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ORIGINAL ARTICLE

Patch depletion behavior differs between sympatric folivorous primates

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Abstract Food competition in group-living animals is commonly accepted as a critical determinant of foraging strategies and social organization. Here we examine food patch depletion behavior in a leaf-eating (folivorous) primate, the guereza (*Colobus guereza*). Snaith and Chapman (2005) studied the sympatric folivorous red colobus (*Procolobus rufomitratus*), which shares many food resources with the guereza. They determined that red colobus deplete the patches (feeding trees) they use, while we found contrary evidence for guerezas using the same methods. We found that the time guerezas spent feeding in a patch was affected by neither tree size, an indicator of food abundance, nor the size of the feeding group, an indicator of feeding competition. For their principal food item (young leaves), intake rate remained constant and coincided with a decrease in the distance moved to find food within a patch, implying that guerezas do not deplete patches. This points to a fundamental difference in the use of food by guerezas and red colobus, which may be linked to the large difference in their group sizes and/or to a disparity in their digestive physiologies. However, further analyses revealed that the number of feeders within a patch did not affect patch depletion patterns in either species, leaving the potential for a physiological basis as the most plausible explanation. Our research highlights the need for a more critical examination of folivorous primate feeding ecology and social behavior, as all folivorous primates are typically lumped into a single category in socioecological models, which may account for conflicting evidence in the literature.

Keywords Black and white colobus · *Colobus guereza* · Folivore paradox · Group size · Kibale National Park

Introduction

Identifying the extent that feeding ecology shapes group size and social structure is a central theme of behavioral ecology (Gartlan and Brian 1968; Eisenberg et al. 1972; Bradbury and Vehrencamp 1976; Terborgh 1983; van Schaik and van Hooff 1983; Jarman and Southwell 1986; Wrangham et al. 1993). Primate feeding ecology is of particular interest in investigating grouping behavior since primate group sizes are highly variable not only within, but also between species. Intraspecific group size for red

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colobus (*Procolobus rufomitratus*), for example, varies between 12 and 150 members (Chapman and Chapman 2000). Interspecific variation may range from a single individual, as seen in orangutans (van Schaik and van Hooff 1996), to over 800 members in mandrills (*Mandrillus sphinx*; Abernethy et al. 2002). Diet and feeding competition are ecological factors often invoked to explain variation in primate socioecology (van Schaik 1983; Janson 1988; Snaith and Chapman 2005), but how a primarily leaf-based (folivorous) diet influences primate grouping patterns is an area of considerable debate.

The most common models to evaluate evolutionary causes of primate group size variation involve comparisons of species that have differing food densities and distributions (Wrangham 1980; Janson 1988; Isbell 1991; Sterck et al. 1997; Snaith and Chapman 2007). One way to unveil more about the evolutionary drivers of the socioecology of folivorous primates may be to look beyond their food density and distribution, and to consider the manner in which they use their food resources. If food resources themselves are a critical determinant of group size, examining two species that share habitats and food resources, but have different group sizes, would be a useful context in which to explore how feeding behavior contributes to social structure. The red colobus and guereza (*Colobus guereza*, also known as the black and white colobus) of Kibale National Park, Uganda (hereafter Kibale) are two species that fit these criteria. They have high overlap in diet and home range, in addition to similarly low local predation pressures and equal body sizes (Delson et al. 2000; Chapman et al. 2002; Chapman et al., unpublished data). Interestingly, red colobus form large social groups (mean 68, range 12–150; Struhsaker 1975; Struhsaker and Oates 1975; Snaith and Chapman 2008), while guerezas form much smaller groups (mean 8, range 4–11; Oates 1974, 1977; Teelen 1994; Harris and Chapman 2007). The colobines of Kibale therefore provide an excellent system in which to explore the interactions between group size and the feeding behavior of folivorous primates. Evidence exists to suggest that there are differences in their use of food resources. For example, the energy budgets of guerezas and red colobus may differ, as indicated by their feeding patterns within a tree: guerezas frequently rest for up to a couple of hours between feeding bouts within a feeding tree, while red colobus typically do not. A closer look at the way they use their food resources may reveal more about differences in selective forces on their group sizes.

