chemistry, and lemur populations. Ecol. 76:2084-2096. https://doi.org/10.2307/1941683

Garber PA, Righini N, Kowalewski MM (2015) Evidence of Alternative Dietary Syndromes and Nutritional Goals in the Genus Alouatta. In: Howler Monkeys: Behavior, Ecology, and Conservation. Springer New York, New York, NY, pp 85–109

Grueter CC, Li D, Ren B, Wei F (2009) Choice of analytical method can have dramatic effects on primate home range estimates. Primates 50:81–84. https://doi.org/10.1007/s10329-008-0113-2

Hankinson EL, Hill RA, Marsh CD, et al (2021) Influences of Forest Structure on the Density and Habitat Preference of Two Sympatric Gibbons (*Symphalangus syndactylus* and *Hylobates lar*). Int J Primatol 42:237–261. https://doi.org/10.1007/s10764-021-00199-2

Hanya G, Chapman CA (2013) Linking feeding ecology and population abundance: a review of food resource limitation on primates. Ecol, Res 28:183–190. https://doi.org/10.1007/s11284-012-1012-y

Hirsch A (1995) Censo de *Alouatta Fusca* Geoffroy, 1812 (Platyrrhini, Atelidae) e Qualidade do Habitat em dois Remanescentes de Mata Atlântica em Minas Gerais. [Master's thesis, Federal University of São Joao del-Rei].

Jung L, Mourthe I, Grelle CEV, et al (2015) Effects of local habitat variation on the behavioral ecology of two sympatric groups of brown howler monkey (*Alouatta clamitans*). PLoS ONE 10. https://doi.org/10.1371/journal.pone.0129789

Kenney M, Gray RD (1993) Can ecological theory predict the distribution of foraging animals? A critical analysis of experiments on the Ideal Free Distribution. Oikos 68: 158-166. https://doi.org/10.2307/3545322

Lambert JE, Rothman JM (2015) Fallback Foods, Optimal Diets, and Nutritional Targets: Primate Responses to Varying Food Availability and Quality. Ann Rev Anthropol 44:493–512. https://doi.org/10.1146/annurev-anthro-102313-025928

Laurance WF, Lovejoy TF, Vasconselos HL, et al. (2002) Ecosystem Decay of Amazonian Forest Fragments: a 22-year Investigation. Conserv Biol 16:605-618. https://doi.org/10.1046/j.1523-1739.2002.01025.x

Lehman SM. Rajaonson A, Day S (2006) Edge effects and their influence on lemur density and distribution in southeast Madagascar. Am J Phys Anthropol 192. https://doi.org/10.1002/ajpa.20241

Lenz BB, Jack KM, Spironello WR (2014) Edge effects in the primate community of the Biological Dyanmics of Forest Fragments project, Amazonas, Brazil. Am J Phys Anthropol 155:436-446. https://doi.org/10.1002/ajpa.22590

Lima M, Mendes SL, Strier KB (2019) Habitat Use in a Population of the Northern Muriqui (*Brachyteles hypoxanthus*). Int J Primatol 40. https://doi.org/10.1007/s10764-019-00098-7

Martins MM (2009) Lianas as a food resource for brown howlers (Alouatta guariba) and southern muriquis (*Brachyteles arachnoides*) in a forest fragment. Anim Biodivers Conserv 32:51–58. https://doi.org/10.32800/abc.2009.32.0051

Mendes SL (1989) Estudo ecológico de *Alouatta fusca* (Primates: Cebidae) na Estação Biológica de Caratinga, MG. Revista Nordestina de Biologia 6:71–104

Oklander LI, Buss G, Bicca-Marques JC, et al (2022) Brown howler monkey (*Alouatta guariba*) In Mittermeier RA, Reuter KE, Rylans AB, Jerusalinksy L, Schwitzer C, Strier KB, Ratszimbasafy J, Humle T (Eds.) Primates in Peril: The World's 25 Most Endangered Primates 2022-2023. International Primatological Society. pp120-125.

Ostro LET, Silver SC, Koontz FW, et al (2001) Shifts in social structure of black howler (*Alouatta pigra*) groups associated with natural and experimental variation in population density. Int J Primatol 22. https://doi.org/10.1023/A:1012013315920

Parker EJ, Koyama NF, Hill RA (2021) Habitat selection of an endangered primate, the samango monkey (*Cercopithecus albogularis schwarzi*): Integrating scales to prioritize habitat for wildlife management. Eco Evol 11:8014–8026. https://doi.org/10.1002/ece3.7631

Pfeifer M, Lefebvre V, Peres CA et al. (2017) Creation of forest edges has global impact on forest vertebrates. Nature 551:187-191. https://doi:10.1038/nature24457.

Possamai CBP, de Melo FR, Mendes SL, Strier KB (2022) Demographic changes in an Atlantic Forest primate Community following a yellow fever outbreak. Am J Primatol e23425 https://doi.org/10.1002/ajp.23425

R Core Team (2021) R: A language and environment for statistical computing.

