

ABSTRACT

DO FOLIVORES DEplete PATCHES? FORAGING BEHAVIOR AND THE DYNAMICS OF RESOURCE USE IN THE COSTA RICAN MANTLED HOWLER (*ALOUATTA PALLIATA*)

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Two general assumptions have often been made about folivorous primates: first, that feeding competition is low or absent because leaves are a superabundant and evenly dispersed resource, and as a result, that feeding competition does not constrain the size of folivorous groups. However, many folivorous primates maintain smaller group sizes. In this study, I aimed to examine this ‘folivore paradox’ by testing the hypothesis that mantled howler monkeys (*Alouatta palliata*) deplete localized patches of young leaves and therefore experience feeding competition. One group of 8 adult individuals was studied July and August 2015 at Piro Research Station in the Osa Peninsula, Costa Rica. Patch occupancy time, intake, and movement were recorded in one minute intervals from the time individuals entered a feeding patch until they left the patch. Patch size and richness was assessed for each patch. Patch depletion was defined as a combination of decreased food intake and increased within-patch movement. Patch depletion occurred in all food types consumed by this group; ripe fruit, young leaves, and mature leaves: in total 36 of 131 patches were depleted. Patch duration was significantly correlated with feeding group size and patch size (DBH). Daily path length was significantly correlated with the number of patches depleted in a day. The occurrence of patch depletion and the fission of howler groups into subgroups while feeding suggest that howler monkey group size is constrained by

scramble competition. Feeding competition also appears to constrain group size, further indicating that there appears to be no paradox for this mostly folivorous primate. These results are imperative to furthering knowledge of folivore feeding competition which can improve conservation efforts aimed at helping to protect folivorous species.

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OF RESOURCE USE IN THE COSTA RICAN MANTLED HOWLER (ALOUATTA
PALLIATA)

BY

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INTRODUCTION

Overview of Ecological Models

Primates are ideal study subjects for examining how ecological factors influence social organization. The Primate order has a high proportion of social species, and these species form a wide variety of social groups including: monogamous pairs, polygynous groups, polyandrous groups, and multi-male multi-female groups, as well as subgroups of these different types, which may form large complex communities (Kappeler and van Schaik, 2001). The term “social group” refers to the size, composition, and spatiotemporal organization of the primate group (Kappeler and van Schaik, 2001). A mating system, however, is both genetic and social, with the social component describing social interactions between individuals and the genetic mating system being determined through paternity analyses of the offspring which result from sexual behavior (Kappeler and van Schaik, 2001). Several ecological factors may influence a group’s size and composition, including predation and competition for food. Early analyses of the evolution of primate groups did not consider sex-based differences in behavior, though it became prominent in subsequent analyses. Instead, early studies focused on the correlations of group size with ecological variables like habitat or diet type (Clutton-Brock and Harvey, 1977). Those correlations then were used to infer the pressures that led to the evolution of group living. Subsequent analyses also included predicted decision making rules for males and females, in order to further understand the evolution of group living, in conjunction with other ecological pressures.

Wrangham (1980) proposed that ecological pressures on females influence their decisions as to what size group to join and who to associate with. While the key strategy for males is to optimize their access to fertile females, the key strategy for females is optimize their access to resources (Wrangham, 1980). Wrangham defined two types of female groups: female-bonded and non-female bonded. “Female-bonded” refers to females who maintain affiliative bonds with each other and stay in their natal group, while “non-female bonded” groups are comprised of unrelated females who emigrated from their natal groups (Wrangham, 1980). Group foraging leads to feeding competition, and one way individuals can reduce competition with kin is to disperse (Hamilton, 1964; Wrangham, 1980). However, some females instead remain with their close relatives in groups (Wrangham, 1980), suggesting that living in a group with related females allows for the potential for cooperation against other unrelated females in order to gain access to high-quality resources. For the cooperation to be effective, feeding sites must be found in defensible patches.

Wrangham’s model predicts that in periods of food abundance female-bonded primates select items found in high-quality but patchily distributed sites, whereas in periods of food scarcity (when individuals may have to travel farther), females may form cooperative sub-groups in order to limit feeding competition (Wrangham, 1980). He also argues that the diets of non-female bonded species are comprised of resources that are not distributed in defensible patches (i.e. colobines, gorillas). Ultimately their choice of a leaf-based diet allows for these species to forage in close proximity without suffering the costs of feeding competition or needing to cooperate (Wrangham, 1980).

The number of females who live together and their social relationships are therefore, the primary determinants of the structure and dynamics of the group as a whole, as males must

associate themselves with these females. Wrangham (1980) predicted that multi-male groups tend to be found in non-territorial female-bonded species because the females benefit by increasing their group's size in order to increase the competitive ability of the group in inter-group interactions. Therefore, females are willing to cooperate with multiple males because they benefit from the males' help in defending high-quality food sources from other groups. This notion of male grouping based on female cooperation (or grouping) has prevailed in the literature, and was an important starting point for subsequent models.

Building from the Wrangham (1980) model, van Schaik (1989) included predation risk as a factor that favors group formation. Animals in small groups may face higher predation risk than animals in larger groups. Individuals in larger groups may be collectively more vigilant, and individuals face a lower probability of being caught if a predator attack occurs (van Schaik and van Hooff, 1983). Van Schaik (1989) outlined a series of predictions regarding female dispersal and social relationships based upon competition for food and safety from predators. In this paper he made a clear distinction between frugivores and folivores, where folivores within groups were classified as facing scramble competition and frugivores within groups were classified as facing contest competition (van Schaik, 1989). van Schaik (1989) assumed that contest competition between groups only occurred among frugivores (van Schaik, 1989). Ultimately the food competition experienced in groups is dependent on the spatiotemporal distribution of resources but any attempt to reduce feeding competition by forming small groups must be balanced with predation risk. This model, as well as Wrangham's work, introduced the socioecological factors influencing female social relationships.

Isbell (1991) provided further refinement of the ecological model, by focusing on the cost incurred by moving between foods within the landscape and how the spatial distribution of foods

may influence social organization. She examined whether contest and scramble competition covary within and among groups (Isbell, 1991). Contest competition refers to direct contests that result in individuals gaining differential access to food, often with a dominant individual (or group) obtaining more food than a subordinate (Snaith and Chapman, 2007). Scramble competition occurs when one individual consumes a resource before another individual arrives (Snaith and Chapman, 2007).

Isbell (1991) proposed that when food is clumped both within-group scramble and within-group contest competition occur and, when food is dispersed, neither occurs. Isbell provided methods for assessing what types of feeding competition were occurring in a group through five indicators (Isbell, 1991). Between-group contest competition is evident if there is between-group aggression and between-group scramble competition is evident if there is a positive relationship between home range size and group size (Isbell, 1991). If there is within-group contest competition, Isbell predicts there will be strong female dominance hierarchies and if there is within-group scramble competition, she predicts there will be a positive relationship between day range (daily travel distance) and group size, and/or a negative relationship between female reproductive rates and group size (Isbell, 1991). Isbell tested these predictions and found that folivore group size did not impact day range which led her to conclude that many folivores experience no competition for food, however, she cautioned that these two variables alone may not adequately demonstrate feeding competition (Isbell, 1991). This last precautionary note was extremely important because it led others to examine whether folivores experience feeding competition using other variables and methods.

Additionally, Chapman *et al* (1995) expanded upon Wrangham's model by considering the influence of group size on travel costs. Chapman and others have proposed that the upper

limit on a group's size is set by the increasing costs of travel that results from adding additional members (Wrangham, 2000; Janson et al., 1995; Chapman et al., 1995). An increase in within-group competition is associated with an increase in day range: when a preferred food source is patchily distributed, larger groups will deplete patches more quickly, individuals in the groups will obtain less food, and groups will have to visit more patches in a day than smaller groups (Chapman and Chapman, 2000). The model is easily applied to frugivores that compete for patchy, high-quality food resources (Strier, 1989; Chapman 1990; Chapman et al., 1995; Wrangham et al., 1996), and has been useful in understanding group size of frugivores, but it is less clear if it applies to folivorous primates.

