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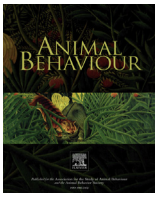

Sharing spaces: niche differentiation in diet and substrate use among wild capuchin monkeys

Rachel E. Williamson [a, *, 1], Shasta E. Webb [a, 1], Colin Dubreuil [a], Ronald Lopez [b], Saúl Cheves Hernandez [b], Linda M. Fedigan [a], Amanda D. Melin [a, c, d, *]

[a] Department of Anthropology and Archaeology, University of Calgary, Calgary, AB, Canada
[b] Área de Conservación Guanacaste, Guanacaste, Costa Rica
[c] Alberta Children's Hospital Research Institute, University of Calgary, Calgary, AB, Canada
[d] Department of Medical Genetics, Cumming School of Medicine, University of Calgary, Calgary, AB, Canada

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Understanding variation in social grouping patterns among animal taxa is an enduring goal of ethologists, who seek to evaluate the selective pressures shaping the evolution of sociality. Cohesive association with conspecifics increases intragroup feeding competition and may impose constraints on group size. Furthermore, in sexually dimorphic species, males and females may have different nutritional requirements, which can lead to suboptimal foraging in mixed-sex groups. How do animals living in permanent social groups mitigate these foraging costs? Niche differentiation is often hypothesized as a mechanism, but rigorous and detailed tests of the extent and context of differences in diet and habitat use, key tenets of this hypothesis, are rare. We investigated the potential for niche differentiation in foraging activity budget and environment use in a population of wild white-faced capuchin monkeys, *Cebus imitator*, in northwestern Costa Rica. Using a robust data set of 15 879 foraging scan samples collected from four groups over 13 months, we found that smaller individuals – e.g. juveniles and females – forage more often on smaller branches. We additionally found clear evidence of predator-sensitive foraging wherein the smallest individuals spent less time on the ground during invertebrate foraging. Importantly, niche differentiation was far more evident overall during invertebrate foraging, likely due to spatial constraints and environmental homogeneity imposed by fruit patches. In summary, we found considerable variation in habitat use across age and sex classes, likely attributable to differences in size and relative predation risk. These variables likely reduce intraspecific feeding competition by promoting differential diet and habitat use. Our results also provide insight into the limits of niche differentiation as a strategy for competition reduction and may shed light on the evolution of fission–fusion dynamics in highly frugivorous species.

Study of animal grouping patterns has long captivated ethologists, who seek to evaluate selective pressures shaping the evolution of sociality and better understand the wide diversity of patterns among extant and past species (Kutsukake, 2009; Port, Kappeler, & Johnstone, 2011; Sterck, Watts, & van Schaik, 1997). Among mammals, permanent associations between males and females extending beyond seasonal breeding groups are uncommon. However, group living is present among pack-hunting carnivores, grazing ungulates and diurnal primates, where permanent social groups are the norm (Dunbar, 1988; Kappeler & van Schaik, 2002). Evolutionary drivers of permanent group living are hypothesized to include decreased risk of predation, increased access to resource-rich areas of the habitat and benefits from shared caregiving (Chapman & Chapman, 2000; Krause & Ruxton, 2002). However, substantial costs of group living are also present and include increased exposure to pathogens (Altizer et al., 2003; Côté & Poulinb, 1995; Kappeler, Cremer, & Nunn, 2015) and increased feeding competition with conspecifics, often including kin (Koenig, 2002; Pinacho-Guendulain & Ramos-Fernández, 2017; Wrangham, 1980). One strategy for decreasing within-group feeding competition is exhibiting flexible grouping patterns, e.g. fission–fusion dynamics, in which group members separate temporarily into smaller parties during foraging (Chapman, 1988; Lehmann,

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* Corresponding authors.
E-mail addresses: rachel.williamson1@ucalgary.ca (R. E. Williamson), amanda.melin@ucalgary.ca (A. D. Melin).
[1] These authors contributed equally to this work.

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Korstjens, & Dunbar, 2007). Alternatively, the niche partitioning hypothesis posits that variation in diet and/or habitat use among group members decreases competition among conspecific, cohesively grouped species (Sheppard et al., 2018).

Intraspecific niche differentiation in diet and foraging strategies, perch use and vertical stratification, among other factors, has been documented in invertebrates (e.g. Johnson, 1986; Polis, 1984), reptiles (e.g. Delaney & Warner, 2016; Houston & Shine, 1993), birds (e.g. De Pascalis et al., 2020; Donald et al., 2007; Sol, Santos, & Cuadrado, 2000) and mammals (e.g. Hirsch, 2011; Voigt, Krofel, Menges, Wachter, & Melzheimer, 2018) and may emerge through one or more proximate mechanisms. Differences in intrinsic factors such as nutritional requirements, physiology, body size, strength or experience may lead individuals to focus their foraging efforts on certain resources or may limit their access to others (Geissler, Daegling, Polvadore, & McGraw, 2021; Lee, 1987; MacKinnon, 2006; Ruckstuhl & Neuhaus, 2002). The capacity for a species to exhibit intraspecific niche differentiation may further vary with the extent of sexual dimorphism in adult body size (Houston & Shine, 1993; Le V. Dit Durell et al., 1993; McGraw, Vick, & Daegling, 2011; Voigt et al., 2018) and with the length of juvenescence, as juvenile animals are smaller, less experienced, less skilful and possess less physical strength than adults. For example, in primates, long periods of juvenescence may contribute to adults and juveniles feeding on different parts of the same resource (Gunst, Leca, Boinski, & Fragaszy, 2010; Nowell & Fletcher, 2008) or selecting different foods altogether (Janson & van Schaik, 1993; O'Malley & Fedigan, 2005).

Differences in size, strength, sex and prior experience may also affect how individuals move through their environments. Sex-specific patterns in perch selection have been observed in different species of woodpeckers, with the smaller females spending more foraging time on smaller perches than do males (Jenkins, 1979; Pechacek, 2006; Peters & Grubb, 1983). For arboreal, quadrupedal animals, horizontal perches are easier to navigate, as individuals are not expending effort to cling and combat gravity while searching for food or feeding (Young, 2009). A number of researchers have hypothesized that, due to their smaller body sizes, immature primates are better suited to utilize thinner branches and move more easily through arboreal environments than adults (Bezanson, 2009; Doran, 1997; Fleagle & Mittermeier, 1980; McGraw, 1998; Young & Shapiro, 2018), and likewise that adult females are more likely to use smaller branch supports than adult males (Agostini & Visalberghi, 2005; Boinski, 1989; Rose, 1994). This is perhaps especially true of more vertically oriented branches (Boinski, 1989).

Habitat use may also be influenced by extrinsic forces such as predation risk, and a growing body of literature has explored predator-sensitive foraging (Altendorf, Laundré, López González, & Brown, 2001; Makin, Payne, Kerley, & Shrader, 2012; Monteza-Moreno, Crofoot, Grote, & Jansen, 2020; Pierce, 1988). Predation risk is not experienced equally by all members of a species or social group (Holmes, 1984; Jenkins, 1979; Longland & Jenkins, 1987; Ramakrishnan & Coss, 2000), and individuals likely exhibit differences in foraging strategies as a consequence. Sex differences in foraging have been hypothesized to reflect differential predation risk in brown anole lizards, *Anolis sagrei*, which experience the greatest threat from aerial predators: adult males (the largest age/sex class) use higher perches than females and juveniles (Delaney & Warner, 2016). In response to predation risk, arboreal monkeys are also predicted to exhibit habitat partitioning between members of the same social group (Janson, 1990; Miller, 2002; Stone, 2007), a pattern that has also been observed among species that form polyspecific associations (Buzzard, 2006, 2010). The predation rate for juvenile platyrrhine primates has been estimated to be three to six times higher than it is for adults (Janson & van Schaik, 1993). Among capuchin monkeys (*Cebus imitator*), adult males travel and forage on the forest floor, a location considered to be particularly risky, while smaller, adult females appear to avoid the forest floor (Fedigan, 1990; Rose, 1994). Potentially supportive of this interpretation, in a population of *C. imitator* living on an island with no terrestrial predators, all group members use the ground more often than do capuchins in mainland populations (Monteza-Moreno et al., 2020).

The type of resource being exploited may also affect the potential for niche differentiation in space use. Fruit is generally considered to be patchily distributed in time and space (Levey, 1988; Saracco, Collazo, & Groom, 2004; Sterck et al., 1997; van Schaik, Terborgh, & Wright, 1993). Furthermore, within a single fruit tree, the ability to select branches of particular sizes, angles or canopy emergence may be limited. Conversely, the wide diversity and more even abundance of invertebrates in the environment may offer opportunities for individuals to exploit different microhabitats (e.g. Gales, 1982; Melin, Fedigan, Young, & Kawamura, 2010). While some invertebrate abundance patterns in tropical dry forests are seasonal (e.g. caterpillar density coincides with the onset of the rainy season; Janzen, 1988, 1993), invertebrates are generally more widely available than fruits due to the high abundance, diversity and temporal availability of arthropods in forest environments (Erwin, 1982; Mosdossy, Melin, & Fedigan, 2015; Stork & Blackburn, 1993; Wardhaugh, Stork, & Edwards, 2014). Because of the more ubiquitous occurrence of invertebrates versus fruit in a forested environment, individuals may be able to use their habitats more strategically when foraging for the former. For example, experimental studies with wild squirrel monkeys (*Saimiri sciureus*) show that when food is abundant, juveniles preferentially forage in relatively concealed patches while avoiding patches more exposed to aerial predators; however, during periods of lower food availability, juveniles do not demonstrate this preference (Stone, 2007). Lending empirical support for these ideas, niche differentiation in use of forest strata between different species travelling and foraging together has been well documented (Grueter, Li, Feng, & Ren, 2010; Heymann & Buchanan-Smith, 2000; Kane & McGraw, 2017; McGraw & Bshary, 2002; Pinheiro, Ferrari, & Lopes, 2011). However, data on the relationship between food type and intraspecific habitat use are sparse for group-living, omnivorous mammals.

In this study, we assess the potential for niche differentiation in a large study population of socially cohesive, wild capuchin monkeys, a sexually dimorphic species with a slow life history and flexible foraging behaviours (Melin, Hiramatsu et al., 2014). We investigate the foraging activity budgets and the use of support substrates and forest strata across different age/sex classes as well as comparing habitat use during fruit foraging and invertebrate foraging. Specifically, we test the following alternative hypotheses against the null hypothesis that diet and habitat use do not vary across individuals or foraging types. Hypothesis 1: individuals exhibit differences in their activity budgets based on their ability to access food items. We predicted that smaller individuals, i.e. younger age classes versus older age classes and females versus males, would (1) spend relatively more time foraging on soft, easy-to-process fruits rather than fruits that require strenuous manual and/or oral processing and (2) spend relatively more time gleaning invertebrates from exposed surfaces rather than extracting invertebrates embedded within substrates. Hypothesis 2: individuals exhibit differences in the use of their environment based on their ability to exploit different branch supports. We predicted that smaller individuals would (1) spend relatively more time using smaller substrates and (2) spend relatively more time using vertically angled substrates. Hypothesis 3: individuals exhibit differences in their use of different canopy strata based on their relative predation risk. We predicted that smaller individuals would (1) spend relatively less time foraging in the upper canopy and (2) spend relatively less time foraging on the ground. Hypothesis 4: the extent of niche differentiation in habitat use varies when foraging on different types of food. We predicted that there would be greater differentiation across age/sex classes in their use of support substrates and forest strata during invertebrate foraging than during fruit foraging.

METHODS

Study System

We conducted our study in Sector Santa Rosa (SSR) in the Área de Conservación Guanacaste in northwestern Costa Rica (10°50′24″N, 85°37′12″W). SSR is a tropical dry forest and UNESCO World Heritage site. Longitudinal study of capuchins and weather (temperature, humidity and rainfall) have been continuously monitored since 1983 and 1978, respectively (reviewed in Melin et al., 2020). Temperature data for the present study were collected using a Kestrel weather meter located in a shaded location near the centre of the study groups' home ranges. The weather meter automatically records the temperature every 30 min. We collect rainfall data using a standard cylindrical rain gauge. Additionally, continuous monitoring of monthly fruit biomass, calculated from phenology surveys and transects of tree density, has been ongoing since 2007 and is detailed in Bergstrom, Hogan, Melin, and Fedigan (2019) and Orkin et al. (2019).