Because of the high abundance and widespread nature of leaves in rainforests, socioecological models often assume that folivorous primates experience little to no feeding competition (Wrangham 1980; Isbell 1991; Sterck et al. 1997). Folivorous primates are therefore theoretically free to form large groups without increasing their travel to find food or the rate at which they deplete patches of food (Charnov 1976; Snaith and Chapman 2005). Increased group size affords a protective advantage against predation and, potentially, infanticide risk (Treves and Chapman 1996; Koenig and Borries 2002; Snaith and Chapman 2005; but see Steenbeek and van Schaik 2001). Many folivores, however, form small groups despite the presumed lack of feeding competition, as is the case with guerezas in Kibale. This contradiction has been termed the folivore paradox (Steenbeek and van Schaik 2001; Koenig and Borries 2002). Recent studies aimed at resolving this issue have found that, contrary to the underlying assumption made by many socioecological models, the preferred foods of some folivorous primates are in fact limited and within-group competition for these foods does occur (Snaith and Chapman 2005, 2008; Saj et al. 2007; Harris et al. 2010). Two studies have also suggested that infanticide actually selects against large groups for some species, including guerezas (see Steenbeek and van Schaik 2001; Chapman and Pavelka 2005).

Snaith and Chapman (2005) investigated the disconnect between theory and empirical data in terms of food competition within folivore groups in a study of the feeding ecology of red colobus monkeys in Kibale, and found clear evidence of food limitation and within-group food competition. Food intake rate (an index of feeding gain) decreased over time despite an increase in distances moved to find food (a proxy for feeding effort), suggesting that red colobus deplete the trees they feed in, also called food patches. In a later study, Snaith and Chapman (2008) found that larger groups occupied larger home ranges and that group size was positively related to the rate of patch depletion, reduced female reproductive success, and decreased foraging efficiency (e.g., longer daily travel distances). Although these findings shed light on the feeding ecology of red colobus, they may not be representative of other folivorous species with smaller groups and therefore different competitive resource regimes.

To better understand how folivory influences smaller primate groups, Harris et al. (2010) studied the response of guerezas to a sharp reduction in food availability. During 4 months of progressive food scarcity, two guereza groups increased their foraging effort by increasing their daily path length, the number of patches visited per day, the percentage of time spent feeding, and their dietary diversity. These results suggest that small folivorous groups may also be food-limited. However, whether folivores that form small groups experience within-group food competition and how they use their food resources in terms of patch depletion remain unclear. For example, if guerezas increase their dietary diversity during times of low food availability, they may need to increase their foraging effort to find the tree species or combination of tree species that will provide them with the nutrient balance that they need or to avoid a buildup of toxins. It is therefore still possible that they do not deplete their food patches like the red colobus do, even when the availability of their more typical (and presumably preferred) foods is low.

Here we evaluate guereza patch depletion behavior, using the same methods as those used by Snaith and Chapman (2005) for red colobus, to compare patch depletion strategies between the two sympatric colobines. If guerezas do not share the same patch depletion behavior as red colobus, this may have implications for within-group competition levels and may provide important clues as to why they form substantially smaller groups.

Methods

Study site and species

Guerezas are diurnal, arboreal primates of medium size, widely distributed across sub-Saharan Africa (Oates et al. 1994). Males weigh 9.1 kg, while females weigh 7.8 kg on average (Delson et al. 2000), and they are strongly folivorous, feeding chiefly on young leaves (Oates 1977; Fashing 2001; National Research Council 2003; Harris and Chapman 2007). Groups are usually composed of either a single or a few males with several females and typically range in size from 4 to 11 individuals in our study area (Harris and Chapman 2007).