Sterck, Watts, and van Schaik (1997) expanded the previous ecological model further to predict how varying levels of competition within groups and between groups shape female social relationships. They also suggest that the risks of predation and infanticide, along with the distribution of food, are the main causal factors of social systems. They argued that although contest competition results in agonistic behaviors, scramble competition does not, and this difference accounts for the presence or absence of nepotism and dominance hierarchies in primate groups (Sterck et al., 1997). They further proposed that agonistic relationships vary along three axes: egalitarian to despotic, individualistic to nepotistic, and tolerant to intolerant (Sterck et al., 1997). Egalitarian females have no dyadic dominance relations while despotic females have clearly established dominance relations and linear dominance hierarchies (Sterck et al., 1997). In nepotistic hierarchies, related females have similar ranks due to coalitionary support from relatives, whereas in individualistic hierarchies the ranks of female relatives are independent of each other (Sterck et al., 1997). Tolerance generally decreases the severity of

aggression: as tolerance decreases, the threats by dominant individuals increases, and “cohesion-enhancing behaviors” increase (Sterck et al., 1997).

When within-group contest (WGC) is strong and between-group-competition (BGC) is low, females should have established hierarchies and agonistic relationships, as dominant individuals will gain access to limited resources (de Waal, 1989). Females should form long-term agonistic dominant relationships with relatives, and also mutualistic coalitions with non-relatives (Sterck et al., 1997). These coalitions are stable, linear, and nepotistic, therefore these societies are termed “Resident-Nepotistic” (Sterck et al., 1997). Females should also remain in their natal group, referred to as philopatry, because females attempting to disperse would lose access to allies and would face strong resistance in their efforts to join other groups (Sterck et al., 1997). In addition, dispersing females would face increased predation risk and reduced foraging efficiency in the new unfamiliar habitat.

When WGC is weak and dispersal costs are low, and BGC is also low, females would gain little from establishing dominance or from using nepotistic or mutualistic coalitions when competing for food and rank (Sterck et al., 1997). Females can disperse because they do not suffer by losing coalition partners and usually face little or no resistance to immigration (Sterck et al., 1997). These societies have been termed “Dispersal-Egalitarian” (Sterck et al., 1997).

If only BGC is strong and WGC is weak, females do not need to form agonistic dominance relationships and within-group coalitions are not necessary (Sterck et al., 1997). However, the cooperation of females in the same group is key to defending resources against other groups. If these females are unrelated, the cooperation can break down due to freeloaders; an individual female may decide to opt out of BGC so that she can gain from others who

participate. This problem is avoided by residing with female relatives (philopatry), and the resulting societies are termed “Resident-Egalitarian” (Sterck et al., 1997).

Where WGC and BGC are both strong, there should be dominance relationships and female philopatry (Sterck et al., 1997). Females should have formal dominance hierarchies and agonistic dominance relationships should be apparent in dyadic contests (Sterck et al., 1997). Females should also form alliances with relatives to counter agonistic behavior from other group members, producing nepotistic hierarchies, but they should also tolerate the presence of non-relatives, because of the assistance they can provide in intergroup encounters (Sterck et al., 1997). Females are philopatric because they risk losing access to allies and face potential strong resistance from females of other groups (Sterck et al., 1997). These societies are labeled “Resident-Nepotistic-Tolerant” (Sterck et al., 1997).

Finally, Sterck et al (1997) suggested that infanticide may have important social consequences for some species (Sterck et al., 1997). Infanticide is one strategy males use to increase their fitness: by eliminating infants who they did not sire, males can cause females to cease lactation and resume cycling, thereby providing the males with mating opportunities (Hrdy, 1979). Females may develop counter-strategies to prevent infanticide, including increasing preferred group sizes and the formation of social alliances to prevent attacks by infanticidal males (Hrdy, 1979).

This model has continued to prevail in the literature as an important predictor of female grouping, and subsequent male grouping in response. This paper made a significant contribution to socioecological models because it incorporated the effects of habitat saturation, predation risk, and infanticide on group size and female social relationships. While this model is important for understanding the ecological pressure under contest conditions, it did not empirically test for the

effects of the pressures of scramble competition and other factors such as predation and infanticide.

The Folivore Paradox and Patch Depletion

Many of the socioecological models outlined above have assumed that feeding competition within folivorous primate groups is absent, and that groups are not limited by the availability of food (Koenig et al., 1998). This is based on studies that have found no relationship between group size and day range among folivores (Clutton-Brock and Harvey, 1977; *Colobus guereza*: Fashing, 2001; Asian Colobines: Yeager et al., 2000, 1998; *Procolobus rufomitratus*: Struhsaker and Leland, 1987).

If feeding competition is absent, then folivores should theoretically be free to form large groups, however, many live in small groups (Snaith and Chapman, 2007). Social factors have been used to solve this “folivore paradox”. Crockett and Janson (2000) found that the rate of infanticide increased with group size in red howlers (*Alouatta seniculus*), thus, they suggested infanticide avoidance could constrain group size below the level where within-group scramble imposes a cost (Crockett and Janson, 2000).

Similarly, Steenbeek and van Schaik (2001) suggested that among Thomas' langurs (*Presbytis thomasi*) group size was limited by the risk of infanticide because larger groups were more at risk of male takeover. Steenbeek and van Schaik (2001) suggest that the overall impact of feeding competition is limited, but in larger groups there was a higher risk of aggressive male take-over. They concluded that the lower limit of group size is set by predation avoidance, while the upper limit is set by infanticide avoidance (Steenbeek and van Schaik, 2001). In addition,

Koenig and Borries (2002) also found that both feeding competition and infanticide risk constrained group size in hanuman langurs (*Semnopithecus entellus*); as group size increased, female nutritional condition was compromised, birth rates decreased, and the risk of infanticide increased due to immigrating males (Koenig and Borries, 2002).

Treves and Chapman (1996) found that infanticide avoidance did not limit group size in a different population of hanuman langurs, but that increasing group size may have been a counter-strategy to prevent takeovers and infanticide. This combined evidence indicates that infanticide may constrain group size in some populations, but it might not provide a complete solution to the folivore paradox for all species. The data also do not rule out the possibility that ecological factors play an important role in limiting folivore group size in some populations.

Another way of understanding the “folivore paradox” is to reject the assumption that folivores do not deplete patches. Charnov’s theorem proposes that a patch is depleted when it is no longer worth exploiting, i.e. when the cost of obtaining food within the patch becomes greater than the cost of moving to the next patch (Charnov, 1976). It is important to note this does not always mean the food is completely gone – there might be some left, but in small quantities it becomes difficult to find. Optimally foraging animals should deplete food patches before travelling to the next patch, and patches should also be depleted more quickly by large groups (Charnov, 1976). If food patches are superabundant, however, patches will not be depleted, and there will be no relationship between how long a group feeds in a patch (patch occupancy time) and group size. Thus, if leaves are assumed to be superabundant, no patch depletion is expected to occur.

On the other hand, if leaves are not superabundant, then patches of leaves may be depleted by folivores. If this is the case, then large leaf patches are expected to be depleted more

quickly by larger groups than smaller groups, and day ranges are expected to increase with group size (Snaith and Chapman, 2007). However, if large groups cannot compensate for increased depletion rates by increasing travel distance, they may increase group spread to maintain fewer individuals per patch (Koenig and Borries, 2002; Snaith and Chapman, 2007). Alternately, individuals may deplete patches but remain in them by feeding on less desirable plant parts (Snaith and Chapman, 2007).

Chapman (1987) first tested patch depletion in howler monkeys and spider monkeys in Santa Rosa National Park, Costa Rica. He found that for spider monkeys, in most tree species the rate of intake of food items during a feeding bout was higher at the start of feeding than the end. There was also a significant positive relationship between subgroup size and the amount of time spent feeding for spider monkeys, an expected result since larger group sizes should spend more time feeding to compensate for the energy expenditure of traveling (Chapman, 1987). In contrast, subgroup size had no significant effect on patch duration in howler monkeys. This study was important for introducing and assessing patch depletion in a frugivorous (*Ateles*) and folivorous (*Alouatta*) species. This set the stage for future studies on scramble competition and patch depletion in folivores by Snaith and Chapman (2005, 2007) and Tombak et al. (2012).