Ramananjato V, Razafindratsima OH (2021) Structure of Microhabitats Used by *Microcebus rufus* Across a Heterogeneous Landscape. Int J Primatol 42:682–700. https://doi.org/10.1007/s10764-021-00224-4

Razafindratsima OH, Brown KA, Carvalho F, et al. (2017) Edge effects on components of diversity and above-ground biomass in a tropical forest. J Applied Ecol 55:977-985. https://doi.org/10.1111/1365-2664.12985

Schreier AL, Voss KA, Bolt LM (2022) A Mathematical Modelling Approach to Functionally Defining Forest Edge and Its Utility for Primate Behavioural Edge Effects. Int J Primatol 43:460-479. https://doi.org/10.1007/s10764-022-00289-9

Sha JCM, Chua SC, Chew PT, et al (2018) Small-scale variability in a mosaic tropical rainforest influences habitat use of long-tailed macaques. Primates 59:163–171. https://doi.org/10.1007/s10329-017-0630-y

Shedden A, Dunn JC, Martínez-Mota R, et al (2022) Forest maturity has a stronger influence on the prevalence of spider monkeys than howler monkeys in an anthropogenically impacted rainforest landscape. Primates 63:283–291. https://doi.org/10.1007/s10329-022-00980-8

Sirovnik J, Voelkl B, Keeling LJ, et al. (2021) Breakdown of the ideal free distribution under conditions of severe and low competition. Behav Ecol Sociobiol 75. https://doi.org/10.1007/s00265-020-02949-3

Stoner KE (1996) Habitat selection and seasonal patterns of activity and foraging of mantled howling monkeys (*Alouatta palliata*) in Northeastern Costa Rica. Int J Primatol 17:1–30. https://doi.org/10.1007/BF02696156

Strier KB (1992) Atelinae adaptations: Behavioral strategies and ecological constraints. Am J Phys Anthropol 88:515–524. https://doi.org/10.1002/ajpa.1330880407

Strier KB (1991) Diet in one group of woolly spider monkeys, or muriquis (*Brachyteles arachnoides*). Am J Primatol 23:113–126. https://doi.org/10.1002/ajp.1350230205

Strier KB (2009) Seeing the Forest through the Seeds: Mechanisms of Primate Behavioral Diversity from Individuals to Populations and Beyond. Curr Anthropol 50:213–228. https://doi.org/10.1086/592026

Strier KB, Boubli JP (2006) A History of Long-term Research and Conservation of Northern Muriquis (*Brachyteles hypoxanthus*) at the Estação Biológica de Caratinga/RPPN-FMA. Primate Conserv 20:53–63. https://doi.org/10.1896/0898-6207.20.1.53

Vieira WF, Kerry C, Hockings KJ (2019) A comparison of methods to determine chimpanzee home-range size in a forest–farm mosaic at Madina in Cantanhez National Park, Guinea-Bissau. Primates 60:355–365. https://doi.org/10.1007/s10329-019-00724-1

Willems EP, Hill RA (2009) A critical assessment of two species distribution models: a case study of the vervet monkey (*Cercopithecus aethiops*). J Biogeogr 36:2300–2312. https://doi.org/10.1111/j.1365-2699.2009.02166.x

QGIS Development Team (2021). QGIS Geographic Information System. QGIS Association. http://www.qgis.org