We studied guerezas for 3 weeks from May to June 2009 and for 4 weeks from June to July 2010; both field seasons were timed to occur during periods of very low food availability for guerezas (Fig. 1). Our study site, Kanyawara, is a moist, evergreen forest in Kibale (795 km^2, 0°13′–0°41′N and 30°19′–30°32′E) with a mean annual rainfall of 1,707 mm (1990–2010) falling mainly during the two rainy seasons (Struhsaker 1997; Chapman and Lambert 2000; C. A. Chapman and L. J. Chapman, unpublished data). We collected feeding data from three groups that inhabit areas less than 1 km apart [“Kasembo” ($n = 6$ individuals), “Zikuru” ($n = 11$), and “Basaija” ($n = 7$); names follow Harris (2006)]. At least two groups of red colobus occupied the same area: “Small Camp” with 86 members and “Large Mikana” with approximately 150 members.

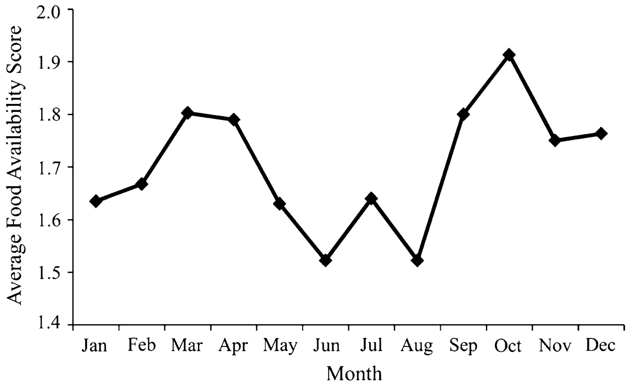

Fig. 1 The average monthly food availability score from a phenology trail that was monitored between January 2007 and September 2010 (C. A. Chapman and L. J. Chapman, unpublished data). Food availability was assessed by visually scanning 300 individuals of 33 tree species once a month to determine the presence of different leaf stages, flowers, and fruit (see Chapman et al. 2005 for exact species and details)

Procedure

We applied the focal patch methods of Snaith and Chapman (2005) to investigate patch depletion in guerezas. We observed the feeding behavior of guereza groups during their occupancy of a given food patch, defined as a single feeding tree. We chose focal patches opportunistically; an observation session began when the first individual of the group entered a patch and ended when the last individual left. The duration of the observation session was recorded as patch occupancy time. We recorded tree species, the food items consumed (e.g., young or mature leaves), and diameter at breast height (DBH), which is a reliable indicator of leaf biomass and therefore food availability in a patch (Harrington 1979; Catchpole and Wheeler 1992; Brown 1997). At 5-min intervals we counted the number of individuals in the patch (patch group size) and the subset of individuals feeding (feeding patch group size).

To assess food limitation in guerezas, we examined trends in feeding gain and effort among the monkeys in the patch. Because we were interested in changes in the feeding behavior of the group as a whole over patch occupancy time, the patch served as the sampling unit rather than individual monkeys. This allowed us to select feeding individuals for observation opportunistically, with preference for adults. We used the number of bites and food items consumed in 1 min (intake rate) as an index of feeding gain. Over 3-min intervals, we recorded the rate of movements to find food within a patch as a proxy for feeding effort [we measured movement frequency (no./3 min) and the distance moved (m/3 min) only for movements that were immediately followed by feeding]. This closely follows Snaith and Chapman (2005), with the exception that they used a single measure of feeding effort: distance moved (m/3 min).

If a slowed intake rate were coupled with a constant or increasing feeding effort over time, this would provide evidence for patch depletion. However, a slowed intake rate paired with a reduced feeding effort may indicate food satiation. Since very few individuals fed simultaneously, the feeding group was easily monitored without bias for particular food types or locations in the tree.

Analysis

We performed all analyses as per Snaith and Chapman (2005), with some additional tests. We used a multiple linear regression to examine the influence of DBH (food availability proxy) and the mean feeding patch group size (calculated over the entire visit to a patch) on patch occupancy time. If patches were depleted in a single visit, a shorter occupancy time would be expected in smaller trees and/or for larger feeding groups. If guerezas do not deplete patches in a single visit, tree size or feeding patch group size should not affect occupancy time. Using a two-sample *t*-test, we compared the DBH of all trees in our data set to that of Snaith and Chapman (2005) to assess whether the two species fed in trees of different sizes (and therefore with different food abundances per patch).