White-faced capuchins, *C. imitator*, are arboreal monkeys found in Honduras, Nicaragua, Costa Rica and Panama and occupy a variety of habitat types (Boubli, Rylands, Farias, Alfaro, & Alfaro, 2012; Fragaszy, Visalberghi, & Fedigan, 2004). Capuchin diets are notoriously variable but are typically composed of 50–80% fruits, 15–45% invertebrates, 0–8% other plant parts (e.g. flowers and pith) and 0–2% vertebrate prey (Eadie, 2015; Fragaszy et al., 2004; Mosdossy et al., 2015; Young, 2005). Capuchins consume an extensive breadth of both plant species and animal prey (Eadie, 2015; Janson & Boinski, 1992), with SSR capuchins feeding on more than 112 different food items (Melin, Young et al., 2014). They live in multimale, multifemale groups of 8–40 individuals (Campos, 2014; Melin et al., 2020).

Capuchins exhibit relatively long periods of juvenescence with females reaching reproductive maturity around age 6 years and males around age 10 years (Fragaszy et al., 2004; Jack et al., 2014). Adult male capuchins are roughly 30% larger than adult females with average males at SSR weighing ca. 3.33 kg and females 2.28 kg. However, this size dimorphism does not become apparent until individuals reach sexual maturity. We follow the established practice of grouping individuals in age classes based on morphological and behavioural developmental milestones: infants (<1 year of age, exclusive or occasional nursing), small immatures (1–3 years, typically weaned, average body size ca. 40% of an adult female, no clear sexual dimorphism, relatively large heads, frequently display slow and clumsy movements when travelling), large immatures (3–5 years, adult-like body proportions but smaller average body size ca. 70% of an adult female), not reproductively mature, males and females of similar body size, smooth and efficient movement) and adults (>5 years, emergence of sexual dimorphism, females reproductively mature, males begin to mature, typically reproducing around age 10 years but with large variation) (reviewed in Melin et al., 2020).

The tropical dry forests of Sector Santa Rosa are protected and boast a healthy population of predators. Given their small to medium body size, capuchins at Sector Santa Rosa are vulnerable to a number of bird species (including collared forest falcons, *Micrastur semitorquatus*, spectacled owls, *Pulsatrix perspicillata*, crane hawks, *Geranospiza caerulescens*, hook-billed kites, *Chondrohierax uncinatus*, common black hawks, *Buteogallus anthracinus*, laughing falcons, *Herpetotheres cachinnans*), snakes (including boa constrictors, *Boa constrictor*, Central American rattlesnakes, *Crotalus simus*) and several felid species (including jaguars, *Panthera onca*, pumas, *Puma concolor*, ocelots, *Leopardus pardalis*, margays, *Leopardus wiedii*, jaguarundi, *Herpailurus yagouaroundi*) (Bianchi & Mendes, 2007; Campos & Fedigan, 2014; Chapman, 1986; Chinchilla, 1997; de Oliveira et al., 2010; Digweed, Fedigan, & Rendall, 2005; Jack et al., 2020; Novack, Main, Sunquist, & Labisky, 2005; Perry, Manson, Dower, & Wikberg, 2003; Rose et al., 2003; Wheeler, 2010). Other carnivores (including coyotes, *Canis latrans*, grey foxes, *Urocyon cinereoargenteus*, tayra, *Eira barbara*) may also be a threat to small or injured monkeys (Campos & Fedigan, 2014; Defler, 1980; Digweed et al., 2005; Hernández-Camacho & Cooper, 1976; Rose et al., 2003; Wheeler, 2010).

Behavioural Data Collection

We collected behavioural data during April 2016 – September 2016 and January 2017 – July 2017. The study population comprised 113 individually identifiable white-faced capuchin monkeys from four social groups, which ranged in size from 15 to 30 individuals in 2016 and from 18 to 33 individuals in 2017. We observed each group during at least one 'rotation' per month, where rotations comprised 2–5 consecutive observation days from dawn (0445–0530 hours) until dusk (1800–1900 hours). We recorded behavioural data using Samsung Galaxy Tab 4 tablets loaded with PrimateLogger (developed by Scott Johnson for Android devices), which recorded a date/time stamp and UTM coordinates for each line of text entered.

During group follows, we conducted instantaneous scans (Altmann, 1974) every 30 min on each hour and half hour mark (e.g. 0500 hours, 0530 hours, 0600 hours, etc.). We identified as many individual monkeys as possible within 10 min and recorded their behavioural states (see Appendix 3, Table A8). As each individual and its behavioural state was identified, we also recorded its relative height in the canopy, the support substrate type and the support substrate angle it was using at the moment it was first observed. During fruit foraging, we recorded the species of fruit; during invertebrate foraging, we recorded whether the behaviour was visual searching/gleaning or extractive in nature. To minimize biasing data collection in favour of central individuals, we sought to begin scans with a different monkey each time and moved around the group.

Classifying Food Types

We observed food-processing behaviours using focal animal samples (Altmann, 1974), which we collected during foraging behaviours that occurred between instantaneous scans. During sampling, we recorded detailed food-processing behaviours such as scrubbing fruits to remove urticating hairs, cracking through fruit husks with teeth, stripping bark, breaking open branches, etc. Focal samples varied in duration (1–10 min), and we ceased data collection after 10 min had passed or once a food patch was left or a food item was fully consumed. Our goal for these focal animal samples was to document processing techniques (Melin, Webb, Williamson, & Chiou, 2018). We used these focal follows to classify foods as 'easy' or 'difficult' with respect to food processing for each type of foraging. For invertebrate foraging, we based our classifications on the estimated amount of manual and/or oral force required to access the invertebrate prey. Invertebrates that are relatively exposed and can be gleaned from the surfaces of branches or leaves, we classified as 'easy'. Invertebrates that are embedded within woody substrates and require extraction prior to ingestion, we classified as ‘difficult’.

For fruits, we classified species binomially as either ‘easy’ or ‘difficult’ based on the manual and/or oral processing required prior to ingestion (if any) and the physical properties of the fruit (Eadie, 2015). Fruits that require more processing steps or processing time were classified as ‘difficult’ (Perry & Ordoñez Jiménez, 2006), and they often had two or more of the following characteristics: (1) thick exocarp; (2) relatively ‘hard’ exocarp; (3) nondehiscent. A thick exocarp requires removal prior to ingestion. We quantified the hardness of a fruit's exocarp using a Lucas Scientific FLS-1 portable mechanical tester (Lucas et al., 2012) to measure their elastic modulus (also known as Young's modulus). We classified fruits with elastic modulus values of >1 megapascal (MPa) as having relatively hard exocarps and classified fruits with values of <1 MPa as having soft exocarps. Finally, some fruits with thick husks dehisce when ripe (i.e. split open along a suture) to expose edible aril around seeds. We classified species in which capuchins typically eat fruits in the dehisced state as ‘easy’ since the monkeys do not need to open the fruits with strength or skill. We collected data on the manual and oral processing of fruits while observing capuchin foraging behaviours and assessed physical properties of the fruits by collecting partially eaten fruits as well as intact samples of fruit species from feeding sites over two sampling seasons in December 2015 – June 2016 and in January 2017 – July 2017 (Chalk et al., 2016; Wright et al., 2008). During our study, we observed capuchins in SSR consuming 53 different fruit species. Of these species, we measured the elastic modulus of a subset of 16 species that we assessed to represent the typical range of values (Fig. 1).

Classifying Support Substrates and Forest Strata

We categorized branches based on their sizes and orientations. We used three different size categories, which were informed by capuchin body sizes (Rose, 1994). We classified branches with circumferences of 1–20 cm as small, 21–50 cm as medium and >50 cm as large. We used two orientation categories where we considered branches between 0° and 45° (relative to the ground) as horizontal and branches >45° as angled (Boinski, 1989; Peters & Grubb, 1983) (Fig. 2). We defined four categorical classifications of forest strata: ground, lower canopy, middle canopy and upper canopy, which refer, respectively, to the forest floor, the lowest third of the canopy, the middle third of the canopy and the highest third of the forest, including emergent trees. All support substrate and forest strata categorizations were made based on visual assessments by researchers in the field.

Statistical Analysis

Over the course of our two behavioural sampling seasons, we collected 30 744 individual scan records of 107 animals over 190 cumulative contact days. For statistical analyses, we grouped our data per individual per rotation. From the complete data set, we created a subset of all foraging scans ($N = 15\ 879$), which includes visually foraging for invertebrates, extracting invertebrates from various substrates (e.g. bark, leaves), feeding on surface invertebrates, foraging for fruit and extracting difficult-to-access fruits. From this foraging data set, we further subset the data according to which hypotheses we were testing. Certain variables (support substrate classifications) were only collected in 2017.

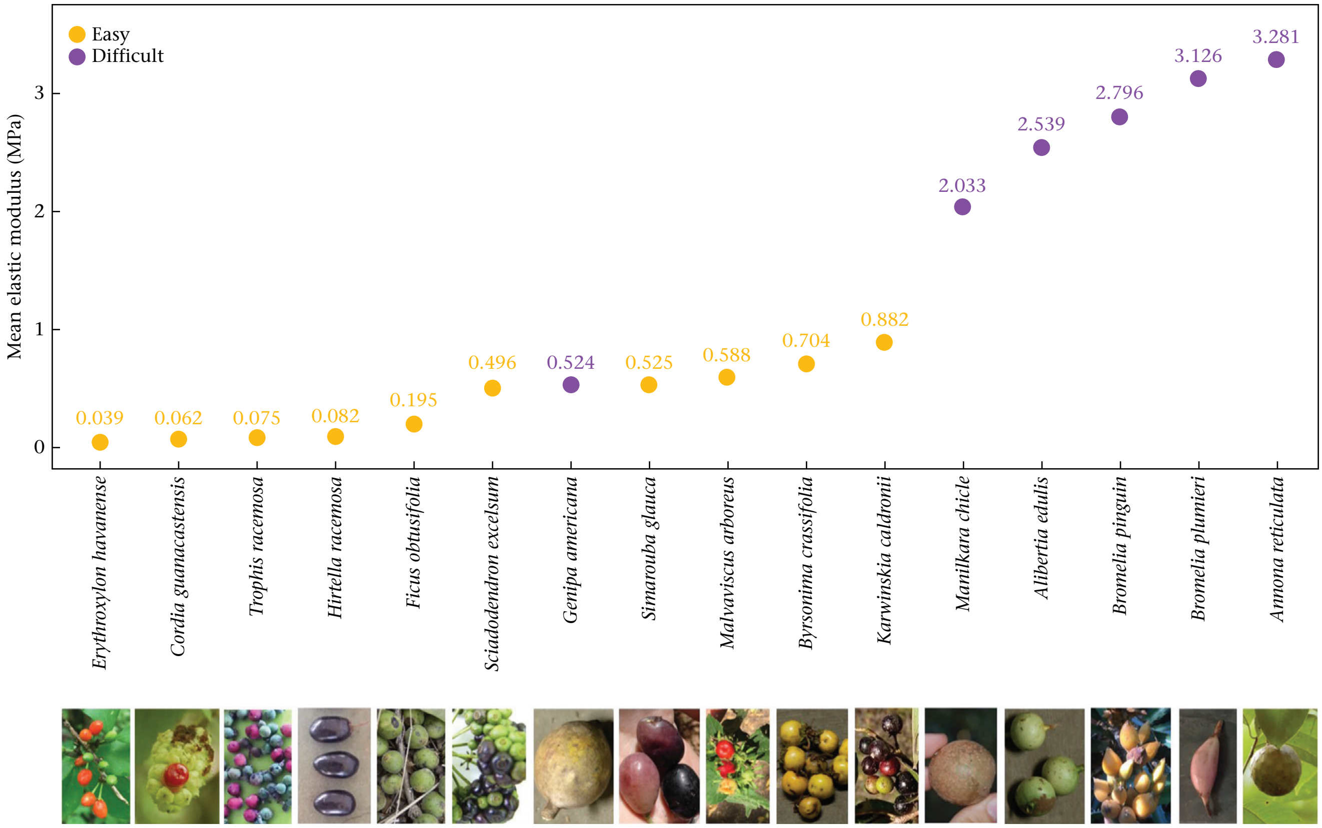

Figure 1. We measured the elastic modulus of 16 fruit species. Fruits with an elastic modulus >1 MPa have soft exocarps while those with an elastic modulus <1 MPa have hard exocarps. Fruits with soft exocarps are typically ‘easy’ fruits, while those with hard exocarps are typically ‘difficult’. *Genipa americana* is an exception: the pulp is very soft, but the exocarp is thick and difficult to puncture and requires moderate effort to peel.