Tables and Figures

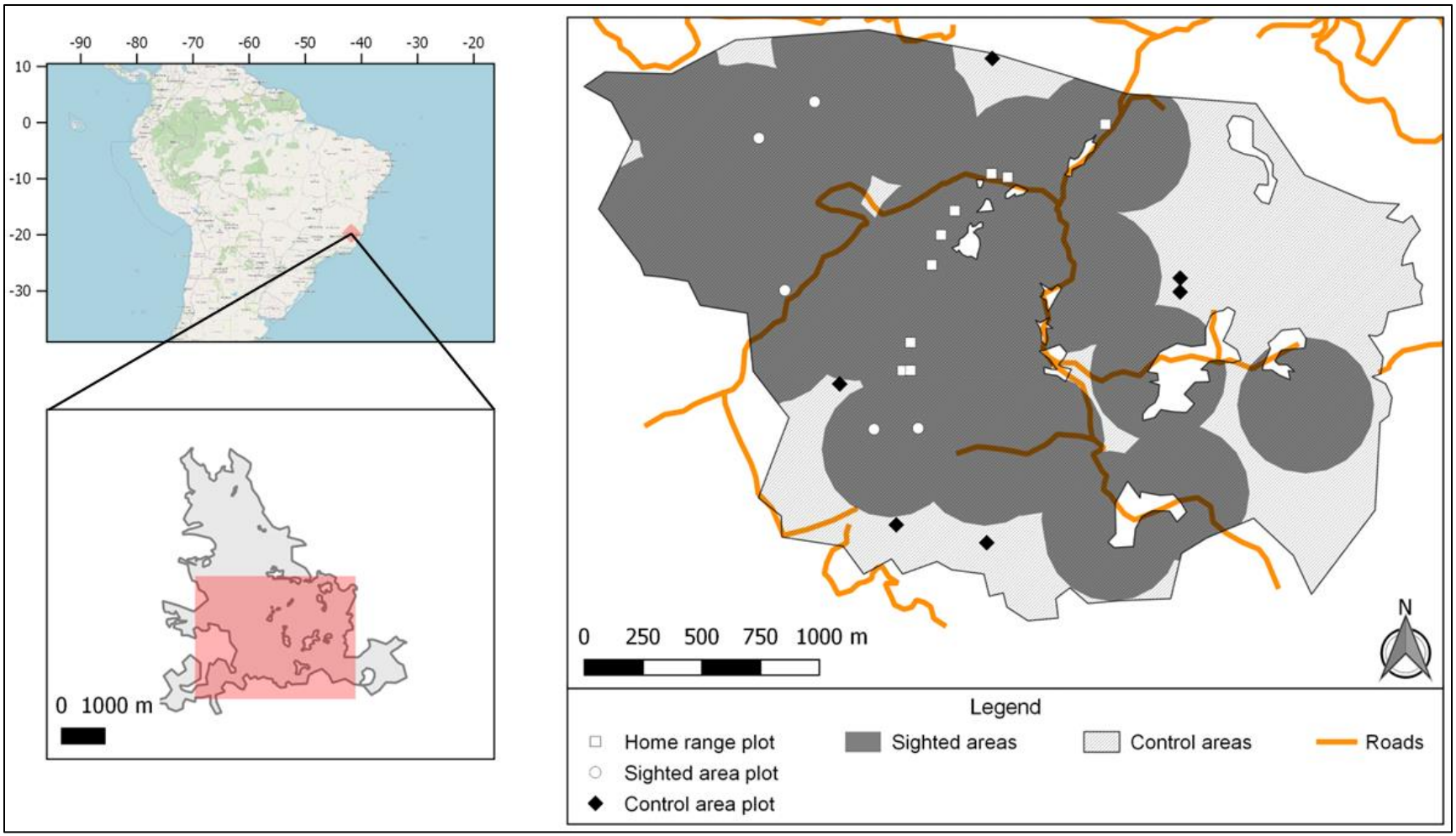

Fig. 1: Map of the RPPN-FMA showing plot locations and categories.

Within the white border is an ESRI/ArcGIS image showing the forested area in and around the RPPN-FMA. Inset is the Matão valley, calculated sighted (including home range) and control areas are indicated by dark gray and light gray, respectively. The locations of home range plots are shown as pink points, sighted plots as light pink points, and control plots as orange points. Dirt roads through the RPPN-FMA are indicated in orange lines.

	Group CM			Group CR			Group RB		
	M	FA	FB	M	FA	FB	M	FA	FB
Sept	63 (17%)	63 (25%)	63 (35%)	51 (37%)	51 (27%)	51 (33%)	NA	NA	NA
Oct	38 (13%)	38 (18%)	38 (21%)	24 (17%)	24 (13%)	24 (25%)	77 (25%)	77 (13%)	77 (23%)
Nov	NA	NA	NA	28 (29%)	28 (18%)	28 (29%)	63 (16%)	63 (14%)	63 (195)
April	96 (17%)	96 (26%)	96 (27%)	78(15%)	78 (12%)	78 (14%)	33 (9%)	33 (9%)	33 (9%)
May	56 (25%)	56 (30%)	56 (33%)	56 (36%)	56 (23%)	56 (34%)	36 (14%)	36 (17%)	36 (14%)

Table 1: Feeding as a percentage of scan samples per individual in each study group.

Monthly number of scan samples and percentage of feeding samples (in parentheses) across individuals and groups. Each group consisted of one adult male (M) and two adult females (FA and FB).