To assess feeding gain and effort, the mean intake rate and movement rates (by both frequency and distance) from the first quarter of each observation session were compared to the last quarter using a paired *t*-test, which controls for the variation among trees. Observation sessions (the full set of individual observations taken during a visit to a patch) with fewer than six individual observations of feeding gain and effort were excluded, and for those with six to seven individual observations we compared the first and last thirds of the session. We analyzed the data for different food items (i.e., young leaves and mature leaves) together, as well as separately by item to evaluate whether only certain foods are depleted (Chapman 1988). For example, young leaves are the preferred food of guerezas in Kibale (Oates 1994), but are patchily distributed (Harris and Chapman 2007), which may influence whether or not they are depleted. To evaluate the effects of individual life stage, time of day, year, or group, we repeated our analyses separating the data by each of these factors.

Finally, we performed multiple regression analyses to determine whether the mean feeding patch group size is a function of patch depletion behavior (change in mean intake rate and in distance moved) in guerezas and/or red colobus (data for red colobus from Snaith and Chapman 2005).

Results

In 2009, 28 patch occupancy periods were collected, and another 38 were obtained in 2010, totaling more than 100 observation hours. Over a patch occupancy period, mean patch group size was 2.86 individuals and mean feeding patch group size was 1.42 individuals, implying that only half of the individuals in a patch were feeding at any given time. Guereza groups fed on 15 tree species, of which *Celtis durandii* was most common (36% of observation sessions). Young leaves were the most frequently consumed food part (78% of bites in 2009 and 65% in 2010).

Patch occupancy time (mean 64.32 min) was not affected by DBH (mean 127.1 cm) or mean feeding patch group size ($R^2 = 0.005$, $p = 0.850$, partial $p = 0.729$ with mean feeding patch group size constant, partial $p = 0.636$ with DBH constant, $n = 64$; one DBH and one occupancy time value were missing). We found no correlation between DBH and mean feeding patch group size ($r = 0.070$, $p = 0.582$, $n = 65$). In addition, we found that guerezas fed in significantly smaller trees than red colobus ($p < 0.0001$, $n = 65$ and 68, respectively).

Feeding gain did not change significantly over patch occupancy time ($p = 0.508$, $n = 66$). When separated by food type, the intake rate of young leaves remained constant ($p = 0.181$, $n = 66$), but the number of mature leaves consumed per minute decreased ($p = 0.019$, $n = 66$). In terms of feeding effort, the distance moved to find food decreased over patch occupancy time for all food items combined ($p = 0.026$, $n = 66$). However, when analyzed separately by dominant food type, this trend was only significant for young leaves (young leaves: $p = 0.014$, $n = 55$; mature leaves: $p = 0.973$, $n = 9$) (Fig. 2). Finally, the frequency of movements within a patch did not

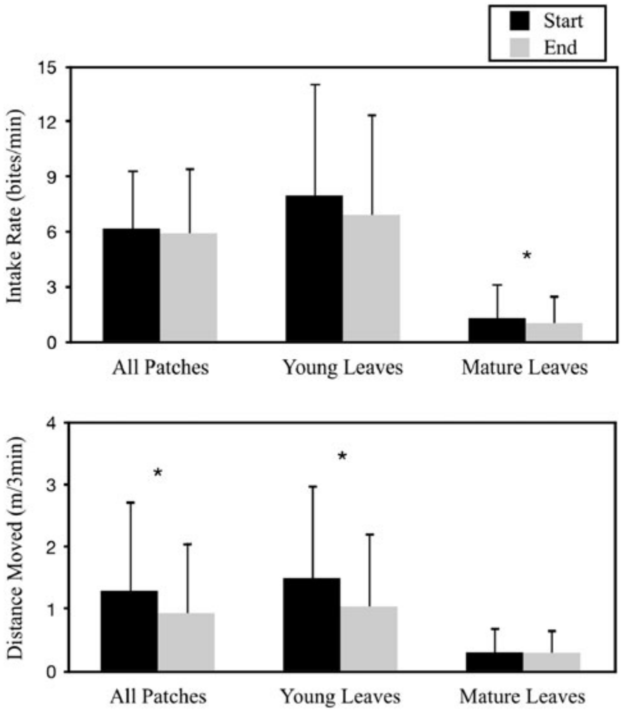

Fig. 2 Changes in the mean intake rate and mean distance moved for all patches combined and for young leaves and mature leaves separately. The *stars* indicate statistically significant differences between the first and last quarters of an observation session

significantly change over patch occupancy time whether food items were separated (young leaves: $p = 0.211$, $n = 55$; mature leaves: $p = 0.521$, $n = 9$) or combined ($p = 0.182$, $n = 66$). We found no change when observation sessions were separated by individual life stage, time of day, year, or group.