Snaith and Chapman (2005) and Tombak et al. (2012) examined whether scramble competition occurs in the folivorous species red colobus (*Procolobus rufomitratu*s), and guereza (*Colobus guereza*), respectively. They tested patch depletion in two ways: intake rate was used as an index of feeding gain and movement within the patch was used as an index of feeding effort or cost (Snaith and Chapman, 2005). They argue that if intake rate slows within a patch, this indicates that either the patch is becoming depleted, or that the animals are becoming satiated (Snaith and Chapman, 2005). However, if intake rate slows while feeding effort remains

constant or increases, satiation is unlikely to be occurring, and instead provides evidence that the patch is becoming depleted (Snaith and Chapman, 2005). Patch depletion was determined to be a behavioral indicator of scramble competition. They also suggested that if scramble competition is absent, then patch occupancy should be unaffected by variation in group size or patch size. However, if group size and patch size influence within-group scramble competition, then occupancy time should increase with increasing patch size and/or decreasing group size (Snaith and Chapman, 2005).

Overall Snaith and Chapman (2005) found that red colobus in Kibale deplete food patches when feeding on young leaves, as indicated by decreasing gains (intake rate) despite increasing feeding effort (movement while feeding). Also, patch occupancy time was affected by patch size and feeding group size. This shows that larger groups deplete patches more quickly, are forced to visit more patches, and therefore accrue greater travel costs than smaller groups. These results suggest that red colobus experience within-group scramble competition, and that this type of competition may be an important factor in determining group size. The methods and findings in these studies guided my approach to a similar study on the mantled howler monkey (*Alouatta palliata*).

Overview of Alouatta palliata

Mantled howler monkeys (*Alouatta palliata*) are 5-7 kg monkeys whose distribution range extends from Mexico south to Peru (Estrada et al., 1999). This range is split into five subspecies: *Alouatta palliata mexicana*, which ranges in south-eastern Mexico, *A. p. palliata*, which ranges from northern Honduras through Nicaragua to Costa Rica, *A. p. trabeata*, which is

endemic to the Azuero Peninsula, Panama, *A. p. coibensis*, which is only found from Coiba Island and Jicarón, and *A. p. aequatorialis*, which occurs in Panama into western Colombia. (Baumgarten and Williamson, 2007).

A. palliata is one of the largest leaf-eaters of the New World primates. They have prehensile tails which allow them to utilize their hands to obtain food sources, and they have molars adapted for shearing leaves (Silver et al., 1998). They are the only New World primate that regularly includes mature leaves in their diet, but soft, less fibrous, young leaves are a preferred food source when available (Silver et al., 1998). Ripe fruit is also an important food item in their diet, especially wild figs (*Ficus*), but they also utilize petioles, buds, flowers, seeds, moss, and stems when mature fruit is scarce (Silver et al., 1998). They are often described as “facultative folivores” because they seem to be frugivorous by choice but folivorous by necessity (Milton, 1980), switching from a leaf-based diet to a fruit-based diet in times of fruit abundance (Stevenson et al., 2000). Their broad diet appears to be the main reason they can survive in fragments and isolated landscapes (Palma et al., 2011). Several researchers have found a positive correlation between the amount of leaves howler monkeys eat and the time they spend resting (Silver et al., 1998; Estrada et al., 1999). This is likely due to the necessity of reducing energy expenditure, especially during periods of leaf eating. Howlers must ferment, digest, and extract energy from the structural carbohydrates in leaves (Milton, 1980). To aid in the fermentation process, howlers have special gut microbacteria (Palma et al., 2011). Although they have some biological aids, they are most known for their long resting periods which they likely use for breaking down leaves.

Mantled howler group size ranges from 10 to 20 members with a sex ratio of four females to every single male (Glander, 1992). Howler groups can maintain a wide range of territory sizes,

from 1 hectare to 50 hectares (Palma et al., 2011). Spacing between these groups is mostly dependent on vocal communication, or howls, between males. Calls occur at dusk and dawn to communicate movement, but are also used in response to disturbances (Palma et al., 2011). Mantled howlers have linear dominance hierarchies which are reflected in their social behavior in behaviors such as grooming (Palma et al., 2011).

Females reach sexual maturity at approximately 36 months, while males reach sexual maturity at approximately 42 months. (Milton, 1980) Breeding occurs year-round with a gestation period of approximately 6 months and an interbirth interval of about 22 months (Glander, 1980). Males generally live an average of seven years and females typically live to eleven years (Glander, 1992). Natal dispersal occurs in both sexes, with males remaining solitary until they can supplant a resident alpha male (Glander, 1992). Alpha male tenure lasts up to four years, while females who rise to alpha status will remain there for their lifetime (Glander, 1992).

Project Goals

I applied methods similar to those used by Snaith and Chapman (2005) and Tombak (2012) to determine if wild howler monkeys (*Alouatta palliata palliata*) in Costa Rica deplete food patches, in order to determine if these platyrrhines experience within-group scramble competition.

Specifically, I tested the following hypothesis and predictions:

H1: If howler monkeys' foods are limited in their abundance then they will experience scramble competition for food resources.

H0: Howler monkey foods are suberabundant, thus they experience no competition for food resources.

P1. Howler monkeys will deplete food patches. Depletion will be defined as a reduction in food intake rate within a single patch coupled with a constant or increasing feeding effort over time.

P2. Patch duration will be affected by variation in feeding subgroup size: the larger the group, the faster a patch will become depleted.

P3. Patch depletion time will be dependent on patch size: the smaller the patch the faster the patch will be depleted.

P4. Feeding subgroups that deplete patches will have longer daily path lengths than groups that do not deplete patches.

METHODS

My study site was located at Piro Research Station in the Osa Peninsula, Costa Rica. This research station (see Figure 1) is within a tract of lowland tropical wet forest on the Pacific side of Central America. On the Osa Peninsula rainfall ranges from 4-7 meters annually, with the rainy season lasting from April to November (Silver et al., 2011). This study was conducted during the wet season of 2015 between July 1 and August 15. I observed one group of howler monkeys that consisted of eight adult individuals, one juvenile, and two infants. Towards the end of the study one adult female gave birth to twins, changing the group composition to 13 individuals. Data were collected on adult individuals (n=8) from dawn until dusk for a total of 30 days.



Figure 1: Study site.

a) Satellite image of the study site with a river lined in blue and gravel roads lined in brown, all trees visited by the howler monkeys are indicated with white dots

I observed the feeding behavior of the mantled howler group using a focal patch method that allowed for collection of data from a feeding subgroup. Each observation period represented the full patch occupancy period (i.e. duration) of a single food patch, which was defined as a single feeding tree. Focal patches were selected opportunistically: whenever monkeys were observed entering a patch to feed, I began data collection. While the feeding subgroup was in a

food patch, I recorded the intake rate (recorded as bites per minute) and feeding effort (recorded as net meters moved per minute) of all individuals in the patch in an *ad hoc* manner. I randomly chose one feeding individual and began simultaneously counting bites and meters for one minute. At the end of the minute I recorded these data, counted and recorded the number of visible individuals in the patch, and moved to another visible individual feeding to begin the next minute recording. I rotated among all individuals before repeating an already recorded individual. I recorded data until all members stopped eating or departed from a patch, whichever occurred first. A feeding subgroup was counted as all of the visible individuals feeding a patch; individuals not feeding were not recorded. Separately, I also recorded the GPS location of the foraging group every 10 minutes along with activity pattern for visible individuals.

I also recorded patch size and an estimate of patch quality using the DBH measurement of the focal tree and a phenology score. At the beginning of a feeding bout I scored the tree's phenology using a five-character scale (0, 1, 2, 3, 4) indicating approximate percentage of branches within the tree crown bearing food where 0=no fruit, flowers, or young leaves, 1 = < 25%, 2 = < 50%, 3 = < 75%, 4 = 75-100% (Schaffer, 2015, *in press*). In addition, all feeding trees were marked with flagging tape and its spatial position was recorded with a hand-held GPS device. At the end of each observation week, I returned to each new feeding tree to record the DBH and to collect botanical samples for identification. If the monkeys returned to the same tree in a new week, the phonological score was recalculated. Species were identified with the aid of the on-site botanical specialist, Max Villabolos, and cross-referenced with photo guide books and existing botanical data located at the site.