Figure 2. Examples of each of the six branch substrate types: (a) small horizontal, (b) medium horizontal, (c) large horizontal, (d) small angled, (e) medium angled, (f) large angled. Photos by: Amanda Melin (a, e); Krisztina Mosdossy (b); Elizabeth Sargeant (c); Fernando Campos (d, f).

We evaluated our hypotheses of niche differentiation by fitting a series of generalized linear mixed models (GLMM) in the R package lme4 (Bates, Mächler, Bolker, & Walker, 2015) and glmmTMB (for 0-inflated models) (Brooks et al., 2017) using a Poisson distribution fitted by Laplace approximation with a log link for all models. We included age class (categorical), sex class and an interaction between age class and sex class in each GLMM. We also included mean rainfall (cm) per rotation, mean high temperature (°C) per rotation and mean estimated monthly fruit biomass (kg/ha) as fixed effects, as evidence suggests that ecological variables influence capuchin foraging behaviour (Campos & Fedigan, 2009; Hogan, Melin, Mosdossy, & Fedigan, 2016; Melin, Young et al., 2014; Orkin et al., 2019; Perry & Ordoñez Jiménez, 2006; Rímoli, Strier, & Ferrari, 2008). Ecological variables were z-transformed to have a mean of 0 in all models. For categorical variables (e.g. age, sex), a reference intercept category was selected by the model (e.g. females for the sex variable, infants for the age variable). We included the individual identity of each animal as a random effect in all models. Our unit of analysis for each model was scans per individual per rotation; each model included an offset that was total scans per animal per rotation, which enabled us to account for differences in sampling effort among rotations.

To examine the effects of our predictor variables, we computed incidence rate ratios (IRR) using the outputs of our GLMMs. For binary variables (e.g. sex), the IRR is the ratio between scans recorded in a given behaviour or substrate in males compared to females. For variables with multiple levels (e.g. age class), the IRR represents the ratio of the number of scans recorded in one level compared to the number of scans recorded in another level. For the multilevel variables, a reference level is selected – in our case, infants – and other levels are compared to the reference level to contextualize the effects of each level on a given behaviour. Because our main interest was the interaction between age and sex, we plotted the predicted outcomes for each age/sex class for each model using the plot_model function in the R package sjPlot. This enabled us to visualize the predicted number of behavioural or habitat use scans for each age and sex combination. Our hypothesis that niche differentiation in habitat use is constrained by foraging context (Hypothesis 4) is tested throughout these analyses. By partitioning our data into invertebrate and fruit foraging contexts, we were able to compare niche differentiation between these two major components of white-faced capuchin foraging.

All statistical analyses and data visualization were conducted in R v.4.0.0 (R Core Team, 2020) within RStudio 1.2.5042. We present plots of all raw data (Appendix 1, Fig. A1, Fig. A2), summary of our raw data (e.g. proportion of scans in each foraging behaviour per age class, Appendix 1, Tables A3–A5) and summary of models and results in the Appendices (Appendix 2, Table A6, Table A7). Data and code used in our analyses are available at https://github.com/webbshasta/NicheDifferentiation.

Ethical Note

This research adhered to the laws of Costa Rica and Canada and complied with protocols approved by the Área de Conservación Guanacaste and by the Canada Research Council for Animal Care through the University of Calgary's Life and Environmental Care Committee.

RESULTS

Hypothesis 1: Individuals Exhibit Differences in Their Activity Budgets Based on Their Ability to Access Food Items

Age class was a significant predictor of total scans spent foraging for fruit (small immature age class: estimate = 0.0460, SE = 0.200, $Z = 2.295$, $P = 0.022$; adult age class: estimate = 0.448, SE = 0.185, $Z = 2.428$, $P = 0.015$). Small immatures were recorded foraging for fruit at 1.58 times the frequency of infants, the reference age class (incidence rate ratio = 1.58, CI = 1.07–2.35, $P = 0.022$), while adults were recorded foraging for fruits at 1.57 times the frequency of infants (incidence rate ratio = 1.57, CI = 1.09–2.25, $P = 0.015$). Mean maximum temperature and mean rainfall were also significant predictors of total scans spent foraging for fruit (Appendix 2, Table A6, Table A7). The interaction effect between age and sex class was not a significant predictor of total fruit foraging scans (Appendix 2, Table A6, Table A7).

Neither age nor sex nor their interaction was significantly associated with the number of scans spent foraging on easy-to-process fruits, nor scans devoted to the ‘easier’ gleaned invertebrates. Mean maximum temperature and estimated fruit biomass were both negatively associated with the number of easy-to-process fruit scans, but these environmental variables did not have an effect on scans devoted to gleaning invertebrates (Appendix 2, Table A6, Table A7) .

Hypothesis 2: Individuals Exhibit Differences in the Use of Their Environment Based on Their Ability to Exploit Different Branch Supports

Age class was a significant predictor of small branch use during invertebrate foraging, with adults using small branches in significantly fewer scans per rotation compared to other age groups (adult age class: estimate: -0.211, SE $= 0.074$, $Z = -2.849$, $P = 0.004$). Adults used small branches during invertebrate foraging at 0.81 times the frequency of infants (incidence rate ratio $= 0.81$, CI $= 0.70-0.94$, $P = 0.004$). The interaction between age class and sex was also significant, with adult males spending significantly fewer scans in small branches (adult males: estimate: -0.215, SE $= 0.096$, $Z = -2.234$, $P = 0.023$). Adult males used small branches during invertebrate foraging at 0.81 times the frequency of infant females (the reference age/sex class) (incidence rate ratios $= 0.81$, CI $= 0.67-0.97$, $P = 0.025$; Fig. 3). No other fixed effects in the model were significantly associated with small branch use during invertebrate foraging scans (Appendix 2, Table A6, Table A7). Predicted counts of small branch use by age/sex during invertebrate foraging are visualized in Fig. 3 and show that adult males are predicted to use small branches less than all other age/sex classes. In our fruit foraging model, none of our predictors were significantly associated with the number of scans on small branches.

When we evaluated whether individuals used support substrates at different angles, we did not observe any significant differences among monkeys based on age and sex variables during either invertebrate foraging or fruit foraging. Only mean maximum temperature was a significant predictor of support substrate angle and was negatively associated with the number of vertically angled support scans during both invertebrate foraging and during fruit foraging (Appendix 2, Table A6, Table A7).

Hypothesis 3: Individuals Exhibit Differences in Their Use of Different Forest Strata Based on Their Relative Predation Risk

We found no differences attributable to age or sex or their interaction in scans spent in the upper canopy for either invertebrate or fruit foraging. However, environmental variables did have an impact. Mean maximum temperature was significantly negatively associated with upper canopy use in both fruit and invertebrate foraging (Appendix 2, Table A6, Table A7). Rainfall and monthly fruit biomass had significant effects on scans spent in the upper canopy; however, the effects were small and inconsistent across invertebrate versus fruit foraging (Appendix 2, Table A6, Table A7).

The interaction between age and sex class was a significant predictor of ground use scans during invertebrate foraging. Female use of the ground did not clearly change with age class, while male ground use steadily increased (Fig. 4). Large immature males and adult males used the ground in significantly more scans per rotation compared to infant females (the reference age/sex class) (large immature male: estimate: 1.86, SE $= 0.876$, $Z = 2.123$, $P = 0.034$; adult male: estimate $= 1.869$, SE $= 0.806$, $Z = 2.32$, $P = 0.020$; Fig. 4). Large immature males foraged on the ground during invertebrate foraging at 6.42 times the frequency of infant females, the reference age/sex class (incidence rate ratios $= 6.42$, CI $= 1.15-35.78$, $P = 0.034$). Adult males foraged on the ground during invertebrate foraging at 6.48 times the frequency of infant females (incidence rate ratios $= 6.48$, CI $= 1.34-31.44$, $P = 0.020$). Environmental variables, including rainfall and temperature, were also positively related to the number of scans where ground locations were used during invertebrate foraging (Appendix 2, Table A6, Table A7). Predicted outcomes of ground use during invertebrate foraging are visualized in Fig. 4.

We attempted to explore ground use during fruit foraging, as there is a small number of fruit species that capuchins access from the ground, including the two bromeliad species, *Bromelia plumieri* and *Bromelia pinguin*. Due to the rarity of ground use during fruit foraging (and a heavily 0-inflated data set), we were forced to run a simpler model to explore this prediction by removing the ecological variables. While the simple model did converge, the standard errors were too large to visualize. Accordingly, we feel the analysis is of limited use but we include the model output in Appendix 2 (Table A6, Table A7).

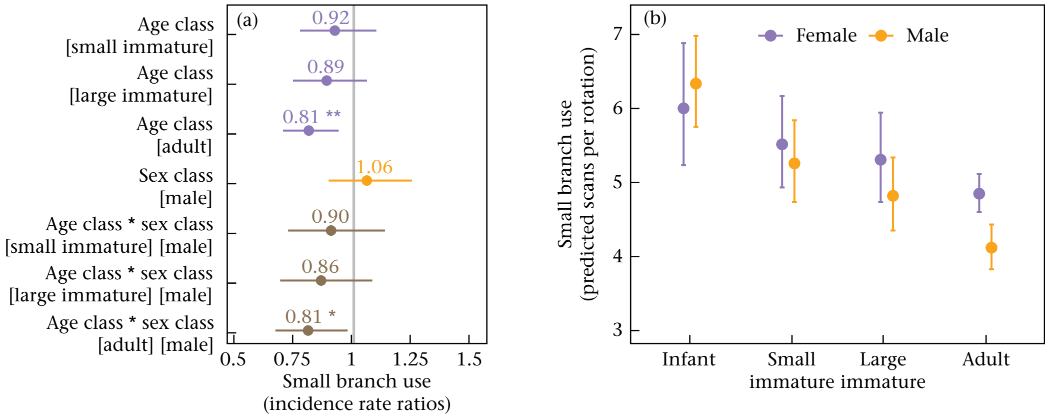

Figure 3. (a) Incidence rate ratios (IRR) and standard error for age and sex variables derived from GLMMs of scans involving small branch substrates during invertebrate foraging. The reference sex class is female, and the reference age class is infants. The vertical grey line represents ‘no effect’. IRR values to the left of the grey line represent negative effects, while values to the right represent positive effects. Significant predictors ($P < 0.05$) are denoted with asterisks. (b) We present an alternative way to visualize the interaction between age and sex classes by plotting the predicted number of small branch scans during invertebrate foraging for each level of our age and sex interaction.

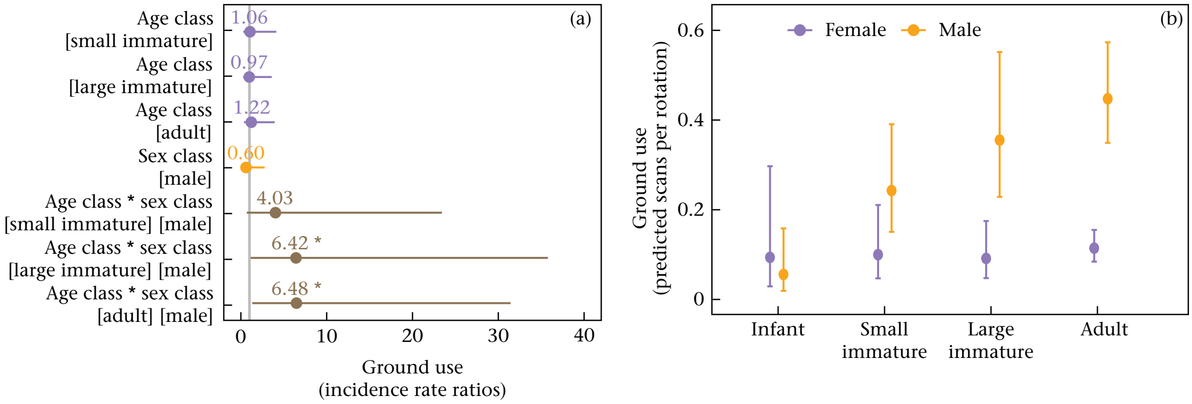

Figure 4. (a) Incidence rate ratios (IRR) and standard error for age and sex variables derived from GLMMs of scans involving ground use during invertebrate foraging. The reference sex class is female, and the reference age class is infants. The vertical grey line represents 'no effect'. IRR values to the left of the grey line represent negative effects, while values to the right represent positive effects. Significant predictors ($P < 0.05$) are denoted with asterisks. (b) We present an alternative way to visualize the interaction between age and sex classes by plotting the predicted number of ground use scans during invertebrate foraging for each level of our age and sex interaction.