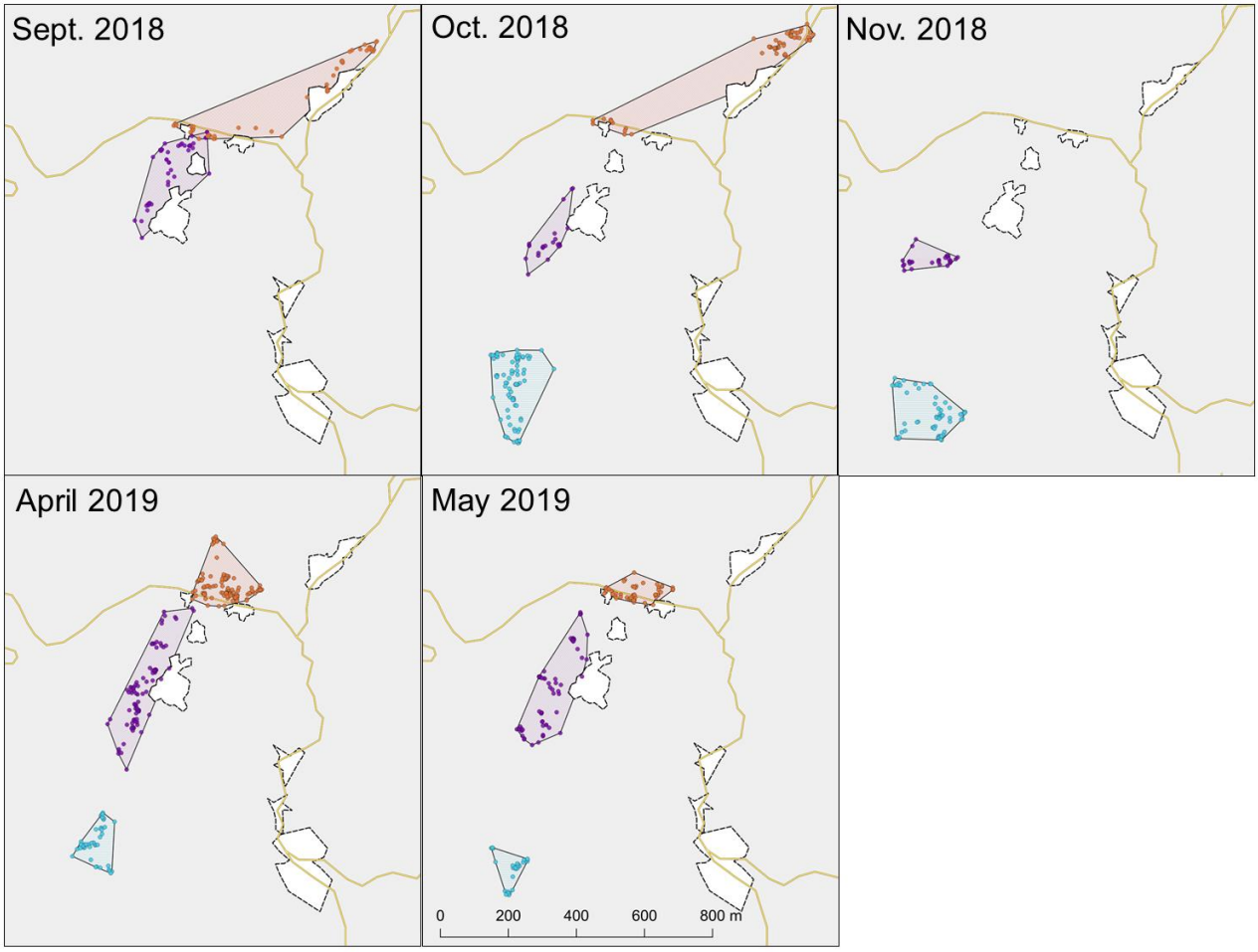

Fig. 2: Monthly home range maps for the three study groups for Sept.-Nov. 2018 and April and May 2019. The home range for group CM is marked with orange points and shaded area, CR with purple points and shaded area, and RB with blue points and shaded area. Forested areas are light gray and unsuitable areas (i.e., pasture, regenerating vegetation) are white, and the dirt road through the RPPN-FMA is yellow. September was the only month with any home range overlap between groups CR and CM: home ranges overlapped by 0.06 ha, or 0.83% and 1.72% of their respective September home ranges.

Variable	Plot type	Median	IQR	χ2	df	*P*	*Post hoc*	*Adj. P*
DBH (cm)	HR	16.26	1.15	21.73	2	*0.000	HR-S	0.109
	S	17.34	3.37				HR-C	*0.000
	C	11.35	4.29				S-C	*0.019
Median tree height (m)	HR	13.31	10.00	12.06	2	*0.000	HR-S	0.524
	S	12.81	10.00				HR-C	*0.001
	C	10.24	5.00				S-C	*0.004
Basal area (m^2/ha)	HR	0.54	0.16	22.51	2	*0.000	HR-S	0.092
	S	1.26	0.72				HR-C	*0.000
	C	0.26	0.17				S-C	*0.019
Canopy height (m)	HR	26.00	3.00	5.24	2	0.070	HR-S	0.404
	S	22.00	5.00				HR-C	0.034
	C	19.00	3.50				S-C	0.505
Number canopy layers	HR	4.00	0.00	8.32	2	*0.020	HR-S	0.669
	S	4.00	0.00				HR-C	*0.006
	C	3.00	0.75				S-C	*0.020
Number emergent trees	HR	0.00	1.00	3.91	2	0.140	HR-S	0.119
	S	2.00	2.00				HR-C	1.000
	C	0.00	0.75				S-C	0.115
Density upper canopy	HR	4.00	1.00	4.55	2	0.100	HR-S	0.687
	S	4.00	0.00				HR-C	0.174
	C	2.00	1.00				S-C	0.060
Density middle canopy	HR	4.00	1.00	2.35	2	0.310	HR-S	1.000
	S	4.00	1.00				HR-C	0.342
	C	2.00	2.75				S-C	0.227
Density understory	HR	3.00	1.00	0.49	2	0.780	HR-S	1.000
	S	2.00	1.00				HR-C	0.740
	C	2.00	1.50				S-C	1.000
Density shrub layer	HR	4.00	2.00	2.18	2	0.340	HR-S	0.462
	S	3.00	2.00				HR-C	0.255
	C	2.00	0.00				S-C	1.000
Density lianas	HR	2.00	2.00	8.49	2	*0.010	HR-S	0.591
	S	3.00	0.00				HR-C	0.036
	C	1.00	0.75				S-C	*0.009
Canopy continuity	HR	4.00	1.00	5.25	2	0.070	HR-S	0.777
	S	4.00	2.00				HR-C	0.034
	C	2.00	0.75				S-C	0.247
Canopy connectivity	HR	4.00	2.00	6.43	2	*0.040	HR-S	0.970
	S	4.00	0.00				HR-C	0.049
	C	2.50	1.75				S-C	0.034

Table 2: Ecological variables compared across plot categories.

Results of Kruskal-Wallis and *post-hoc* Dunn's tests comparing ecological variables among home range (HR), other sighted (S), and control (C) plots. Variable, plot type (HR, S, or C), median for the metric of each given variable, interquartile range (IQR) for each metric, Kruskal Wallis chi squared value, degrees of freedom, and *P*-values. *Post hoc* pairwise comparisons are listed with Bonferroni adjusted *P*-values ($\alpha = 0.025$).