Analysis

I tested for patch depletion and satiation by examining intake rate (bites/min) and movement (m/min). If intake rate slowed while feeding effort remained constant or increased, the patch was considered depleted (Snaith and Chapman, 2007). If intake rate slowed while feeding effort also decreased, the individual was considered satiated (Snaith and Chapman, 2007). I examined each patch duration and split the total database of one-minute samples into quartiles corresponding to their temporal position within the time of patch residency. The first and last quartiles were compared to determine if there was an increase, decrease, or no change in the intake and movement over that period. If there were more than twelve samples, I compared the first three samples to the last three samples. If a patch was used for less than 8 minutes it was not included in analyses. A “depletion rate” was also determined, calculated as the total time from when depletion began until the time at which the individual left the patch.

To determine the activity pattern for the howler group I used a technique that accounted for calculating visible animals. I used the scan sampling technique described by Altmann (1974) and Milton (1980) at 10-minute intervals. During each scan I recorded the behavior of every group member I could see in 10 seconds. Percentages for each activity – feeding, traveling, resting, and social interaction – were then expressed as a proportion of the total number of individuals in the group. These percentages were added and divided by the total number of 10-minute intervals in the sample day to arrive at the percent of time spent at each activity.

Patch richness was calculated using a general patch density calculation. I calculated patch richness by cubing the DBH, in place of crown height and crown volume estimates, and multiplied that by 100. The resulting figure was then compared across numerous variables and patch behavior, using Pearson correlation. If the correlation was moderate ($0.3 < r < 0.5$ or $-0.3 >$

$r > -0.5$) or strong ($0.5 < r < 0.7$; $-0.5 > r > 0.5$) multiple linear regression was conducted to test the effects of various predictors on the independent variable to be tested. One-way ANOVA was utilized to test the difference between means of various patch characteristics. Chi-square analysis was used to test for differences in food type use between depleted and satiated patches. All statistical tests were conducted with in IBM Statistics SPSS 22 with a significance of $\alpha = 0.05$. Significant outliers and a food type where $n = 1$ were excluded from analysis.

The GPS points I recorded on group travel and feeding patch locations were plotted in ArcGIS (version 10.3). Daily path length was calculated using the GIS locations taken at 10 minutes throughout a day using the Point to Line feature in ArcMap. In cases where the 10 minute sample occurred when monkeys were feeding, the focal feeding group was used to determine group location.

Home range boundaries were estimated using the minimum convex polygon with the convex hull method in ArcMap. To determine the distribution (clustering versus dispersal) of feeding trees, I utilized the nearest neighbor index analysis and kernel density estimation in ArcMap. The nearest neighbor index calculates the distance between each point and its nearest neighbor, as well as the mean of those distances for the entire data set (Clark and Evans, 1954). The observed average distance is then divided by the expected average distance for a hypothetical distribution. If the means are the same, the ratio equals 1 and the pattern is random, if the ratio is greater than 1 the pattern is dispersed, and if the ratio is less than 1, the pattern is clustered. The calculated observed mean distance is also useful for providing the extent of clustering. The output also includes a z-score, which is calculated as the observed mean distance minus the expected mean distance, divided by the standard error. This z-score is then compared to the normal distribution to assess significance; $z < -1.96$ indicating significant clustering, and

$z > 1.96$ indicating significant clustering. The output for the nearest neighbor index also includes a p-value, which was interpreted in this study by a significance level of $p = 0.05$. Kernel density estimation is a non-parametric method that estimates the probability density function of a random variable. For this study I edited the minimum convex polygon home range, removing outliers to reduce error in the kernel density estimation.

RESULTS

The howling monkey study group utilized a home range of approximately 14 hectares (see Figure 2). The average daily path length was approximately 581 meters (see Figure 2). The distribution of trees was found to be significantly clustered on all days (e.g. the nearest neighbor ratio for the feeding trees was 0.0273, z-score = -17.555, p-value < 0.001). Since feeding trees were clustered on all days (using both home ranges generated by the minimum convex polygon and kernel density method), tree distribution was not included in further analyses since it lacked the ability to be compared to dispersed trees.

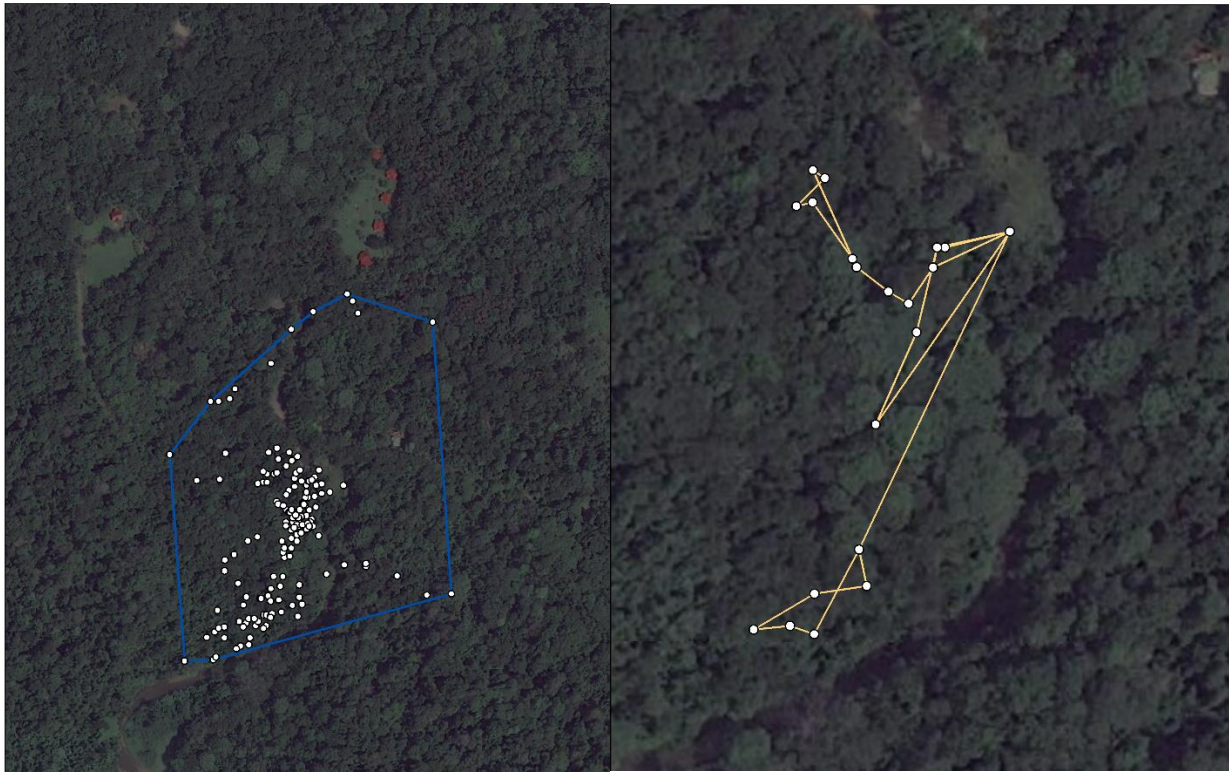


Figure 2: Study group home range and daily path.

a) Home range of the study group outlined in blue using the Minimum Convex Polygon feature of ArcMap, all trees visited by the howler monkeys are indicated with white dots; b) example of one daily path length of the study group on July 25th, 2015, the white dots indicate location points at 10 minute intervals, the yellow line indicates the daily path length as calculated by the point-to-line feature of ArcGIS. Both figures are overlaid on an image of the study site taken from GoogleEarth.

The monkeys' activity pattern was dominated by rest and feeding/foraging, with less time spent traveling and in social behavior (Figure 3). The monkeys spent the majority of their feeding time consuming ripe fruit (47%; $n = 55$ bouts) and young leaves (45%; $n = 53$ bouts), compared to mature leaves (8%; $n = 10$ bouts). The monkeys spent an average of 10.5 minutes feeding in a patch they visited (range 1.1 – 54.8 minutes, $n = 118$; Figure 4). On average the

monkeys spent the longest time in fruit patches (12.1 minutes), followed by young leaf (9.5 minutes) and mature leaf (7.5 minutes) patches (Table 1). However, these differences were not statistically significant, as determined by one-way ANOVA ($F(2,115) = 0.074$, $p = 0.874$: Table 1).