Hypothesis 4: The Extent of Niche Differentiation in Habitat Use Varies When Foraging on Different Types of Food

Variation in the use of branch supports and forest strata was more extensive and prevalent during invertebrate foraging than during fruit foraging. Our models revealed that age/sex class was not clearly associated with habitat use during fruit foraging (i.e. the use of small branches, vertically angled branches or the upper canopy or ground). Conversely, during invertebrate foraging, differences across age/sex classes emerged, specifically in use of small branches and time spent foraging on the ground.

DISCUSSION

Revealing the patterns of intraspecific niche differentiation and evaluating the conditions in which it occurs can improve the broader understanding of the dynamics, costs and benefits of group living. Here we studied the activity budgets and patterns of habitat use of four social groups of individually identified, wild capuchin monkeys. Our aim was to assess the potential for foraging niche differentiation as a mechanism for reducing intraspecific competition in a social species with relatively cohesive grouping patterns. We analysed a robust data set of >15 000 foraging scan samples collected over 13 months. Our primary findings are three-fold: (1) individuals of smaller body size – juveniles and females – used smaller branch supports more often during invertebrate foraging than did adults and males; (2) smaller individuals were recorded less often on the ground, i.e. the area associated with the highest risk of predation; (3) differentiation in habitat use via the support substrates and the forest strata used was greater during invertebrate foraging than during fruit foraging, which may indicate constraints of frugivory on habitat partitioning. Overall, we found niche differentiation attributable to age and sex, which likely reflects the impacts of size and relative predation risk on individual foraging choices. Such differences may contribute to a reduction in intraspecific feeding competition by promoting different food acquisition strategies. We discuss the significance of these results with respect to our hypotheses below.

Individuals Do Not Exhibit Differences in Their Activity Budgets Based on Their Ability to Access Food Items

We did not observe evidence of smaller individuals spending more time on easier-to-access foods than did larger individuals, i.e. foraging for easy (versus difficult) fruit or for gleaned (versus embedded) invertebrates. Our data suggest that small immature capuchins forage on all or most fruit species in their dietary repertoire (demonstrating that difficult fruits are accessible to young, inexperienced monkeys). This pattern is broadly consistent with reports that capuchins across age classes have similar diets (MacKinnon, 2006). Given our use of scan data, we examined gross-scale time budgets and cannot directly speak to the issue of foraging competency; however, previous research using continuous focal animal follows (Eadie, 2015; Visalberghi et al., 2016) and experimental evidence (Barrett, McElreath, & Perry, 2017) have found that juvenile capuchins take many years to reach adult level foraging competency and/or demonstrate the most efficient processing techniques – particularly for food items that require complex manual/oral processing. While we did not observe niche differentiation in broad foraging activity budgets, our result provides different insight. Our results may reflect constraints imposed by travelling and foraging in a cohesive group, which likely limits the opportunities for individual capuchins to choose between different food items at any given time. Emerging evidence shows the cost of group living on individual decision making (Conradt & Roper, 2005; Tórrez-Herrera, Davis, & Crofoot, 2020), and synchronous behaviour may be an expression of this constraint (red deer, *Cervus elaphus*: Conradt, 1998; coatis, *Nasua nasua*: Gompper, 1996; ungulates: Ruckstuhl & Neuhaus, 2000; kiang, *Equus kiang*: St-Louis & Côté, 2017; Vickery, Giraldeau, Templeton, Kramer, & Chapman, 1991).

Individuals Exhibit Differences in the Use of Their Environment Based on Their Ability to Exploit Different Branch Supports

Due to differences in joint loading and manoeuvrability, we predicted that during foraging, smaller individuals would use vertically angled branches and smaller branches to support their body weight more frequently than larger individuals. We did not find evidence that monkeys of different age/sex classes selected branches based on their relative angles. However, we did find support for the branch size prediction: during invertebrate foraging, all age/sex classes used small branches more often than adult males, and large immature males were also observed using small branches less than the remaining age/sex classes. While this pattern lends support to our prediction that body size affects branch size selection, these differences may additionally arise from male and female patterns of associations and social behaviour, wherein juvenile males spend more time in proximity to adult males and juvenile females spend more time in proximity to adult females. This interesting idea is supported by evidence suggesting that an individual's social environment can have profound effects on their foraging behaviour (Barrett et al., 2017; Galef & Laland, 2005; van de Waal, Borgeaud, & Whiten, 2013). Sex biases in association patterns have been suggested to drive the development of sex-typical foraging strategies in immature tufted capuchins, *Sapajus nigritus*, (Agostini & Visalberghi, 2005). Juveniles of other species also demonstrate a preference for associating with individuals of the same sex (bottlenose dolphins, *Tursiops aduncus*: Krzyszczyk, Patterson, Stanton, & Mann, 2017; spider monkeys, *Ateles geoffroyi*: Rodrigues, 2014; pheasants, *Phasianus colchicus*: Whiteside et al., 2017). It is conceivable, then, that sex differences in association patterns could result in sex-specific differences in habitat use during foraging, including branch support use, and may subsequently contribute to a broader pattern of intraspecific niche differentiation.

Individuals Exhibit Differences in Their Use of Different Forest Strata Based on Their Relative Predation Risk

As with many animals, smaller individuals appear to face higher predation risk (passerines: Andreasson, Nord, & Nilsson, 2019; hoary marmot, *Marmota caligata*: Holmes, 1984; ground squirrels *(Spermophilus spp.)*: Matrosova, Volodin, Volodina, & Babitsky, 2007; broad-headed snakes, *Hoplocephalus bungaroides*: Webb & Whiting, 2005), and our results are consistent with other observations of predation-sensitive foraging patterns in platyrrhine primates (Campos & Fedigan, 2014; Rose & Fedigan, 1995; Stone, 2007). We found that smaller capuchins were recorded on the ground less often, while the largest monkeys, adult males, were recorded to forage there most often. This stratum is widely thought to be more exposed to predators in SSR, and previous research on SSR capuchins has shown that alarm calls directed towards snakes and terrestrial predators (‘alerting calls’, Digweed, 2005), are more frequent near or on the ground (Campos & Fedigan, 2014). While this study also found that alarm call types typically given in response to raptors flying overhead (‘aerial predator alarms’, Digweed, 2005) generally originate from higher in the forest strata (both in terms of absolute height and relative height in the vegetation layer) (Campos & Fedigan, 2014), we did not find strong evidence that smaller individuals avoid the upper canopy during foraging. The presence of fruit or invertebrate resources in the upper canopy may outweigh the potential risk of avian predators. This is consistent with similar findings in closely related squirrel monkeys *(S. sciureus)* (Stone, 2007). Perhaps smaller individuals avoid the upper canopy during other behaviours, such as travelling and social behaviours, however, our study was focused only on habitat use during foraging behaviours. Given that it is more difficult to locate small primates in the upper canopy, especially when trees are fully foliated, data collection biases may have obscured an effect. However, the canopy height in Sector Santa Rosa is typically rather low (<20 m), so we do not anticipate a strong impact of low visibility. Our result that adult males, the largest age/sex class, used the ground most often is also consistent with predator-sensitive foraging. Surprisingly, juvenile males also used the ground more than the similar-sized females in their age cohort. As with small branch use discussed above, the patterns observed in the current study may indicate the emergence of sex-specific habitat use early in development.

The Extent of Niche Differentiation in Habitat Use Varies When Foraging on Different Types of Food

As we predicted, variation in the use of branch supports and forest strata was more extensive and prevalent during invertebrate foraging than during fruit foraging. It is perhaps unsurprising that foraging on different types of food items affects capuchins’ ability to use parts of their habitat given the constraints in time and space associated with harvesting fruit. Invertebrates are found throughout the vertical and horizontal surfaces in the forest and are eaten by capuchins in SSR at all canopy heights, even though capture efficiency is highest on the forest floor (Melin et al., 2007, 2010; Rose, 1994).

Trees fruit periodically and, while branch sizes vary, individual tree canopies are relatively homogeneous with respect to the forest more generally. In SSR, intragroup competition during fruit foraging may be especially high because many fruit trees are small and can support only one to three individuals at a time (Melin, Young et al., 2014). A number of studies on capuchin monkeys have observed that as more individuals attempt to feed in the same fruit patch, the rate of agonism increases, highlighting the costs associated with resource competition in this taxon (Phillips, 1995a; Vogel, 2005; Vogel & Janson, 2007). Our result that niche differentiation in space use is constrained during fruit foraging has important implications for intragroup feeding competition, as group-living species may face selection pressure to develop alternative strategies for reducing competition among group members. For example, such pressures have likely contributed to the repeated evolution of fission–fusion grouping patterns in frugivorous species, which includes spider monkeys (*Ateles* sp.) and chimpanzees, *Pan troglodytes* (Symington, 1990). In group-living species that exhibit high fission–fusion dynamics, variable foraging parties break away from the main group and change in size and composition throughout the day, which has long been predicted to be a mechanism for reducing intragroup feeding competition (Aureli et al., 2008; Koenig, Scarry, Wheeler, & Borries, 2013; Pinacho-Guendulain & Ramos-Fernández, 2017). While capuchins in our study remained cohesive, there is evidence that at least some capuchin monkeys exhibit flexible foraging and grouping patterns (Phillips, 1995b). For example, during a period of low fruit availability, Izar (2004) observed that social groups of tufted capuchins in the Brazilian Atlantic forest fissioned into smaller subgroups that foraged and slept separately, only to rejoin more cohesively several months later. Future studies examining grouping behaviour in such typically cohesive, but occasionally flexible, species may provide further insight regarding the evolution of fission–fusion versus cohesive systems.

Limitations and Future Directions

Our study has several limitations, one being that, because we chose to analyse our data using coarse age/sex classes, we did not assess differences within each age/sex group. For example, the increased energetic demands of pregnancy and lactation can impact foraging behaviours and lead to foraging differences between cycling, gestating or lactating females (mouflans, *Ovis gmelini*: Bourgoin, Marchand, Hewison, Ruckstuhl, & Garel, 2018; plains zebras, *Equus quagga*: Neuhaus & Ruckstuhl, 2002; squirrel monkeys *(Saimiri collinsi)*: Ruivo, Stone, & Fienup, 2017; Weddell seal, *Leptonychotes weddellii*: Shero, Goetz, Costa, & Burns, 2018). In white-faced capuchins, reproduction has been found to drive differences in the foraging behaviour of females, where lactating females consume a higher number of food items during periods of foraging (McCabe & Fedigan, 2007). The impact of reproduction on foraging and habitat choices in long-lived organisms is best addressed using a longitudinal data set tracking a large sample of adult females across different reproductive stages (Altmann, Gesquiere, Galbany, Onyango, & Alberts, 2010). Future work in SSR and at other field sites will hopefully make this ambitious endeavour possible. In addition, we do not examine the capacity for differentiation within age/sex classes due to individual specialization (which has been observed in other generalist foragers such as sea otters, *Enhydra lutris*: Fujii, Ralls, & Tinker, 2017; Tinker, Costa, Estes, & Wieringa, 2007). Furthermore, future long-term studies focusing on intraspecific niche differentiation would benefit from gathering and incorporating more data on sex differences in infant and juvenile foraging behaviour. This would allow an understanding of niche differentiation through a developmental lens, with a focus on the ontogeny of sex-specific foraging patterns.

Conclusions

Capuchins are the largest-brained monkeys, and approximately half of their day is devoted to foraging and fuelling their metabolic needs (McCabe, 2005; Melin, Fedigan, Hiramatsu, & Kawamura, 2008). Finding sufficient food may be particularly difficult in tropical dry forests, which undergo strong seasonal fluctuations in food abundance, and marked lean seasons that can lead to negative energy balance and high infant mortality (Bergstrom, Thompson, Melin, & Fedigan, 2017; Campos et al., 2020; Orkin et al., 2019, 2021). Our findings support and extend previous work in other taxa demonstrating foraging strategies of this cohesive, group-living species include variability in microhabitat choice between members of the same species (fish: Gratwicke, Petrovic, & Speight, 2006; amphibians: Da Silva Neto, Sutton, & Freake, 2019; reptiles: Delaney & Warner, 2016; Montgomery, Lips, & Ray, 2011; Stamps, 1983; birds: Gall, Hough, & Fernández-Juricic, 2013; Phillips, Silk, Phalan, Catry, & Croxall, 2004; mammals: Beerman, Ashe, Preedy, & Williams, 2016; Safi, König, & Kerth, 2007). We also contribute new insight on a facet of niche differentiation not commonly explored: the limitations of food type, i.e. fruit versus invertebrate foraging, on the capacity for differentiating habitat use. We find greater variation in space use during invertebrate foraging, which also highlights the potential for further individual specialization. Taken together, our results support the hypothesis of niche differentiation as a mechanism for lowering intragroup feeding competition and also highlight important constraints in the ability of individuals living in cohesive social groups to occupy different spaces or diverge in diet.