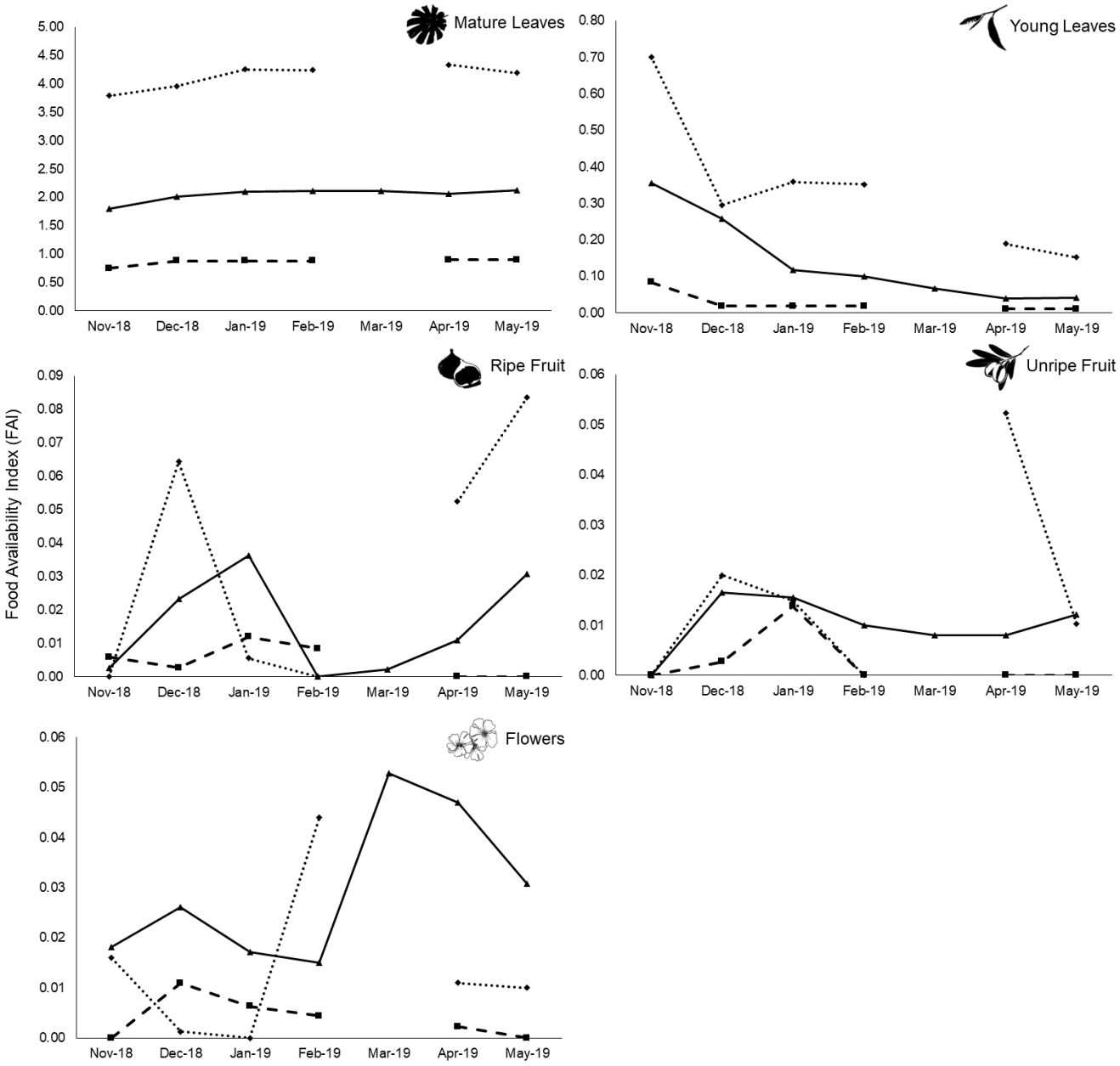

Fig. 3: Monthly FAI values for each plant part across plot categories.

Mature leaf, young leaf, ripe fruit, unripe fruit, and flower FAI values are shown for each month and each plot category. Home range plots are solid black lines, sighted plots are dotted black lines, and control plots are dashed black lines. Note: scales of y-axes are different.

Month	Food item	Median (IQR) percent feeding scans			Test statistic[a]	*P*
		CM	CR	RB		
Sept	Buds	0.33 (0.50)	0.17 (0.50)	NA	161.50	0.9060
	Fruit	0.00 (0.00)	0.00 (0.00)	NA	135.00	0.1405
	Flowers	0.00 (0.00)	0.00 (0.00)	NA	135.00	0.1409
	Leaves	0.67 (0.50)	0.50 (1.00)	NA	198.50	0.1799
Oct	Buds	0.00 (0.00)	0.00 (0.25)	0.25 (0.67)	3.44	0.1790
	Fruit	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	NA	NA
	Flowers	0.00 (0.50)	0.00 (0.00)	0.00 (0.00)	8.18	*0.0168
	Leaves	0.50 (1.00)	0.75 (0.63)	0.50 (0.67)	0.25	0.8833
Nov	Buds	NA	0.00 (0.00)	0.00 (0.33)	32.00	0.0867
	Fruit	NA	0.00 (0.00)	0.00 (0.13)	41.50	0.5066
	Flowers	NA	0.00 (0.00)	0.00 (0.00)	NA	NA
	Leaves	NA	1.00 (0.00)	0.67 (0.50)	69.50	0.6469
April	Buds	0.00 (0.00)	0.00 (0.00)	NA	NA	NA
	Fruit	0.25 (0.15)	0.00 (0.00)	NA	202.50	*0.0000
	Flowers	0.00 (0.00)	0.50 (0.83)	NA	45.00	*0.0006
	Leaves	0.75 (0.08)	0.33 (0.58)	NA	120.00	0.3506
May	Buds	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	1.50	0.4724
	Fruit	0.00 (0.00)	0.00 (0.00)	0.50 (1.00)	12.89	*0.0016
	Flowers	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	4.00	0.1353
	Leaves	1.00 (0.00)	1.00 (0.00)	0.38 (0.94)	14.33	*0.0008

Table 3: Differences in monthly diet composition among the three study groups.