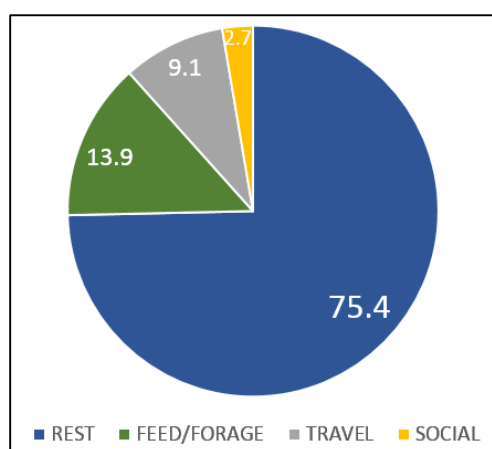


Figure 3: Mean activity budget of study group (n = 2551).

Table 1

Physical characteristics and related foraging behavior for food patches used by howler monkeys

Food Type	Sample Size	Mean Feeding Group Size (number of monkeys)	Mean Patch Duration (seconds)	Mean DBH (centimeters)	Mean Phenological Score	Mean Patch Richness	Number of Patches Where Depletion Occurred	Number of Patches Where Satiation Occurred
Young Leaves	53	2.07	570.4	71	1.8	5309576	15	12
Ripe Fruit	55	3	724.5	123	3.07	8298005	16	24
Mature Leaves	10	1.48	450.2	32	3.5	1232435	4	1
Total	118	2.45	632	91.92	2	64004937	35	37
Test for Equality of Means		$F(3,115) = 1.071$ $p = 0.346$	$F(3,115) = 0.074$ $p = 0.874$	$F(3,115) = 0.277$ $p = 0.758$	$F(3,115) = 3.772$ $p < 0.05$	$F(3,115) = 1.640$ $p = 0.190$		

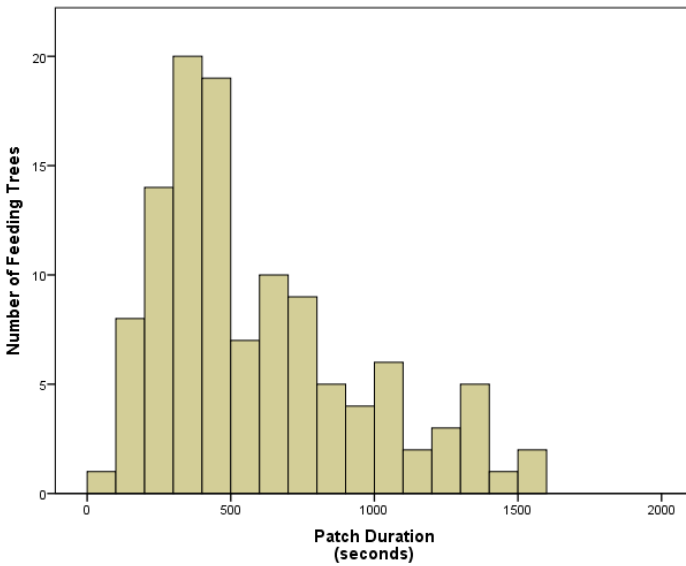


Figure 4: Patch duration in all feeding trees.

The average DBH of the food trees used was 91 cm with a range of 5 to 250 cm (Figure 5). Fruit patches had on average the largest DBH (mean 123 cm), followed by young leaf patches (mean 71 cm) and mature leaf patches (mean 32 cm: Figure 5, Table 1). However, these differences were not statistically significant, as determined by one-way ANOVA ($F(2,115) = 0.277, p = 0.758$: Table 1).

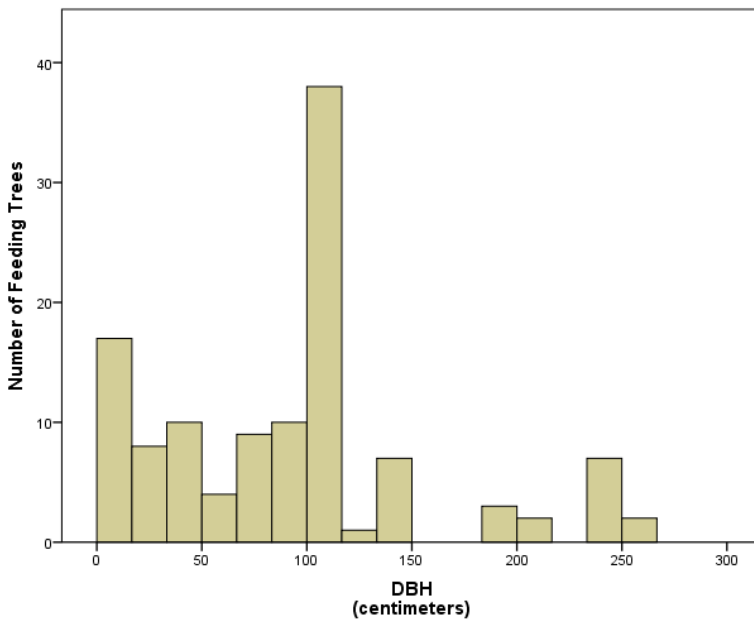


Figure 5: DBH of all feeding trees.

The food trees the monkeys visited had phenology scores ranging from 0 to 4 (Figure 6). The patches used to obtain mature leaves had the highest mean phenology scores (mean 3.5), followed by ripe fruit (mean 3.07), and young leaf patches (mean 1.8: Table 1). There was a statistically significant difference between phenological score means based on food type as determined by one-way ANOVA ($F(2,115) = 3.772$, $p < 0.05$: Table 1). There was no significant difference between mean phenological scores in ripe fruit and young leaves.

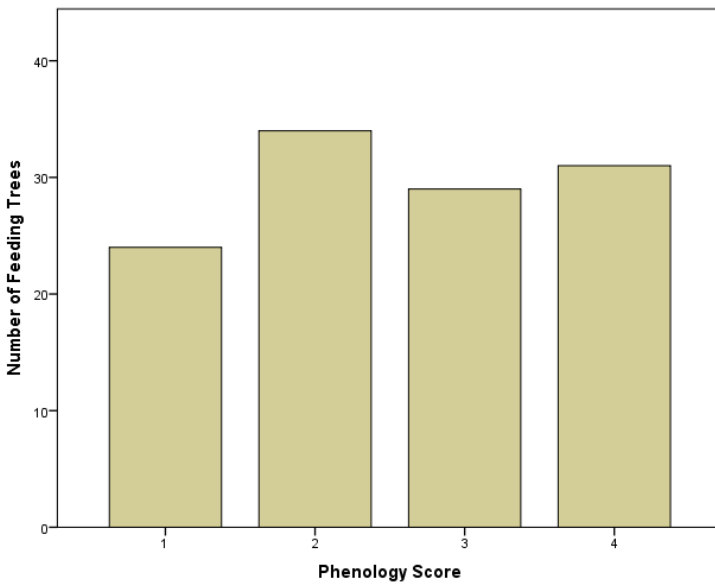


Figure 6: Weekly phenological scores for all feeding trees.

Patch richness ranged from 298 to 64,004,937 food units (leaf or fruit), with a mean of 625,705 (Figure 7). On average ripe fruit patches had the highest richness (mean = 8,298,005), followed by young leaves (mean = 5,309,576), and lastly, by mature leaves (mean = 1,232,435: Table 1). However, these differences were not statistically different, as determined by one-way ANOVA ($F(2,114) = 1.640$, $p = 0.199$).

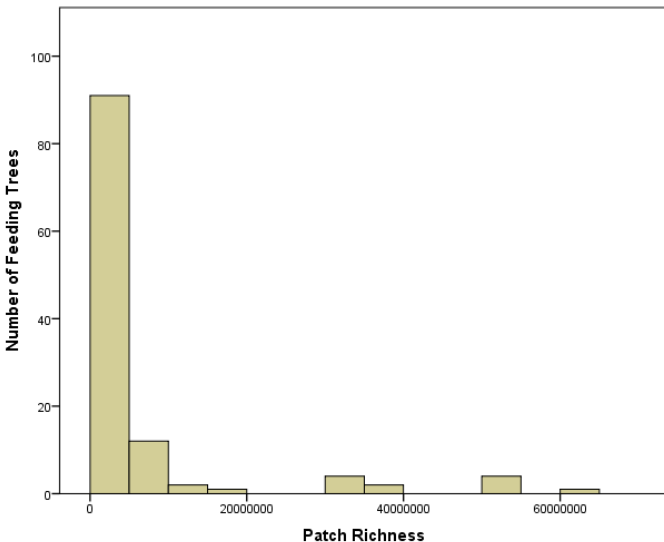


Figure 7: Patch richness scores for all feeding trees.