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Appendix 1

Table A1

Group composition for each of the four study groups during each period of data collection

Group	Age/sex class	No. of individuals	
		2016	2017
AD	Infant female	0–1	2–3
	Infant male	0	1–4
	Small immature female	1	1
	Small immature male	1	1
	Large immature female	1–0	0
	Large immature male	2–1	1
	Adult female	7	6
	Adult male	5	5–4
	Total	**17–16**	**17–20**
GN	Infant female	0	0–3
	Infant male	1–2	2–4
	Small immature female	4	3–2
	Small immature male	1	2
	Large immature female	5	6
	Large immature male	1	1
	Adult female	8	8
	Adult male	2	2–3
	Total	**22–23**	**24–29**
LV	Infant female	0	0–2
	Infant male	0	1–3
	Small immature female	2	2
	Small immature male	1	1
	Large immature female	2	1
	Large immature male	2–3	2
	Adult female	7	8–7
	Adult male	8	8–7
	Total	**22–23**	**23–25**
RM	Infant female	0–2	2–4
	Infant male	0–2	2–3
	Small immature female	1	1
	Small immature male	4	3
	Large immature female	3	2
	Large immature male	3	4
	Adult female	7	8
	Adult male	8	8
	Total	**26–30**	**30–33**

Table A2

We observed capuchins eating 53 fruit species over the course of our two study periods and classified each fruit as either easy or difficult based on their physical properties and the intensity of manual and/or oral processing they require during foraging

Family	Species	Elastic modulus (MPa)	Tough exocarp (yes/no)	Husk cracking (yes/no)	Dehiscent (yes/no)	Classification
Anacardiaceae	*Spondias mombin*	–	No	No	No	Easy
Anacardiaceae	*Spondias purpurea*	–	No	No	No	Easy
Annonaceae	*Annona reticulata*	3.281	Yes	Yes	No	Difficult
Annonaceae	*Sapranthus palanga*	–	No	No	No	Easy
Annonaceae	*Sciadodendron excelsum*	0.496	No	No	No	Easy
Apocynaceae	*Stemmadenia obovata*	–	Yes	Yes	Yes	Difficult
Arecaceae	*Acrocomia aculeata*	–	Yes	Yes	Yes	Difficult
Bignoniaceae	*Tabebuia ochracea*	–	No	Yes	No	Easy
Boraginaceae	*Cordia guanacastensis*	0.062	No	No	No	Easy
Bromeliaceae	*Bromelia pinguin*	2.796	Yes	Yes	No	Difficult
Bromeliaceae	*Bromelia plumieri*	3.126	No	Yes	No	Difficult
Burseraceae	*Bursera simaruba*	–	Yes	Yes	Yes	Difficult
Cactaceae	*Hylocereus costaricensis*	–	Yes	Yes	No	Difficult
Chrysobalanaceae	*Hirtella racemosa*	0.082	No	No	No	Easy
Connaraceae	*Rourea glabra*	–	No	No	Yes	Easy
Dilleniaceae	*Curatella americana*	–	No	No	Yes	Easy
Dilleniaceae	*Davila kunthii*	–	No	No	Yes	Easy
Dilleniaceae	*Doliocarpus dentatus*	–	No	Yes	Yes	Easy
Elaeocarpaceae	*Sloanea ternifolia*	–	Yes	Yes	Yes	Difficult
Erythroxyaceae	*Erythroxylon havanense*	0.039	No	No	No	Easy
Fabaceae	*Vachellia collinsii*	–	No	Yes	Yes	Easy
Fagaceae	*Quercus oleoides*	–	Yes	Yes	No	Easy
Malpighiaceae	*Byrsonima crassifolia*	0.704	No	No	No	Easy
Malvaceae	*Malvaviscus arboreus*	0.588	No	No	No	Easy
Melastomatacea	*Miconia argentea*	–	No	No	No	Easy
Moraceae	*Ficus cotinifolia*	–	No	No	No	Easy
Moraceae	*Ficus goldmanii*	–	No	No	No	Easy
Moraceae	*Ficus hondurensis*	–	No	No	No	Easy
Moraceae	*Ficus obtusifolia*	0.195	No	No	No	Easy
Moraceae	*Ficus ovalis*	–	No	No	No	Easy
Moraceae	*Maclura tinctoria*	–	No	No	No	Easy
Moraceae	*Trophis racemosa*	0.075	No	No	No	Easy
Poaceae	*Lasiacis sorghoidea*	–	No	No	No	Easy
Rhamnaceae	*Karwinskia caldronii*	0.882	No	No	No	Easy
Rubiaceae	*Alibertia edulis*	2.539	No	No	No	Easy
Rubiaceae	*Genipa americana*	0.463[a]	Yes	Yes	No	Difficult
Rubiaceae	*Guettarda macrosperma*	–	No	No	No	Easy
Rubiaceae	*Randia monantha*	–	Yes	Yes	No	Difficult
Rubiaceae	*Randia thurberi*	–	No	No	No	Easy
Salicaceae	*Casearia arguta*	–	Yes	Yes	No	Difficult
Salicaceae	*Casearia sylvestris*	–	No	No	No	Easy
Salicaceae	*Xylosma flexuosa*	–	No	No	No	Easy
Salicaceae	*Zuelania guidonia*	–	Yes	Yes	Yes	Difficult
Sapindaceae	*Allophylus occidentalis*	–	No	No	No	Easy
Sapindaceae	*Dipterodendron costaricensis*	–	Yes	No	Yes	Easy
Sapindaceae	*Paullinia cururu*	–	No	No	Yes	Easy
Sapotaceae	*Manilkara chicle*	2.033	No	No	No	Easy
Simaroubaceae	*Simarouba glauca*	0.5254	No	No	No	Easy
Theophrastaceae	*Jacquinia pungens*	–	Yes	Yes	No	Difficult
Tiliaceae	*Apeiba tibourbou*	–	Yes	Yes	No	Difficult
Tiliaceae	*Luehea candida*	–	Yes	No	Yes	Difficult
Tiliaceae	*Luehea speciosa*	–	Yes	Yes	Yes	Difficult
Tiliaceae	*Muntingia calabura*	–	No	No	No	Easy

[a] Values are from overripe fruit and underestimate the elastic modulus of ripe fruit.

Table A3

Summary of proportion of scans spent foraging and proportions of scans spent foraging on fruit, invertebrates and nonfruit, noninvertebrate items (‘other’)

Age/sex class	Fruit foraging	Invertebrate foraging	Other foraging	Total foraging
Infant female	0.09	0.90	<0.01	0.21
Infant male	0.08	0.91	<0.01	0.23
Small immature female	0.14	0.84	0.02	0.65
Small immature male	0.14	0.84	0.01	0.65
Large immature female	0.13	0.86	0.02	0.62
Large immature male	0.15	0.83	0.02	0.60
Adult female	0.14	0.83	0.03	0.55
Adult male	0.13	0.84	0.03	0.52

Table A4
Summary of substrate use during fruit foraging

Age/sex class	Substrate use								
	Ground	Lower canopy	Mid-canopy	Upper canopy	Small branch	Medium branch	Large branch	Horizontal substrate	Vertical substrate
Infant female	<0.01	0.04	0.73	0.23	0.88	0.12	<0.01	0.48	0.52
Infant male	0.02	0.09	0.47	0.42	0.90	0.10	<0.01	0.52	0.48
Small immature female	0.01	0.10	0.73	0.17	0.84	0.15	0.01	0.50	0.50
Small immature male	0.05	0.22	0.50	0.22	0.88	0.11	0.01	0.59	0.41
Large immature female	0.03	0.07	0.69	0.21	0.88	0.12	<0.01	0.59	0.41
Large immature male	0.03	0.13	0.59	0.25	0.79	0.18	0.03	0.56	0.44
Adult female	0.03	0.10	0.56	0.31	0.82	0.17	0.01	0.59	0.41
Adult male	0.03	0.09	0.54	0.33	0.79	0.18	0.03	0.58	0.42

All values are proportions of scans.

Table A5
Summary of substrate use during invertebrate foraging

Age/sex class	Substrate use								
	Ground	Lower canopy	Mid-canopy	Upper canopy	Small branch	Medium branch	Large branch	Horizontal substrate	Vertical substrate
Infant female	0.01	0.03	0.73	0.23	0.80	0.16	0.04	0.48	0.52
Infant male	0.01	0.09	0.72	0.19	0.85	0.12	0.03	0.51	0.49
Small immature female	0.02	0.13	0.69	0.15	0.74	0.21	0.05	0.48	0.52
Small immature male	0.06	0.17	0.63	0.14	0.70	0.24	0.06	0.45	0.55
Large immature female	0.02	0.13	0.71	0.13	0.71	0.23	0.06	0.45	0.55
Large immature male	0.06	0.17	0.58	0.19	0.64	0.27	0.08	0.48	0.52
Adult female	0.02	0.10	0.63	0.26	0.65	0.30	0.05	0.49	0.51
Adult male	0.08	0.14	0.59	0.20	0.55	0.37	0.08	0.48	0.52

All values are proportions of scans.

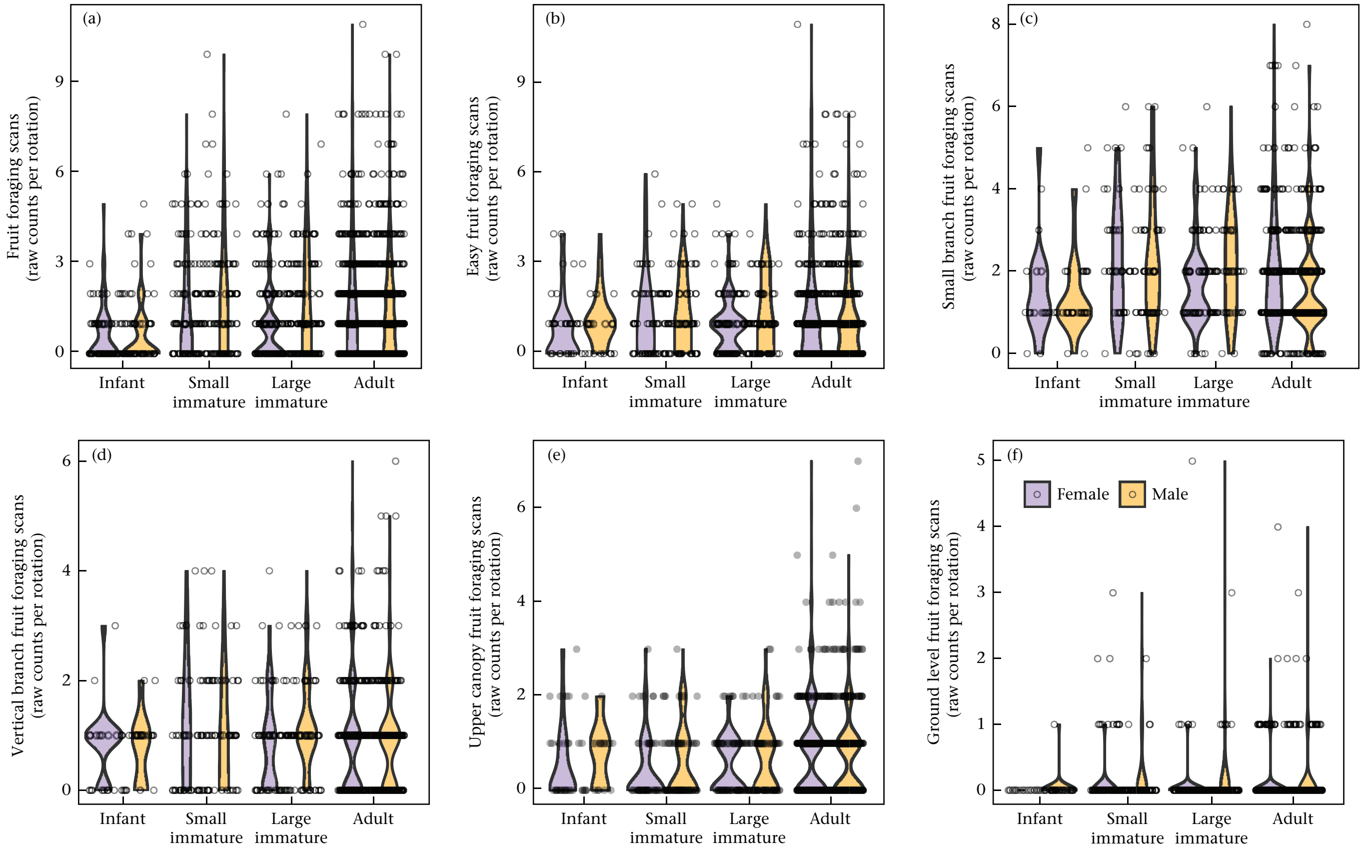

Figure A1. We plotted raw scan counts per rotation of (a) all fruit foraging, (b) easy fruit foraging, (c) small branch use during fruit foraging, (d) vertical branch use during fruit foraging, (e) upper canopy use during fruit foraging and (f) ground level use during fruit foraging. Circles represent raw scan counts per individual per rotation overlaid on violin plots. Age classes are plotted along the *X* axis.