[a] For months with data from only two groups, Wilcoxon rank sum tests were used with the test statistic *W*. For months with all three groups, Kruskal-Wallis tests were used with the test statistic being the Kruskal-Wallis chi squared.

*Indicates significant *P* values, results of post hoc comparisons are provided in text.

Conclusion

The degree to which primates can adjust behavior along different temporal scales in response to environmental changes directly impacts both individual and species-level survival in an increasingly unpredictable world. As brown howler monkeys confront extinction pressures from shrinking habitats, a changing climate, and other factors like disease outbreaks active population management may become a more intensive part of conservation planning for this species, and thus understanding local ecology and where populations are most likely to be successful will be critical (Bicca-Marques et al., 2020).

Here we presented a summary of current research describing primate dietary flexibility across the order and provided context for understanding the degree to which species can adjust their diets and behavior given morphological, physiological, or phylogenetic constraints. Additionally, we described the intra-group social dynamics of three small groups of brown howler monkeys and the negative correlation between proximity to anthropogenic disturbance and the stability of dyadic female social relationships. We further provided a test of the ideal free model and demonstrated that the areas of the RPPN-FMA with howler monkey sightings were of higher quality than the surrounding forest. We also found no quantitative difference in the vegetation characteristics of group home ranges despite proximity to a dirt road that bisects the RPPN-FMA.

This work contributes data from a population of brown howler monkeys living at unusually low density and in very small groups to the rich body of work documenting behavioral variation of howler monkeys throughout Central and South America. Throughout the work, we highlighted the importance of behavioral variability (and ultimately flexibility) as one of the factors influencing the ability of individuals and species to persist in a variety of habitats and with varying degrees of anthropogenic disturbance. Howler monkeys are widely considered resilient in the face of ecological changes, including shrinking habitats or decreasing habitat

quality. However, as suggested by Bicca-Marques et al. (2020), the ability of individual howler monkeys to survive life in disturbed or fragmented forests does not equate to the long-term survival of species in this genus.

As forests shrink, isolated populations are likely to face local extinction due to genetic isolation and inbreeding depression (Bicca-Marques et al., 2020). The increased pressure on isolated individuals to cross matrices such as farmland or roads leads to heightened risks of serious injury or death from dog attacks or vehicle collisions (Chaves et al., 2022). And encroaching forest edges and anthropogenic disturbance can force behavioral and dietary modifications that could have long-term consequences for populations (McKinney, 2019; Negrín et al., 2016). Among these other threats, disease also poses a significant risk to howler monkey populations throughout the Americas. Yellow fever outbreaks in 2007-2009 and again in 2016-2017 decimated brown howler monkey populations across northern Argentina and southeastern Brazil, leading to population decreases of approximately 80% at many sites (Agostini et al., 2014; Moreno et al., 2015; Possamai et al., 2022).

Largely as a result of the considerable population declines as a result of successive yellow fever outbreaks, brown howler monkeys are included among the world's 25 most endangered primates, with the northern population (*A. guariba guariba*) listed as critically endangered and the southern population (*A. guariba clamitans*) listed as vulnerable in Brazil and critically endangered in Argentina (Ministério do Meio Ambiente do Brasil, 2022; Oklander et al., 2022). Future research with this species should seek to clarify genetic relationships among populations and subspecies and assess genetic variation within populations to facilitate conservation planning and implementation of wildlife management strategies.

Additional future research with brown howler monkeys should also seek to identify physiological mechanisms by which individuals are able to persist in degraded habitats with higher degrees of disturbance. Non-invasive methods for understanding primate energetics (i.e., urinary C-peptide analyses) are well developed in other species and have recently been

biologically validated in other platyrrhine taxa (Sacco et al., 2021), which shows promise for researchers interested in using similar methods with howler monkeys. While the behavioral and digestive mechanisms by which howler monkeys are able to consume large quantities of leaves across their range are well documented (Glander, 1978; Lambert, 1998), non-invasive monitoring of individual physiology could elucidate when and how howler monkeys experience energetic stress.

Howler monkeys, while able to adjust their behavior and diets and thus persist for many years in degraded habitats, will suffer health and fitness consequences if they are forced to endure energetic or nutritional deficits for prolonged periods. Understanding these thresholds and physiological limits will be an important part of conservation planning and management for these primates, alongside continued study of their diets, behavior, and biology. Research and conservation planning must incorporate an understanding of the scale or scope of the variability we are investigating – whether we are looking at individuals, groups, populations, or species (e.g., Bicca-Marques et al. 2020) or whether we are considering resilience in the face of short-term challenges or long-term pressures (e.g., Strier, 2021). Many of the lingering questions concerning brown howler monkeys will require long-term research to understand the extent to which behavior varies within this species, among members of the genus *Alouatta,* and across the order Primates.