The howling monkeys frequently formed two or more subgroups separated by distances of up to 20 m when feeding. Sometimes after the last individual of one subgroup left the patch, a new subgroup entered, unless the rest of the group had already moved on. Often, a feeding subgroup rejoined the rest of the group to rest once the feeding bout had ended. In this way, the subgroup size varied throughout the day, by activity, and by food patch type. The average number of animals in a feeding subgroup was 2.4 individuals with a range of 1 to 5 adult individuals (Figure 8). Mean feeding subgroup sizes were largest in fruit patches (mean = 3.0), followed by young leaf patches (mean = 2.07), and mature leaf patches (mean = 1.48 Table 1). However, these differences were not statistically significant, as determined by one-way ANOVA ($F(2,115) = 1.071$, $p = 0.346$: Table 1).

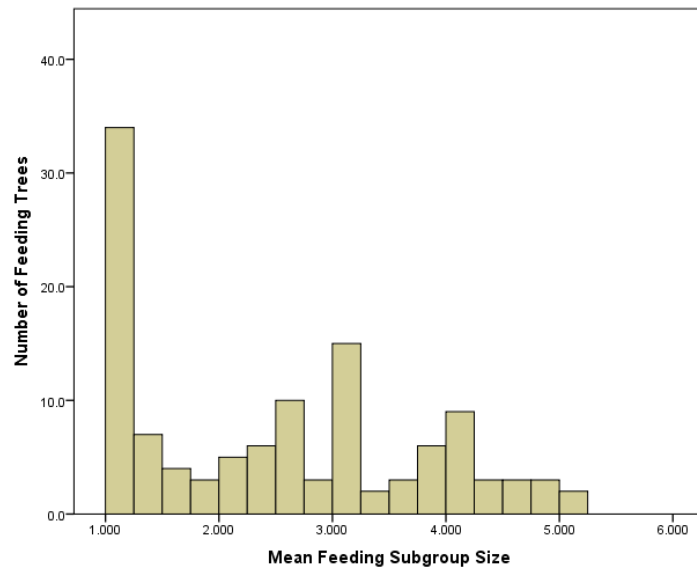


Figure 8: Mean feeding subgroup sizes during all foraging bouts.

Patch Use Analysis

A strong linear relationship was found between patch duration and feeding subgroup size (Pearson correlation = 0.504, $p < 0.001$: Table 2), explaining 25.4% of the variance in patch duration for all patch types ($r^2 = 0.254$; $F(1,114) = 38.724$, $p < 0.001$: Table 3). Therefore, as feeding group size increased, patch duration also increased. When broken down by food type, feeding group size continued to maintain a positive linear relationship with patch duration (Table 2, 3). Feeding group size explained 28.8% - 46.4% of the variance of different food types (see Table 3).

Table 2
Patch use correlation results

		Patch Duration	Feeding Subgroup Size	DBH	Patch Richness	Food Type
Patch Duration	Pearson Correlation		.498**	.218*	.136	.023
	Sig. (2-tailed)		.000	.019	.148	.810
Feeding Subgroup Size	Pearson Correlation	.498**		.507**	.128	-.063
	Sig. (2-tailed)	.000		.000	.172	.506
DBH	Pearson Correlation	.218*	.507**		.005	.057
	Sig. (2-tailed)	.019	.000		.957	.549
Patch Richness	Pearson Correlation	.136	.128	.005		.002
	Sig. (2-tailed)	.148	.172	.957		.980
Food Type	Pearson Correlation	.023	-.063	.057	.002	
	Sig. (2-tailed)	.810	.506	.549	.980	

** . Correlation is significant at the 0.01 level (2-tailed).

* . Correlation is significant at the 0.05 level (2-tailed).

Table 3

The correlation coefficients of feeding subgroup size on patch duration by food type

Patch Type	r	r ²	df	F	p
Ripe Fruit	0.537	0.288	50	20.218	0.000
Young Leaves	0.479	0.229	52	15.488	0.000
Mature Leaves	0.681	0.464	8	6.929	0.030

A weak linear relationship was observed between patch duration and DBH (Pearson correlation = 0.218, $p < 0.05$: Table 2). There was no relationship between patch duration and food type, or patch duration and patch richness (Table 2).

A weak linear relationship between patch size (DBH) and patch duration was found (Pearson correlation = 0.218, $p < 0.05$: Table 4). A strong linear relationship was found between patch size (DBH) and feeding subgroup size (Pearson correlation = 0.506, $p < 0.001$: Table 2), and DBH predicted 25.6% of the variance in feeding subgroup size ($r^2 = 0.256$, $F(1,114) = 39.184$, $p < 0.001$). When broken down by food type, feeding subgroup size in all patch types had a positively linear relationship with patch size (DBH) (see Table 4).

Table 4

The correlation coefficients of DBH on feeding subgroup size by food type

Predictor	R	R Square	df	F	Significance
Ripe Fruit	0.537	0.288	50	20.255	0.000
Young Leaves	0.429	0.184	52	11.739	0.001
Mature Leaves	0.771	0.594	8	11.694	0.009

Patch Depletion

The monkeys depleted 35 out of 118 patches, the majority of these were ripe fruit (45.7%), followed by young leaves (42.9%), and lastly, mature leaves (11.4%). There is no

statistically significant association between food type and patch depletion ($\chi^2 = 0.692$, $p = 0.707$, $df = 3$). Therefore, no food type was depleted more than others.

When considering only depleted patches, there was no linear relationship between patch duration and feeding subgroup size, DBH, patch richness, or food type (Table 5). However, there was a strong linear relationship between DBH and feeding subgroup size in depleted patches (Pearson correlation = 0.558, $p < 0.001$: Table 5), and DBH explained 31.1% of the variance in feeding subgroup size ($r^2 = 0.311$, $F(1,32) = 5.976$, $p < 0.05$).

Table 5
Patch use correlation results in depleted patches

		Patch Duration	Feeding Subgroup Size	DBH	Patch Richness	Food Type
Patch Duration	Pearson Correlation		.272	-.026	-.106	-.145
	Sig. (2-tailed)		.115	.884	.546	.407
Feeding Subgroup Size	Pearson Correlation	.272		.558**	.480**	-.017
	Sig. (2-tailed)	.115		.000	.003	.925
DBH	Pearson Correlation	-.026	.558**		.750**	.034
	Sig. (2-tailed)	.884	.000		.000	.847
Patch Richness	Pearson Correlation	-.106	.480**	.750**		-.071
	Sig. (2-tailed)	.546	.003	.000		.684
Food Type	Pearson Correlation	-.145	-.017	.034	-.071	
	Sig. (2-tailed)	.407	.925	.847	.684	

** . Correlation is significant at the 0.01 level (2-tailed).

There was a moderate linear relationship between patch richness and feeding subgroup size (Pearson correlation = 0.480, $p < 0.01$: Table 5), and patch richness predicts 23% of the variance in feeding group size in depleted patches ($r^2 = 0.230$, $F(1,32) = 4.003$, $p < 0.01$). There was also a strong linear relationship between DBH and patch richness (Table 5), likely due to the fact that patch richness is calculated using DBH. Therefore, further analysis was not conducted on this relationship.

I also examined whether patch size (DBH) influenced depletion rate, and found there was no linear relationship ($r = 0.035$, $F(1,26) = 0.144$, $p=0.707$). Therefore, the size of the patch does not influence the time it takes to deplete a patch.

An independent samples t-test was conducted to compare the following variables between depleted and non-depleted patches: feeding subgroup size, patch duration, patch richness, and DBH. There was not a significant difference in each variable between depleted and non-depleted patches (See Tables 6 and 7). Therefore, the occurrence of depletion does not have an effect on the variation in feeding subgroup size, patch duration, patch richness, and DBH.