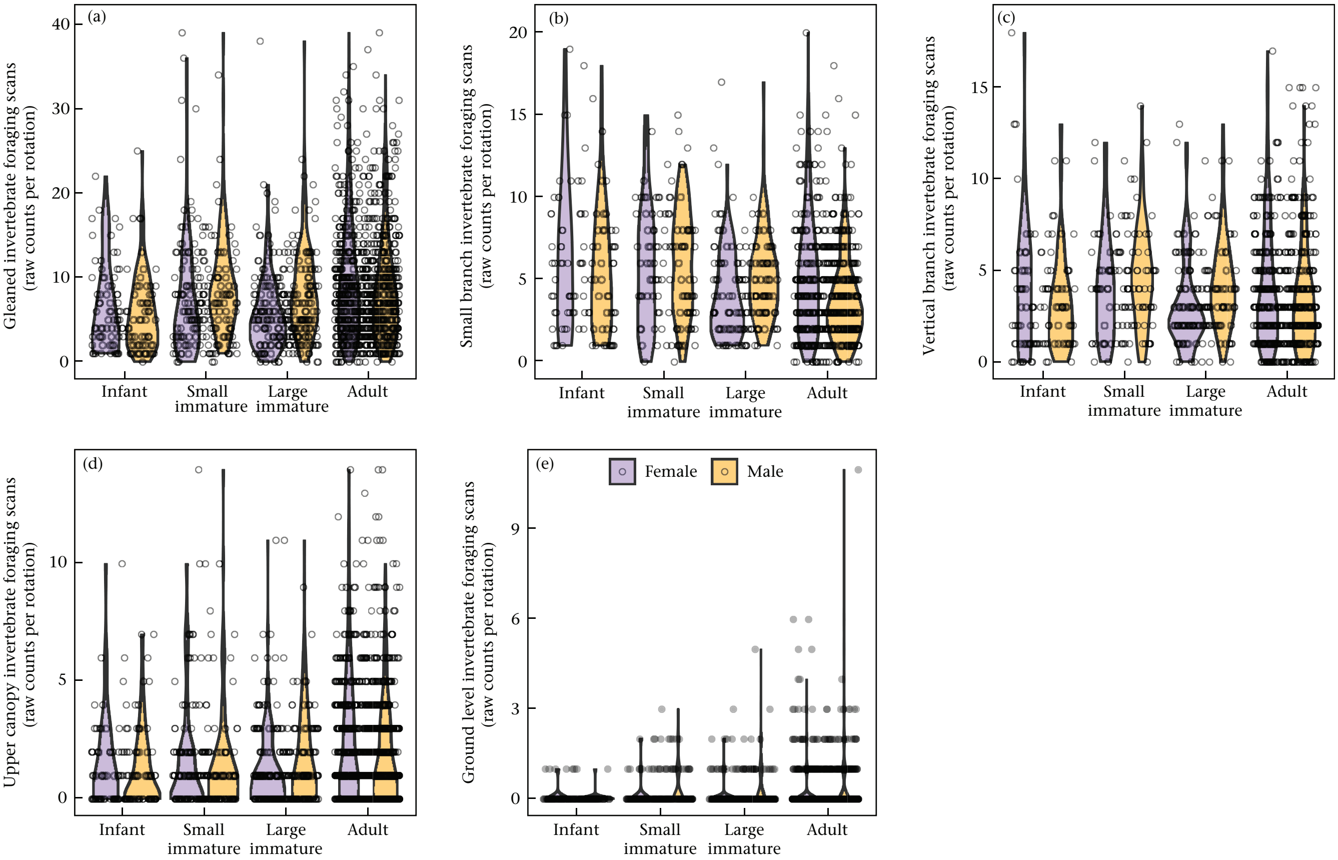

Figure A2. We plotted raw scan counts per rotation of (a) all invertebrate foraging, (b) small branch use during invertebrate foraging, (c) vertical branch use during invertebrate foraging, (d) upper canopy use during invertebrate foraging and (e) ground level use during invertebrate foraging. Circles represent raw scan counts per individual per rotation overlaid on violin plots. Age classes are plotted along the *X* axis.

Appendix 2

Summary of Hypotheses, Predictions, Data sets, Generalized Linear Mixed Models and Results from All Models Run in the Analysis

To test whether individuals differ in behaviour based on their ability to access foods (Hypothesis 1), we fitted two GLMMs. To test our prediction that smaller individuals, i.e. juveniles and females, spend relatively more time foraging for soft rather than hard-to-access fruits, our first model included scans in which easy fruits were processed as the response variable. To test our prediction that smaller individuals spend relatively more time foraging for gleaned invertebrates rather than invertebrates extracted from substrates, our second model included scans in which invertebrates were gleaned as the response variable. Both models included age/sex class, mean maximum temperature and mean rainfall as predictors. We calculated incidence rate ratios for each predictor to understand the size of each effect in the model. To understand how our models predicted interaction effects, we visualized predicted outcomes of our response variable.

To evaluate whether individuals differ in use of their environment based on their ability to use different supports (Hypothesis 2), we fitted a series of GLMMs with branch use and substrate angle as response variables. We first split our data into an invertebrate foraging data set and a fruit foraging data set. To test our prediction that smaller individuals, i.e. juveniles and females, spend more time using smaller/thinner substrates during invertebrate foraging, we fitted a GLMM with small branch use as the response variable and the same predictor variables as listed previously. We repeated this model with the fruit foraging data. To test our prediction that smaller individuals use more vertically angled substrates during invertebrate foraging, we fitted a similar model, except with vertical substrate use scans as the response variable. We repeated this model with the fruit foraging data.

We examined whether individuals differ in the use of different forest strata based on relative predation risk using a similar approach (Hypothesis 3). To examine our prediction that smaller individuals spend less time foraging on the ground or in the upper canopy, areas that potentially increase predation risk, we fitted a series of GLMMs. First, we fitted a model with upper canopy use during arboreal invertebrate foraging as the response variable and previously described variables as predictors. We then repeated this model but with upper canopy use during arboreal fruit foraging. Second, we fitted a model with ground use during invertebrate foraging as the response variable. Finally, to examine ground use differences across age/sex classes during fruit foraging, we fitted a final model with ground use during fruit foraging as response variable.

Table A6
Reults from generalized linear mixed models

Hypothesis/Prediction	Generalized linear mixed model	Results	Estimate	SE	Z	P
Hypothesis 1						
Smaller individuals, i.e. juveniles and females, will spend relatively more time foraging for fruit than larger individuals, i.e. males, adults	glmmTMB(FruitScans ~ AdjustedAge + SexClass + (AdjustedAge*SexClass) + MeanTempMax + MeanRainfall + MonthlyFruitBiomass_kg_ha + offset(log(TotalForagingScans)) + (1 | Animal), data = df.overallStates, ziformula=~0, family = poisson)	(Intercept)	−2.427976	0.181348	−13.388	<2e-16
		AdjustedAgesmall immature	**0.460263**	**0.200545**	**2.295**	**0.02173**
		AdjustedAgelarge immature	0.288395	0.200638	1.437	0.150608
		AdjustedAgeadult	**0.448254**	**0.18463**	**2.428**	**0.015189**
		SexClassmale	−0.091758	0.228317	−0.402	0.687767
		MeanTempMax	**0.29048**	**0.027827**	**10.439**	**<2e-16**
		MeanRainfall	**0.132538**	**0.037741**	**3.512**	**0.000445**
		MonthlyFruitBiomass_kg_ha	−0.007381	0.022775	−0.324	0.745865
		AdjustedAgesmall immature:SexClassmale	0.082148	0.254854	0.322	0.7472
		AdjustedAgelarge immature:SexClassmale	0.331958	0.253886	1.308	0.191041
		AdjustedAgeadult:SexClassmale	0.03589	0.235179	0.153	0.878708
Smaller individuals will spend relatively more time foraging for soft, rather than hard-to-access, fruits	glmer(EasyFruitScans ~ AdjustedAge + SexClass + AdjustedAge*SexClass + MeanTempMax + MeanRainfall + MonthlyFruitBiomass_kg_ha + offset(log(TotalFruitScans)) + (1 | Animal), data = dfh1.difficulty, family = poisson(link = "log"))	(Intercept)	−0.73264	0.25839	−2.835	0.00458
		AdjustedAgesmall immature	0.10644	0.28441	0.374	0.70823
		AdjustedAgelarge immature	0.06399	0.28428	0.225	0.82192
		AdjustedAgeadult	0.20634	0.26237	0.786	0.43159
		SexClassMale	0.35444	0.30792	1.151	0.2497
		MeanTempMax	**−0.06653**	**0.03282**	**−2.027**	**0.04264**
		MeanRainfall	−0.06082	0.04452	−1.366	0.17188
		MonthlyFruitBiomass_kg_ha	**−0.14875**	**0.03456**	**−4.304**	**1.67E-05**
		AdjustedAgesmall immature:SexClassMale	−0.39937	0.3465	−1.153	0.24908
		AdjustedAgelarge immature:SexClassMale	−0.3487	0.34385	−1.014	0.31054
		AdjustedAgeadult:SexClassMale	−0.46348	0.31714	−1.461	0.14389
Smaller individuals will spend relatively more time foraging for gleaned invertebrates rather than invertebrates extracted from within substrates	glmer(GleanedInvertebrateScans ~ AdjustedAge + SexClass + (AdjustedAge*SexClass) + MeanTempMax + MeanRainfall + MonthlyFruitBiomass_kg_ha + offset(log(TotalInvertebrateScans)) + (1 | Animal), data = dfh1.invertebrates, family = poisson(link = "log"))	(Intercept)	−0.07967	0.05979	−1.332	0.1827
		AdjustedAgesmall immature	−0.12372	0.07124	−1.736	0.0825
		AdjustedAgelarge immature	−0.0985	0.06975	−1.412	0.1579
		AdjustedAgeadult	−0.02091	0.06163	−0.339	0.7344
		SexClassmale	0.01842	0.07396	0.249	0.8034
		MeanTempMax	0.0132	0.01232	1.071	0.2841
		MeanRainfall	−0.02084	0.01601	−1.302	0.193
		MonthlyFruitBiomass_kg_ha	−0.01138	0.0102	−1.116	0.2643
		AdjustedAgesmall immature:SexClassmale	−0.01471	0.08972	−0.164	0.8698
		AdjustedAgelarge immature:SexClassmale	−0.01663	0.08822	−0.188	0.8505
		AdjustedAgeadult:SexClassmale	−0.03925	0.07761	−0.506	0.613
Hypothesis 2						
Invertebrate foraging						
Smaller individuals will spend more time using smaller/thinner substrates	glmer(SmallBranch ~ AdjustedAge + SexClass + (AdjustedAge*SexClass) + MeanRainfall + MeanTempMax + MonthlyFruitBiomass_kg_ha + offset(log(TotalInvertebrate ForagingBranchUseScans)) + 1 | Animal), data = supportDF.invertebrates, family = poisson(link = "log"))	(Intercept)	−0.22245	0.06946	−3.203	0.00136
		AdjustedAgesmall immature	−0.08376	0.08936	−0.937	0.34859
		AdjustedAgelarge immature	−0.12191	0.08993	−1.356	0.17522
		AdjustedAgeadult	**−0.21148**	**0.07423**	**−2.849**	**0.00439**
		SexClassmale	0.05374	0.08494	0.633	0.52697
		MeanRainfall	−0.01288	0.04557	−0.283	0.77739
		MeanTempMax	0.01403	0.0201	0.698	0.4852
		MonthlyFruitBiomass_kg_ha	0.01624	0.03088	0.526	0.59893
		AdjustedAgesmall immature:SexClassmale	−0.10119	0.11492	−0.881	0.37858
		AdjustedAgelarge immature:SexClassmale	−0.14924	0.11467	−1.301	0.19311
		AdjustedAgeadult:SexClassmale	**−0.21512**	**0.09628**	**−2.234**	**0.02546**