References

Agostini, I., Holzmann, I., Bitetti, M. S. D., Luciani, I., Kowalewski, M. M., Beldomnico, P. M., ... Miller, P. (2014) Conservation letter Building a species conservation strategy for the brown howler monkey (*Alouatta guariba clamitans*) in Argentina in the context of yellow fever outbreaks. *Tropical Conservation Science* 7(1), 26-34. https://doi.org/10.1177/194008291400700107

Bicca-Marques JC, Chaves ÓM, Hass GP (2020) Howler monkey tolerance to habitat shrinking: Lifetime warranty or death sentence? Am J Primatol 82. https://doi.org/10.1002/ajp.23089

Chaves OM, Souza Junior JC, Buss G, et al (2022) Wildlife is imperiled in peri-urban landscapes: threats to arboreal mammals. Sci Total Environ 821. https://doi.org/10.1016/j.scitotenv.2021.152883

Glander, K. E. (1978). Howling monkey feeding behavior and plant secondary compounds: a study of strategies. *In* Montgomery, C. G. (Ed.) *The Ecology of Arboreal Folivores*. Smithsonian Institution Press.

Lambert, J. E. (1998) Primate digestion: interactions among anatomy, physiology, and feeding ecology. *Evolutionary Anthropology*. 7(1), 8-20. https://doi.org/10.1002/(SICI)1520-6505(1998)7:1%3C8::AID-EVAN3%3E3.0.CO;2-C

McKinney, T. 2019. Ecological and Behavioural Flexibility of Mantled Howlers (*Alouatta palliata*) in Response to Anthropogenic Habitat Disturbance. *Folia Primatologica* 90(6), 456-469. https://doi.org/10.1159/000499825

Ministério do Meio Ambiente do Brasil (2022) Portaria MMA Nº 148, de 7 de junho de 2022 Lisa Oficial de Espécies da Flora Brasileira Ameaçadas de Extinção. https://www.icmbio.gov.br/cepsul/images/stories/legislacao/Portaria/2020/P_mma_148_2022_altera_anexos_P_mma_443_444_445_2014_atualiza_especies_ameacadas_extincao.pdf

Moreno, E. S., Spinola, R., Tengan, C. H., Brasil, R. A., Siciliano, M. M., Coimbra, T. L. M., ... Suzuki, A. (2013) Epizootias de febre amarela em primatas não humanos no estado de São Paulo, Brasil 2008-2009. *Revista Do Instituto de Medicina Tropical de São Paulo.* 55(1), 45-50. https://doi.org/10.1590/S0036-46652013000100008

Negrín, A. R., Fuentes, A. C., Espinosa, D. C., Dias, P. A. D. 2016. The loss of behavioral diversity as a consequence of anthropogenic habitat disturbance: the social interactions of black howler monkeys. *Primates*.

Oklander, L.I., Buss, G., Bicca-Marques, J.C., Hirano, Z. B., Chaves, O. M., ... Jerusaliksky L. (2022) Brown Howler Monkey *In* Mittermeier, R. A., Reuter, K. E., Rylands, A. B., Jerusalinsku, L., Schwitzer, C., Strier, K. B., Ratsimbazafy, J., & Humle, T. *Primates in Peril: The World's 25 Most Endangered Primates 2022-2023*. IUCN SSC Primate Specialist Group, International Primatological Society, and Re:wild, Washington, D.C.

Possamai CBP, de Melo FR, Mendes SL, Strier KB (2022) Demographic changes in an Atlantic Forest primate Community following a yellow fever outbreak. *American Journal of Primatology* e23425 https://doi.org/10.1002/ajp.23425

Sacco AJ, Granatosky MC, Laird MF, Milich KM. (2021) Validation of a method for quantifying urinary C-peptide in platyrrhine monkeys. *General and Comparative Endocrinology* (300) https://doi.org/10.1016/j.ygcen.2020.113644

Strier, K.B. The limits of resilience. *Primates.* 62, 861–868 (2021). https://doi.org/10.1007/s10329-021-00953-3

Appendix

Appendix 1: Supplementary materials for Chapter 3

Group	Month	N GPS sightings	MCP (ha)	Adj MCP (ha)	Grid Cell (ha)	KDE *H_ref* (ha)	KDE *H_ad hoc* (ha)
CM	Sept.	40	6.26	5.98	1.25	40.69	15.70
	Oct.	68	6.94	6.49	1.44	21.95	41.40
	Nov.	NA	NA	NA	NA	NA	NA
	April	113	2.60	2.60	1.94	4.20	2.07
	May	57	1.22	1.17	0.94	2.91	2.91
CR	Sept.	29	3.87	3.19	1.06	8.22	7.28
	Oct.	24	1.50	1.49	1.00	5.43	3.81
	Nov.	54	0.94	0.94	0.69	3.32	2.68
	April	70	4.46	4.26	2.13	11.41	6.59
	May	83	4.04	3.92	1.44	10.16	5.59
RB	Sept.	NA	NA	NA	NA	NA	NA
	Oct.	81	3.66	3.66	2.00	8.91	6.35
	Nov.	63	3.00	3.00	1.63	6.40	5.78
	April	37	1.39	1.39	1.06	3.31	3.03
	May	37	0.81	0.81	0.63	2.81	2.61

Table S1: Monthly sample sizes and home range estimates by group.