Table 6

Mean comparison of patch characteristics in depleted vs. non-depleted patches

	Depletion	N	Mean	Std. Deviation
Feeding Subgroup Size	0	81	2.50	1.28
	1	34	2.31	1.20
Patch Duration	0	81	550.32	329.22
	1	34	660.53	418.26
Patch Abundance	0	81	6813342.98	13398904.35
	1	34	5274242.62	10916593.32
DBH	0	81	96.72	63.73
	1	34	82.84	62.30

Table 7

T-test results for patch characteristics in depleted vs. non-depleted patches

	t	Significance	Mean Difference	Std. Error Difference
Feeding Subgroup Size	0.718	0.474	0.18	0.257
Patch Duration	1.369	0.177	110.21	80.521
Patch Richness	0.592	0.555	1539100.36	2600132.3
DBH	1.072	0.286	13.88	12.939

I also tested to see if daily path length was influenced by the following variables: the number of patches visited per day, the number of depleted patches per day, mean patch production per day, and mean feeding subgroup size per day. Of these, the number of patches per day that were depleted was the only variable that significantly influenced daily path length (Table 8). There was a strong linear relationship between daily path length and the number of patches depleted in a day (Pearson correlation = 0.565, $p < 0.01$: Table 8), with the number of patches depleted in a day explaining 31.9% of the variance in daily path length ($r^2 = 0.319$, $F(1,29) = 13.110$, $p < 0.01$). All other variables were insignificant.

Table 8

Mean patch use per day and daily path length correlation results

	Daily Path Length	Patches Depleted Per Day	Patches Visited Per Day	Mean Feeding Subgroup Size Per Day	Mean Patch Production Per Day
Daily Path Length		.565 .001	.143 .451	-.242 .198	.285 .127
Patches Depleted Per Day	.565 .001		.182 .337	-.069 .719	.233 .216
Patches Visited Per Day	.143 .451	.182 .337		-.203 .281	.102 .592
Mean Feeding Subgroup Size Per Day	-.242 .198	-.069 .719	-.203 .281		.165 .383
Mean Patch Production Per Day	.285 .127	.233 .216	.102 .592	.165 .383	

Satiation

Satiation was detected in 37 out of 118 patches, the majority was ripe fruit (64.86%, n=24), followed by young leaves (32.43%, n=12), and lastly, mature leaves (2.7%, n=1; excluded from analysis). There is no statistically significant association between food type and satiation ($\chi^2 = 0.633$, $p = 0.729$).

I examined whether feeding group size, DBH, food type and patch richness influenced patch duration in patches where satiation occurred. There was a strong linear relationship between patch duration and feeding group size in satiated patches (Pearson correlation = 0.662, $p < 0.001$: Table 9), and feeding group size predicts 43.8% of the variance in patch duration in satiated patches ($r^2 = 0.438$, $F(1,33) = 25.742$, $p < 0.001$: Table 10). There was a moderate linear

relationship between patch duration and DBH (Pearson correlation = 0.489, $p < 0.01$: Table 9), and DBH explains 23.9% of the variance in patch duration in satiated patches ($r^2 = 0.239$, $F(1,33) = 10.382$, $p < 0.01$: Table 10). There was also a moderate linear relationship between patch duration and patch richness (Pearson correlation = 0.422, $p < 0.05$: Table 9), and patch richness explains 17.8% of the variance in patch duration in satiated patches ($r^2 = 0.178$, $F(1,33) = 7.161$, $p < 0.05$: Table 10). All other results were not significant.

Table 9
Patch use correlation results in satiated patches

		Food Type	Patch Duration	Feeding Subgroup Size	DBH	Patch Richness
Food Type	Pearson Correlation		.138	.153	.203	-.051
	Sig. (2-tailed)		.430	.379	.243	.770
Patch Duration	Pearson Correlation	.138		.662**	.489**	.422*
	Sig. (2-tailed)	.430		.000	.003	.012
Feeding Subgroup Size	Pearson Correlation	.153	.662**		.694**	.198
	Sig. (2-tailed)	.379	.000		.000	.255
DBH	Pearson Correlation	.203	.489**	.694**		.154
	Sig. (2-tailed)	.243	.003	.000		.378
Patch Richness	Pearson Correlation	-.051	.422*	.198	.154	
	Sig. (2-tailed)	.770	.012	.255	.378	

** . Correlation is significant at the 0.01 level (2-tailed).

* . Correlation is significant at the 0.05 level (2-tailed).

Table 10

Effects of mean feeding subgroup size, DBH, and patch richness on patch duration in patches where satiation occurred

Predictor	R	R Square	df	F	Significance
Feeding Group Size	0.662	0.438	(1,33)	3.007	0.000
DBH	0.489	0.239	(1,33)	0.884	0.003
Patch Richness	0.422	0.178	(1,33)	4.221	0.012

For a summary of all study data analysis results, see Table 11. In total I found 13 significant relationships between the dependent variables and the predictors tested.

Table 11
Summary of the analyses in the study

Dependent Variable	Predictor	Results*
Patch Duration	Feeding Subgroup Size	
<i>All Patches</i>		Significant positive, moderate influence
<i>Ripe Fruit Only</i>		Significant positive, moderate influence
<i>Young Leaves Only</i>		Significant positive, moderate influence
<i>Mature Leaves Only</i>		Significant positive, strong influence
<i>Depleted Patches</i>		No significant influence
<i>Satiation Occurred</i>		No significant influence
Patch Duration	DBH (Patch Size)	
<i>All Patches</i>		Significant positive, weak influence
<i>Ripe Fruit Only</i>		Significant positive, moderate influence
<i>Young Leaves Only</i>		No significant influence
<i>Mature Leaves Only</i>		No significant influence
<i>Depleted Patches</i>		No significant influence
<i>Satiation Occurred</i>		No significant influence
Patch Duration	Patch Abundance	
<i>All Patches</i>		No significant influence
<i>Ripe Fruit Only</i>		No significant influence
<i>Young Leaves Only</i>		No significant influence
<i>Mature Leaves Only</i>		No significant influence
<i>Depleted Patches</i>		No significant influence
<i>Satiation Occurred</i>		Significant positive, moderate influence
Feeding Subgroup Size	DBH (Patch Size)	
<i>All Patches</i>		Significant, positive, strong influence
<i>Ripe Fruit Only</i>		Significant positive, moderate influence
<i>Young Leaves Only</i>		Significant positive, moderate influence
<i>Mature Leaves Only</i>		Significant positive, strong influence
<i>Depleted Patches</i>		Significant, positive, strong influence
Depletion Rate	DBH (Patch Size)	No significant influence
Daily Path Length	Patches Visited Per Day	No significant influence
	# Depleted Patches Per Day	Significant positive, moderate influence
	Mean Patch Production Per Day	No significant influence
	Mean Feeding Group Size Per Day	No significant influence

*significance was set at $p \leq 0.05$; a “weak” influence is defined as $-0.3 > r < 0.3$, “moderate” influence is defined as $0.3 < r < 0.5$ or $-0.3 > r > -0.5$, “strong” influence defined as $r > 0.5$ or $-1 > r < -0.5$

DISCUSSION

The howler monkey study group ate ripe fruit and young leaves more than mature leaves. Similar dietary profiles are exhibited by other howler monkey species (*Alouatta pigra*, mean 40.8% fruit, 37.2% young leaves, 7.9% mature leaves, 91% ripe fruit (when maturity could be determined), Silver et al., 1998; *Alouatta palliata*, 28.5% fruit, 49% leaves (immature and mature not differentiated), Chapman, 1998; *Alouatta seniculus*, 30.1% fruit, 59.7% young leaves; 7.3% mature leaves, Palma et al., 2011).

On average the group split into two feeding subgroups. Even when the monkeys were in large fruit patches, the average feeding group size was only 3 adult individuals (ranging up to 5 individuals), whereas the total number of adult members was 8 individuals. This may have been a behavioral strategy the monkeys used to reduce feeding competition.

The monkeys also spent the most time resting, followed by feeding, traveling, and interacting socially. Resting is generally the most common howler monkey activity, as is evident in the activity budgets of other howler species (*Alouatta pigra*, 61.9% resting Silver et al., 1998; *Alouata seniculus*, 62.4% resting Palma et al., 2011). Howler monkeys do not have specialized stomachs or caecums in which leaves can be digested through the aid of microbes, instead they rely on long retention times to allow for the fermentation of leaves in the intestines (Silver et al., 1998). Recently, a study found that mantled howlers in Mexico produce tannin-binding salivary proteins that inactivate tannins from food sources that typically induce a loss of dietary protein and produce toxins that are hydrolyzed in the gut (Espinosa-Gómez, 2015). The concentration of

tannin did not differ between a fruit and leaf diet, suggesting that these salivary proteins enable howlers to consume diets with varying tannin content (Espinosa-Gómez, 2015).