(*continued on next page*)

Table A6 (*continued*)

Hypothesis/Prediction	Generalized linear mixed model	Results	Estimate	SE	*Z*	*P*
Fruit foraging						
	glmer(SmallBranch ~ AdjustedAge + SexClass + (AdjustedAge*SexClass) + MeanRainfall + MeanTempMax + MonthlyFruitBiomass_kg_ha + offset(log(TotalFruitForaging BranchUseScans)) + (1 | Animal), data = supportDF.fruit, family = poisson(link = "log"))	(Intercept)	−0.1136545	0.2135212	−0.532	0.595
		AdjustedAgesmall immature	0.0464409	0.2395618	−0.194	0.846
		AdjustedAgelarge immature	0.014558	0.2395957	0.061	0.952
		AdjustedAgeadult	−0.0696859	0.2188649	−0.318	0.75
		SexClassmale	0.0237292	0.2681286	0.088	0.929
		MeanRainfall	−0.0009442	0.0709868	−0.013	0.989
		MeanTempMax	−0.0387095	0.0346473	−1.117	0.264
		MonthlyFruitBiomass_kg_ha	0.0609086	0.0511861	1.19	0.234
		AdjustedAgesmall immature:SexClassmale	0.0300125	0.3053166	0.098	0.922
		AdjustedAgelarge immature:SexClassmale	−0.1394311	0.3031814	−0.46	0.646
		AdjustedAgeadult:SexClassmale	−0.0591029	0.2793372	−0.212	0.832
Invertebrate foraging						
Smaller individuals will spend more time using more vertically angled substrates	glmer(VerticalScans ~ AdjustedAge + SexClass + (AdjustedAge*SexClass) + MeanRainfall + MeanTempMax + MonthlyFruitBiomass_kg_ha + offset(log(TotalInvertebrate ForagingBranchUseScans)) + (1 | Animal), data = supportDF.invertebrates, family = poisson(link = "log"))	(Intercept)	−0.6349128	0.0861174	−7.373	1.67E-13
		AdjustedAgesmall immature	−0.0060136	0.1090773	−0.055	0.956034
		AdjustedAgelarge immature	0.0635076	0.1077524	0.589	0.555603
		AdjustedAgeadult	−0.0352866	0.0911034	−0.387	0.698516
		SexClassmale	−0.0690529	0.1074499	−0.643	0.52045
		MeanRainfall	0.0739756	0.0491618	1.505	0.132392
		MeanTempMax	**−0.0829635**	**0.0228666**	**−3.628**	**0.000285**
		MonthlyFruitBiomass_kg_ha	−0.0247516	0.0347862	−0.712	0.476752
		AdjustedAgesmall immature:SexClassmale	0.1296963	0.1401411	0.925	0.354722
		AdjustedAgelarge immature:SexClassmale	−0.0007801	0.1379186	−0.006	0.995487
		AdjustedAgeadult:SexClassmale	0.1002551	0.117744	0.851	0.39451
Fruit foraging						
	glmer(VerticalScans ~ AdjustedAge + SexClass + (AdjustedAge*SexClass) + MeanRainfall + MeanTempMax + MonthlyFruitBiomass_kg_ha + offset(log(TotalFruitForaging BranchUseScans)) + (1 | Animal), data = supportDF.fruit, family = poisson(link = "log"))	(Intercept)	−0.62491	0.27773	−2.25	0.0244
		AdjustedAgesmall immature	−0.05293	0.31188	−0.17	0.8652
		AdjustedAgelarge immature	−0.22512	0.3204	−0.703	0.4823
		AdjustedAgeadult	−0.24914	0.28606	−0.871	0.3838
		SexClassmale	−0.10952	0.35663	−0.307	0.7588
		MeanRainfall	−0.02744	0.09758	−0.281	0.7785
		MeanTempMax	**−0.10461**	**0.04773**	**−2.192**	**0.0284**
		MonthlyFruitBiomass_kg_ha	0.04518	0.0715	0.632	0.5275
		AdjustedAgesmall immature:SexClassmale	−0.06569	0.40955	−0.16	0.8726
		AdjustedAgelarge immature:SexClassmale	0.17078	0.40912	0.417	0.6764
		AdjustedAgeadult:SexClassmale	0.15095	0.37282	0.405	0.6856
Hypothesis 3						
Invertebrate foraging						
Smaller individuals will spend less time foraging in the upper canopy	glmmTMB(UpperScans ~ AdjustedAge + SexClass + (AdjustedAge*SexClass) + MeanRainfall + MeanTempMax + MonthlyFruitBiomass_kg_ha + offset(log(TotalInvertebrateForaging ArborealScans)) + (1 | Animal), data = supportDF.invertebrates.arboreal, ziformula=~0, family = poisson)	(Intercept)	−1.44756	0.12342	−11.728	<2e-16
		AdjustedAgesmall immature	−0.22008	0.1494	−1.473	0.1407
		AdjustedAgelarge immature	−0.23822	0.1462	−1.629	0.1032
		AdjustedAgeadult	0.0561	0.12691	0.442	0.6584
		SexClassmale	−0.17982	0.15704	−1.145	0.2522
		MeanRainfall	**0.05934**	**0.03**	**1.978**	**0.0479**
		MeanTempMax	**−0.18952**	**0.02585**	**−7.333**	**2.25E-13**
		MonthlyFruitBiomass_kg_ha	**0.08158**	**0.02059**	**3.961**	**7.46E-05**
		AdjustedAgesmall immature:SexClassmale	−0.07473	0.19539	−0.382	0.7021
		AdjustedAgelarge immature:SexClassmale	0.15581	0.18978	0.821	0.4117
		AdjustedAgeadult:SexClassmale	0.02608	0.16461	0.158	0.8741
Fruit foraging						
	glmer(UpperScans ~ AdjustedAge + SexClass + (AdjustedAge*SexClass) + MeanRainfall + MeanTempMax + MonthlyFruitBiomass_kg_ha + offset(log(TotalFruitForaging ArborealScans)) + (1 | Group/Animal), data = supportDF.fruits.arboreal, family = poisson(link = "log"))	(Intercept)	−1.22703	0.33355	−3.679	0.000234
		AdjustedAgesmall immature	−0.67538	0.40172	−1.681	0.092721
		AdjustedAgelarge immature	−0.0785	0.37285	−0.211	0.833252
		AdjustedAgeadult	0.15252	0.33891	0.45	0.652686
		SexClassmale	0.43036	0.392	1.098	0.272266
		MeanRainfall	−0.05286	0.05853	−0.903	0.366419
		MeanTempMax	**−0.18566**	**0.04496**	**−4.13**	**3.63E-05**

		MonthlyFruitBiomass_kg_ha	**−0.10202**	**0.04849**	**−2.104**	**0.035375**
		AdjustedAgesmall immature:SexClassmale	0.04498	0.47903	0.094	0.925193
		AdjustedAgelarge immature:SexClassmale	−0.51455	0.44889	−1.146	0.251687
		AdjustedAgeadult:SexClassmale	−0.47184	0.40423	−1.167	0.2431
Invertebrate foraging						
Smaller individuals will spend less time foraging on the ground	glmmTMB(GroundScans ~ AdjustedAge + SexClass + (AdjustedAge*SexClass) + MeanRainfall + MeanTempMax + MonthlyFruitBiomass_kg_ha + offset(log(TotalInvertebrateForaging CanopyLevelScans)) + (1 | Animal), data = supportDF.invertebrates.all, ziformula = ~0, family = poisson)	(Intercept)	−4.67645	0.5838	−8.01	1.14E-15
		AdjustedAgesmall immature	0.06156	0.692	0.089	0.9291
		AdjustedAgelarge immature	−0.02553	0.66625	−0.038	0.9694
		AdjustedAgeadult	0.19544	0.60021	0.326	0.7447
		SexClassmale	−0.51246	0.78249	−0.655	0.5125
		MeanRainfall	**0.20593**	**0.09602**	**2.145**	**0.032**
		MeanTempMax	**0.62044**	**0.07133**	**8.698**	**<2e-16**
		MonthlyFruitBiomass_kg_ha	0.09638	0.05315	1.813	0.0698
		AdjustedAgesmall immature:SexClassmale	1.3938	0.89825	1.552	0.1207
		AdjustedAgelarge immature:SexClassmale	**1.86003**	**0.87617**	**2.123**	**0.0338**
		AdjustedAgeadult:SexClassmale	**1.86901**	**0.80561**	**2.32**	**0.0203**
Fruit foraging						
	glmmTMB(GroundScans ~ AgeClass + SexClass + (AgeClass*SexClass) + offset(log(TotalFruitForaging CanopyLevelScans)) + (1 | Animal), data = support DF.fruit.all, ziformula = ~0, family = poisson)	(Intercept)	−20.82	5864.21	−0.004	0.997
		AgeClasssmall immature	17.25	5864.21	0.003	0.998
		AgeClasslarge immature	16.98	5864.21	0.003	0.998
		AgeClassadult	17.27	5864.21	0.003	0.998
		SexClassmale	16.85	5864.21	0.003	0.998
		AgeClasssmall immature:SexClassmale	−15.71	5864.21	−0.003	0.998
		AgeClasslarge immature:SexClassmale	−15.71	5864.21	−0.003	0.998
		AgeClassadult:SexClassmale	−16.05	5864.21	−0.003	0.998

Bold denotes statistically significant results ($P < 0.05$).

Table A7

Incidence rate ratios from generalized linear mixed models

Hypothesis/Prediction	Generalized linear mixed model	Predictor	Incidence rate ratio	Confidence interval	*P*
Hypothesis 1					
Smaller individuals, i.e. juveniles and females, will spend relatively more time foraging for fruit than larger individuals, i.e. males, adults	glmmTMB(FruitScans ~ AdjustedAge + SexClass + (AdjustedAge*SexClass) + MeanTempMax + MeanRainfall + MonthlyFruitBiomass_kg_ha + offset(log(TotalForagingScans)) + (1 | Animal), data = df.overallStates, ziformula=~0, family = poisson)	(Intercept)	0.09	0.06–0.13	**<0.001**
		AgeClass [small immature]	**1.58**	**1.07–2.35**	**0.022**
		AgeClass [large immature]	1.33	0.90–1.98	0.151
		AgeClass [adult]	**1.57**	**1.09–2.25**	**0.015**
		SexClass [male]	0.91	0.58–1.43	0.688
		MeanTempMax	**1.34**	**1.27–1.41**	**<0.001**
		MeanRainfall	**1.14**	**1.06–1.23**	**<0.001**
		MonthlyFruitBiomass_kg_ha	0.99	0.95–1.04	0.746
		AgeClass [small immature]*SexClass [male]	1.09	0.66–1.79	0.747
		AgeClass [large immature]*SexClass [male]	1.39	0.85–2.29	0.191
		AgeClass [adult]*SexClass [male]	1.04	0.65–1.64	0.879
Smaller individuals will spend relatively more time foraging for soft, rather than hard-to-access, fruits	glmer(EasyFruitScans ~ AdjustedAge + SexClass + AdjustedAge*SexClass + MeanTempMax + MeanRainfall + MonthlyFruitBiomass_kg_ha + offset(log(TotalFruitScans)) + (1 | Animal), data = dfh1.difficulty, family = poisson(link = "log"))	(Intercept)	0.48	0.29–0.80	**0.005**
		AgeClass [small immature]	1.11	0.64–1.94	0.708
		AgeClass [large immature]	1.07	0.61–1.86	0.822
		AgeClass [adult]	1.23	0.73–2.06	0.432
		SexClass [Male]	1.43	0.78–2.61	0.250
		MeanTempMax	**0.94**	**0.88–1.00**	**0.043**
		MeanRainfall	0.94	0.86–1.03	0.172
		MonthlyFruitBiomass_kg_ha	**0.86**	**0.81–0.92**	**<0.001**
		AgeClass [small immature]*SexClass [Male]	0.67	0.34–1.32	0.249
		AgeClass [large immature]*SexClass [Male]	0.71	0.36–1.38	0.311
		AgeClass [adult]*SexClass [Male]	0.63	0.34–1.17	0.144

(*continued on next page*)

Table A7 (*continued*)