Number of GPS locations for each group are given by month. Home range estimates are given in hectares for five different methods of home range estimation: minimum convex polygon (MCP); adjusted minimum convex polygon (adj. MCP; Grueter 2009); grid cell; kernel density estimate with 95% CI and a reference smoothing parameter (KDE *H_ref*); and kernel density estimate with a 95% CI and *ad hoc* smoothing parameter (KDE *H_ad hoc*).

Month	Plant part	Plot type	Median FAI	IQR FAI	χ2	df	*P*	*Post hoc*	Adj. *P*
Nov.	ML	HR	1.880	0.760	10.250	2	*0.006	HR-S	0.770
		S	4.170	3.030				HR-C	*0.012
		C	0.742	0.674				S-C	*0.005
	YL	HR	0.401	0.358	4.638	2	0.098		
		S	0.256	0.929					
		C	0.021	0.081					
	RF	HR	0.000	0.000	0.885	2	0.643		
		S	0.000	0.000					
		C	0.000	0.000					
	UF	HR	0.000	0.000		NA			
		S	0.000	0.000					
		C	0.000	0.000					
	FL	HR	0.000	0.028	4.066	2	0.131		
		S	0.000	0.000					
		C	0.000	0.000					
Dec.	ML	HR	1.970	0.986	8.769	2	*0.012	HR-S	0.764
		S	4.610	3.030				HR-C	*0.023
		C	0.951	0.664				S-C	*0.010
	YL	HR	0.127	0.168	6.685	2	*0.035	HR-S	0.524
		S	0.057	0.256				HR-C	*0.015
		C	0.007	0.024				S-C	0.248
	RF	HR	0.000	0.047	4.087	2	0.130		
		S	0.074	0.077					
		C	0.000	0.000					
	UF	HR	0.016	0.027	2.454	2	0.293		
		S	0.000	0.026					
		C	0.000	0.000					
	FL	HR	0.024	0.033	4.491	2	0.106		
		S	0.000	0.000					

		C	0.000	0.000					
Jan.	ML	HR	2.030	0.573	9.785	2	*0.008	HR-S	0.738
		S	4.430	2.790				HR-C	*0.015
		C	0.951	0.664				S-C	*0.006
	YL	HR	0.059	0.154	4.674	2	0.097		
		S	0.168	0.575					
		C	0.007	0.024					
	RF	HR	0.026	0.033	2.453	2	0.293		
		S	0.000	0.000					
		C	0.005	0.023					
	UF	HR	0.000	0.033	0.422	2	0.810		
		S	0.000	0.000					
		C	0.007	0.028					
	FL	HR	0.000	0.033	2.180	2	0.336		
		S	0.000	0.000					
		C	0.000	0.004					
Feb.	ML	HR	2.030	0.469	9.209	2	*0.010	HR-S	0.797
		S	4.610	3.030				HR-C	*0.018
		C	0.951	0.664				S-C	*0.009
	YL	HR	0.059	0.127	5.153	2	0.076		
		S	0.256	0.575					
		C	0.007	0.024					
	RF	HR	0.000	0.000	4.912	2	0.086		
		S	0.000	0.000					
		C	0.000	0.013					
	UF	HR	0.000	0.000		NA			
		S	0.000	0.000					
		C	0.000	0.000					
	FL	HR	0.000	0.000	0.742	2	0.690		
		S	0.000	0.000					
		C	0.000	0.007					

April	ML	HR	1.970	0.319	9.923	2	*0.007	HR-S	0.652
		S	4.970	2.930				HR-C	*0.017
		C	1.010	0.696				S-C	*0.005
	YL	HR	0.000	0.059	1.543	2	0.462		
		S	0.057	0.256					
		C	0.007	0.019					
	RF	HR	0.000	0.000	1.271	2	0.530		
		S	0.000	0.000					
		C	0.000	0.000					
	UF	HR	0.000	0.000	1.271	2	0.530		
		S	0.000	0.000					
		C	0.000	0.000					
	FL	HR	0.039	0.066	8.031	2	*0.018	HR-S	*0.019
		S	0.000	0.000				HR-C	*0.042
		C	0.000	0.000				S-C	1.000
May	ML	HR	2.030	0.603	9.785	2	*0.008	HR-S	0.738
		S	4.970	2.930				HR-C	*0.015
		C	1.010	0.694				S-C	*0.006
	YL	HR	0.010	0.059	1.465	2	0.481		
		S	0.057	0.179					
		C	0.007	0.019					
	RF	HR	0.000	0.041	3.378	2	0.185		
		S	0.000	0.026					
		C	0.000	0.000					
	UF	HR	0.000	0.000	1.438	2	0.487		
		S	0.000	0.000					
		C	0.000	0.000					
	FL	HR	0.038	0.055	7.540	2	*0.023	HR-S	0.040
		S	0.000	0.000				HR-C	0.029
		C	0.000	0.000				S-C	1.000

Table S2: Phenological variation measured using a simplified Food Availability Index among plot types across seven months. Here we report, by month, median plot values for mature leaves (ML), young leaves (YL), ripe fruit (RF), unripe fruit (UF), and flowers (FL) across plot categories of home range (HR), sighted (S), and control (C). Median Fruit Availability Index (FAI) values and interquartile ranges are reported, as are Kruskal-Wallis chi squared values with degrees of freedom (df) and *P*-values for Kruskal-Wallis tests. Pairwise comparisons and Bonferroni adjusted *P*-values ($\alpha = 0.025$). Significant results of Kruskal-Wallis tests and *post hoc* pairwise Dunn's tests are indicated with an asterisk.