Young leaves are assumed to be richer in digestible protein content than mature leaves and have less fiber and toxic compounds (Ganzhorn, 1992). Milton (1984) found that young leaves eaten by howler monkeys on Barro Colorado Island in Panama contained approximately 33% more protein and 35% less fiber, than mature leaves, and the monkeys ate young leaves more than mature leaves. However, howler monkeys rest often even when their diet contains large quantities of fruits (Palma et al., 2011), indicating that they may not rest for large time periods only for leaf fermentation. My study group ingested the entire fruit of *Spondias mombin*, passing the 5-8cm seeds intact. If howler monkeys swallow whole fruit, they may rest in order to break down the fibrous fruit, or to allow time for seeds to pass through their gastrointestinal tract before resuming feeding. Other studies found a strong relationship with the abundance of individual bacterial taxa and changes in host diet, suggesting that gut microbiota provide additional energy and nutrients to compensate for changes in diet (Amato et al., 2014: *Alouatta pigra*). This provides additional evidence for the strategies used by howlers to offset the complex chemical breakdown of various components of their diet.

I found a significant positive relationship between DBH and feeding group size. However, other studies have found no correlation between tree size and feeding group size (Chapman, 1988; Snaith and Chapman, 2005; Tombak et al., 2012). The differences in these results indicate that while DBH may have been an appropriate measure of patch size at my study site, this may not be the case in other regions, or that other factors are shaping subgroup foraging sizes in other species.

In addition to determining which factors influence foraging group size, my results also suggest which factors influence patch duration. Foraging subgroup size positively influenced patch duration for the howling monkeys in this study for all food types they consumed. Chapman (1988) found similar results in the howling monkeys at Santa Rosa National Park, Costa Rica. Snaith and Chapman (2005) studying red colobus at Kibale National Park found that patch duration was significantly positively affected by foraging subgroup size, but only once patch size (DBH) was accounted for, suggesting a weaker relationship between these variables than was observed for my study group. Individuals in large groups might spend more time feeding per day than individuals in small groups to compensate for added energy expended in travel (Chapman, 1988). Alternatively, members of large subgroups may obtain fewer food items per minute, likely due to increased interference, and therefore they may need to spend more time in a food patch before they are satiated, as compared to small subgroups (Chapman, 1988). It is also possible that the effect of foraging group size on patch duration is an indication of scramble competition occurring.

Patch size (measured by DBH) also had a significant positive, weak influence on patch duration. When broken down by food type, however, only ripe fruit patches maintained this relationship. These results indicate that increasing patch size allows for larger feeding group sizes. This is likely due to the fact that a larger patch size can accommodate a larger feeding group. It is also intuitive, since the patch size of fruit patches were on average twice as large as other food patches.

I also tested to see which factors influenced the howler monkeys' daily path lengths. The percentage of depleted patches visited per day was the only variable with a significant (positive) correlation with daily path length. These results indicate that the monkeys would travel farther

on days in which they depleted more patches of food, likely to obtain adequate resources. As fruits formed the majority of depleted patches, the energetic gains from foraging on this food source must outweigh the costs of traveling to obtain this resource

Satiation and Depletion

Satiation was detected in 37 out of 118 patches, and the majority of these patches contained ripe fruit. Thus, in 31% of food patches the howler monkeys are unlikely to experience feeding competition. The only significant predictor of patch duration, in patches where satiation was detected, was patch richness, indicating that larger crops allowed the howler monkeys to stay longer and “fill up”.

Patch richness also positively influenced patch duration, but only in patches where satiation occurred. These results are intuitive, showing that a more abundant food patch would allow monkeys to stay longer. These results may simply result from individuals remaining in a patch, even when satiated, while others continue feeding. Alternatively, individuals may have more time to be selective in a relatively abundant patch, causing them to stay longer as they forage more slowly. However, when broken down by food type, these results remained significant for ripe fruit and young leaves but not for mature leaves. Surprisingly there was only a significant positive correlation in satiated patches, indicating that other factors may contribute to different results in depleted patches.

Howler monkeys also depleted 30% of the patches they fed in when feeding on young leaves and ripe fruits. Patch depletion has also been detected in mantled howlers at Santa Rosa

National Park (Chapman, 1988) and red colobus at Kibale National Park (Snaith and Chapman, 2005). However, not all folivores deplete patches: Tombak et al. (2012) tested for patch depletion in *Colobus guereza* at Kibale, but found no indication of patch depletion.

I examined which factors specifically influenced howler monkey behavior in depleted patches. The only linear relationship was found between the patch size (DBH) and feeding subgroup size. This indicates that as patch size increases, so does feeding subgroup size. Even in patches where depletion occurred, it's likely that a larger patch can accommodate a larger feeding subgroup size.

Tombak et al (2012) argue that within-group competition for food among guerezas, who typically form groups of 4-11, is lower than in red colobus, which have group sizes of 12-150 monkeys (Chapman, 2007). They suggest that folivores in small groups do not experience feeding competition, but caution that this may not be the case for other species that form large groups (Tombak et al., 2012). The results of this study suggest that these mantled howler monkeys at Piro Research Station, Costa Rica, which formed a group of 8 individuals, similar to guereza group sizes, do deplete patches. This is an indication that these monkeys experience within-group scramble competition, and that this type of competition may be an important factor determining group size. Furthermore, the number of patches where depletion occurred in a day had a positive, moderate influence on daily path length. This indicated that my study group had to travel further on days in which they depleted patches, likely so that all individuals could obtain the necessary nutritional intake.

Thus, patch depletion is an indicator that these folivores experience within-group scramble competition. Furthermore, my results suggest that the scramble competition constrains group size. These findings challenge the notion of the "folivore paradox" for this study group

and suggest that patch depletion should be analyzed to better understand scramble competition in folivorous species. Acknowledging the presence of scramble competition in folivores can aid in understanding its effects on social behavior.

Future Directions

Further studies are required to examine the effect of group size on travel costs, habitat quality, and nutritional ecology of preferred food sources. One interesting future study could compare a significantly larger howler group (approximately 20-30 individuals) on the Osa Conservation property with the study group I observed. The larger group at Osa has a home range that is enclosed by the ocean, a service road, and a field station. It would be interesting to compare depletion rates and habitat quality of this substantially larger group to the smaller group at Piro in order to compare their foraging strategies and test optimal foraging models. There was no linear relationship between patch duration and feeding subgroup size in depleted patches for my study group. Optimal foraging theory suggests that “giving-up time” should occur faster in habitats which contain high quality and more feeding patches than in habitats with scarce resources because animals can more quickly find another food patch (Charnov, 1976). In contrast, monkeys should give-up later (and deplete patches further) in poorer habitats where the inter-patch difference is greater or where there only a few high quality patches (Snaith and Chapman, 2005). It would be useful to compare habitat quality at this study site, with those at other study sites by measuring feeding patch quantity, quality, and abundance, and then compare

feeding patch durations. In this way, it would be possible to determine if the monkeys are optimizing patch use based on their environment.

Nutritional analyses of fruits and leaves consumed by the howlers, and further studies of the digestive capabilities of the howlers, would allow for direct estimates of benefits gained by eating different food sources. These nutritional analyses in combination with a more complete map of food sources and an analysis of the travel costs incurred by travelling among feeding trees would allow for a better evaluation of the costs involved in leaving a patch. In this way it would be possible to conduct a cost/benefit analysis to determine if monkeys are balancing the costs of leaving a patch and moving to a new patch with the benefits of staying in a particular food source.

Other folivorous species should be studied to determine the presence of patch depletion and aid in offering more results to help explain the “folivore paradox”. In addition, these studies should carry out an analysis of food availability versus food intake and choice. Other spatial analyses would also be interesting to test if the paths chosen are direct to known sources or not. Thus, a variety of valuable follow-up projects could be done on howler monkeys, especially in varying habitat types, to better understand their foraging and social behavior.

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