Hypothesis/Prediction	Generalized linear mixed model	Predictor	Incidence rate ratio	Confidence interval	*P*
Smaller individuals will spend relatively more time foraging for gleaned invertebrates rather than invertebrates extracted from within substrates	glmer(GleanedInvertebrateScans ~ AdjustedAge + SexClass + (AdjustedAge*SexClass) + MeanTempMax + MeanRainfall + MonthlyFruitBiomass_kg_ha + offset(log(TotalInvertebrateScans)) + (1 | Animal), data = dfh1.invertebrates, family = poisson(link = "log"))	(Intercept)	0.92	0.82–1.04	0.183
		AgeClass [small immature]	0.88	0.77–1.02	0.082
		AgeClass [large immature]	0.91	0.79–1.04	0.158
		AgeClass [adult]	0.98	0.87–1.11	0.734
		SexClass [male]	1.02	0.88–1.18	0.803
		MeanTempMax	1.01	0.99–1.04	0.284
		MeanRainfall	0.98	0.95–1.01	0.193
		MonthlyFruitBiomass_kg_ha	0.99	0.97–1.01	0.264
		AgeClass [small immature]*SexClass [male]	0.99	0.83–1.17	0.870
		AgeClass [large immature]*SexClass [male]	0.98	0.83–1.17	0.850
		AgeClass [adult]*SexClass [male]	0.96	0.83–1.12	0.613
Hypothesis 2					
Invertebrate foraging					
Smaller individuals will spend more time using smaller/thinner substrates	glmer(SmallBranch ~ AdjustedAge + SexClass + (AdjustedAge*SexClass) + MeanRainfall + MeanTempMax + MonthlyFruitBiomass_kg_ha + offset(log(TotalInvertebrate ForagingBranchUseScans)) + 1 | Animal), data = supportDF.invertebrates, family = poisson(link = "log"))	(Intercept)	0.80	0.70–0.92	**0.001**
		AgeClass [small immature]	0.92	0.77–1.10	0.349
		AgeClass [large immature]	0.89	0.74–1.06	0.175
		AgeClass [adult]	**0.81**	**0.70–0.94**	**0.004**
		SexClass [male]	1.06	0.89–1.25	0.527
		MeanRainfall	0.99	0.90–1.08	0.777
		MeanTempMax	1.01	0.97–1.05	0.485
		MonthlyFruitBiomass_kg_ha	1.02	0.96–1.08	0.599
		AgeClass [small immature]*SexClass [male]	0.90	0.72–1.13	0.379
		AgeClass [large immature]*SexClass [male]	0.86	0.69–1.08	0.193
		AgeClass [adult]*SexClass [male]	**0.81**	**0.67–0.97**	**0.025**
Fruit foraging					
	glmer(SmallBranch ~ AdjustedAge + SexClass + (AdjustedAge*SexClass) + MeanRainfall + MeanTempMax + MonthlyFruitBiomass_kg_ha + offset(log(TotalFruitForaging BranchUseScans)) + (1 | Animal), data = supportDF.fruit, family = poisson(link = "log"))	(Intercept)	0.89	0.59–1.36	0.595
		AgeClass [small immature]	0.95	0.60–1.53	0.846
		AgeClass [large immature]	1.01	0.63–1.62	0.952
		AgeClass [adult]	0.93	0.61–1.43	0.750
		SexClass [male]	1.02	0.61–1.73	0.929
		MeanRainfall	1.00	0.87–1.15	0.989
		MeanTempMax	0.96	0.90–1.03	0.264
		MonthlyFruitBiomass_kg_ha	1.06	0.96–1.17	0.234
		AgeClass [small immature]*SexClass [male]	1.03	0.57–1.87	0.922
		AgeClass [large immature]*SexClass [male]	0.87	0.48–1.58	0.646
		AgeClass [adult]*SexClass [male]	0.94	0.55–1.63	0.832
Invertebrate foraging					
Smaller individuals will spend more time using more vertically angled substrates	glmer(VerticalScans ~ AdjustedAge + SexClass + (AdjustedAge*SexClass) + MeanRainfall + MeanTempMax + MonthlyFruitBiomass_kg_ha + offset(log(TotalInvertebrate ForagingBranchUseScans)) + (1 | Animal), data = supportDF.invertebrates, family = poisson(link = "log"))	(Intercept)	0.53	0.45–0.63	**<0.001**
		AgeClass [small immature]	0.99	0.80–1.23	0.956
		AgeClass [large immature]	1.07	0.86–1.32	0.556
		AgeClass [adult]	0.97	0.81–1.15	0.699
		SexClass [male]	0.93	0.76–1.15	0.520
		MeanRainfall	1.08	0.98–1.19	0.132
		MeanTempMax	**0.92**	**0.88–0.96**	**<0.001**
		MonthlyFruitBiomass_kg_ha	0.98	0.91–1.04	0.477
		AgeClass [small immature]*SexClass [male]	1.14	0.87–1.50	0.355
		AgeClass [large immature]*SexClass [male]	1.00	0.76–1.31	0.995
		AgeClass [adult]*SexClass [male]	1.11	0.88–1.39	0.395
Fruit foraging					
	glmer(VerticalScans ~ AdjustedAge + SexClass + (AdjustedAge*SexClass) + MeanRainfall + MeanTempMax + MonthlyFruitBiomass_kg_ha + offset(log(TotalFruitForaging BranchUseScans)) + (1 | Animal), data = supportDF.fruit, family = poisson(link = "log"))	(Intercept)	0.54	0.31–0.92	**0.024**
		AgeClass [small immature]	0.95	0.51–1.75	0.865
		AgeClass [large immature]	0.80	0.43–1.50	0.482
		AgeClass [adult]	0.78	0.44–1.37	0.384
		SexClass [male]	0.90	0.45–1.80	0.759
		MeanRainfall	0.97	0.80–1.18	0.779
		MeanTempMax	**0.90**	**0.82–0.99**	**0.028**

		MonthlyFruitBiomass_kg_ha	1.05	0.91–1.20	0.527
		AgeClass [small immature]*SexClass [male]	0.94	0.42–2.09	0.873
		AgeClass [large immature]*SexClass [male]	1.19	0.53–2.64	0.676
		AgeClass [adult]*SexClass [male]	1.16	0.56–2.41	0.686
Hypothesis 3					
Invertebrate foraging					
Smaller individuals will spend less time foraging in the upper canopy	glmmTMB(UpperScans ~ AdjustedAge + SexClass + (AdjustedAge*SexClass) + MeanRainfall + MeanTempMax + MonthlyFruitBiomass_kg_ha + offset(log(TotalInvertebrateForaging ArborealScans)) + (1 | Animal), data = supportDF.invertebrates.arboreal, ziformula=~0, family = poisson)	(Intercept)	0.24	0.18–0.30	**<0.001**
		AgeClass [small immature]	0.80	0.60–1.08	0.141
		AgeClass [large immature]	0.79	0.59–1.05	0.103
		AgeClass [adult]	1.06	0.82–1.36	0.658
		SexClass [male]	0.84	0.61–1.14	0.252
		MeanRainfall	**1.06**	**1.00–1.13**	**0.048**
		MeanTempMax	**0.83**	**0.79–0.87**	**<0.001**
		MonthlyFruitBiomass_kg_ha	**1.08**	**1.04–1.13**	**<0.001**
		AgeClass [small immature]*SexClass [male]	0.93	0.63–1.36	0.702
		AgeClass [large immature]*SexClass [male]	1.17	0.81–1.69	0.412
		AgeClass [adult]*SexClass [male]	1.03	0.74–1.42	0.875
Fruit foraging					
	glmer(UpperScans ~ AdjustedAge + SexClass + (AdjustedAge*SexClass) + MeanRainfall + MeanTempMax + MonthlyFruitBiomass_kg_ha + offset(log(TotalFruitForaging ArborealScans)) + (1 | Group/ Animal), data = supportDF.fruits.arboreal, family = poisson(link = "log"))	(Intercept)	0.29	0.15–0.56	**<0.001**
		AgeClass [small immature]	0.51	0.23–1.12	0.093
		AgeClass [large immature]	0.92	0.45–1.92	0.833
		AgeClass [adult]	1.16	0.60–2.26	0.653
		SexClass [male]	1.54	0.71–3.32	0.272
		MeanRainfall	0.95	0.85–1.06	0.366
		MeanTempMax	**0.83**	**0.76–0.91**	**<0.001**
		MonthlyFruitBiomass_kg_ha	**0.90**	**0.82–0.99**	**0.035**
		AgeClass [small immature]*SexClass [male]	1.05	0.41–2.67	0.925
		AgeClass [large immature]*SexClass [male]	0.60	0.25–1.44	0.252
		AgeClass [adult]*SexClass [male]	0.62	0.28–1.38	0.243
Invertebrate foraging					
Smaller individuals will spend less time foraging on the ground	glmmTMB(GroundScans ~ AdjustedAge + SexClass + (AdjustedAge*SexClass) + MeanRainfall + MeanTempMax + MonthlyFruitBiomass_kg_ha + offset(log(TotalInvertebrateForaging CanopyLevelScans)) + (1 | Animal), data = supportDF.invertebrates.all, ziformula = ~0, family = poisson)	(Intercept)	0.01	0.00–0.03	**<0.001**
		AgeClass [small immature]	1.06	0.27–4.13	0.929
		AgeClass [large immature]	0.97	0.26–3.60	0.969
		AgeClass [adult]	1.22	0.37–3.94	0.745
		SexClass [male]	0.60	0.13–2.78	0.513
		MeanRainfall	**1.23**	**1.02–1.48**	**0.032**
		MeanTempMax	**1.86**	**1.62–2.14**	**<0.001**
		MonthlyFruitBiomass_kg_ha	1.10	0.99–1.22	0.070
		AgeClass [small immature]*SexClass [male]	4.03	0.69–23.44	0.121
		AgeClass [large immature]*SexClass [male]	**6.42**	**1.15–35.78**	**0.034**
		AgeClass [adult]*SexClass [male]	**6.48**	**1.34–31.44**	**0.020**
Fruit foraging					
	glmmTMB(GroundScans ~ AgeClass + SexClass + (AgeClass*SexClass) + offset(log(TotalFruitForagingCanopyLevelScans)) + (1 | Animal), data = supportDF.fruit.all, ziformula = ~0, family = poisson)	(Intercept)	0.00	0.00–Inf	0.997
		AgeClass [small immature]	31164303.41	0.00–Inf	0.998
		AgeClass [large immature]	23746684.14	0.00–Inf	0.998
		AgeClass [adult]	31744170.93	0.00–Inf	0.998
		SexClass [male]	20715170.75	0.00–Inf	0.998
		AgeClass [small immature]*SexClass [male]	0.00	0.00–Inf	0.998
		AgeClass [large immature]*SexClass [male]	0.00	0.00–Inf	0.998
		AgeClass [adult]*SexClass [male]	0.00	0.00–Inf	0.998

Bold denotes statistically significant results ($P < 0.05$).

Appendix 3

Table A8
Ethogram of behavioural states used during data collection

Behaviour	Description
Drink	Drinking
Excretion	Excretion of faeces, urine or vomit
Foraging: flower	Foraging for flowers; feeding on flowers
Foraging visually	Actively visually investigating areas around for edible objects, often while moving through the forest at a moderate pace; includes gleaning small insects, investigating leaves or bark and looking around at short distances for fruit or vertebrates
Foraging: fruit	Foraging for fruits; feeding on fruit
Foraging: fruit (extractive)	Pounding *Luehea*, scrubbing *Sloanea* or breaking open *Genipa*
Foraging: invertebrate	Foraging for nonembedded invertebrates; feeding on invertebrates
Foraging: invertebrate (extractive)	Foraging for embedded invertebrates by altering substrates (e.g. tearing branches, ripping bark, reaching into tree holes)
Foraging: other	Foraging for bromeliad leaves, pith, vertebrates, vertebrate eggs, etc.
Intergroup encounter	Intergroup encounter with another capuchin group
Mobbing	Mobbing a predator
Other	Any behaviour not covered
Out of sight	Focal individual not visible or partially covered such that its state/behaviours cannot be reliably determined by observer
Play	Playing (e.g. biting, chasing, hitting, bouncing, pushing, pulling, etc. in exaggerated and/or nonaggressive manner)
Self-directed	Autogrooming
Social active	Affiliative/allogrooming; includes monkeys receiving grooming while resting and while nursing or being nursed
Social aggressive	Agonistic behaviour towards conspecifics (e.g. chasing, lunging, biting, etc.)
Social rest	Inactive or sleeping <3 body lengths away from other individuals
Solitary rest	Inactive or sleeping >3 body lengths away from other individuals
Travel	Moving relatively quickly in a unified direction, often in response to intergroup encounters or predators, while moving towards sleep trees or towards high-quality resources; during travel, monkeys do not forage or socialize
Vigilant	Scanning intently at a long range (not for food)