The number of feeders (mean feeding patch group size) had no effect on change in the intake rate or distance moved for any measures of patch depletion that significantly changed over patch occupancy time (guereza distance moved: $R^2 = 0.009$, $p = 0.438$, $n = 66$; red colobus intake rate and distance moved: $R^2 = 0.001$, $p = 0.823$ and $R^2 = 0.004$, $p = 0.693$, respectively, $n = 45$). Repeating these regressions with the patch occupancy time as a second independent variable (controlling for this factor) did not result in a change in significance. Our results are summarized and compared to those of Snaith and Chapman (2005) in Table 1.

Discussion

The folivore paradox is based on the assumption that all folivorous primates have low levels of food competition within their groups, allowing them to have large groups as an anti-predator or anti-infanticide strategy (Treves and Chapman 1996; Koenig and Borries 2002; Snaith and Chapman 2005). Our findings suggest that within-group competition for food among guerezas is lower than in red colobus. Thus, the assumption of low food competition among folivores may hold only for those that form small groups, as in guerezas, but may be invalid for species that form large groups, such as the red colobus.

In contrast to red colobus groups, the time guerezas spent in a patch was not a function of tree size or the number of individuals feeding, which is evidence against patch depletion. For all food items combined, the constant feeding gain coupled with a decrease in the distance moved to find food may indicate that satiation, rather than patch depletion, is occurring. On the other hand, when data were separated by food type, there was a significant decrease in mature leaf intake, while the decrease in feeding effort only applied to young leaf consumption. These trends can be explained based on three assumptions backed by our observations and by other studies: (1) mature leaves are less digestible than young leaves, (2) mature leaves are more abundant than young leaves, and (3) young leaves are preferred over mature leaves by folivorous primates (Oates 1994; Isbell 1998; Chapman and Chapman 2002). If mature leaves are less digestible, guerezas feeding in a patch with mostly mature leaves may take longer to process their food, requiring them to slow down their intake rate towards the end of their visit. This does not exclude the possibility that guerezas also satiate on young leaves; their constant intake rate may be explained by intermittent clearing of the foregut of these more digestible foods during the long and frequent resting periods observed. If mature leaves are more abundant but less preferred, a group may move more upon entering a patch because individuals need to search for concentrations of young leaves. In trees where mature leaves are the main food item consumed, these movements to find feeding spots are less necessary, and so the distance moved remains constant at a low rate.

Our results run counter to the findings of Snaith and Chapman (2005) in red colobus, where a decrease in

Table 1 A comparison of patch depletion results for guereza and red colobus monkeys of Kibale National Park, Uganda, with red colobus data from Snaith and Chapman (2005)

	Guereza	Red colobus
Multiple regressions		
Patch occupancy time		
Sample size	64	44
Mean patch occupancy time (min)	64.32	36
Mean DBH (cm)	127.1	205.9
Mean feeding patch group size (no. of feeders)	1.42	3.63
Effect of DBH and feeding patch group size (R^2)	0.005	0.145*
Change in intake rate and distance moved		
Sample size	66	45
Effect of no. of feeders on Δ intake rate (R^2)	NA	0.001
Effect of no. of feeders on Δ distance moved (R^2)	0.009	0.004
Paired *t*-tests		
Feeding gain		
Sample size	66	68
Δ Bites/min for all food items	−0.24	−2.38**
For young leaves	−1.06	−2.91**
For mature leaves	−0.28*	0.32
Feeding effort		
Sample size	66	45
Δ Movement rate (no./3 min) for all food items	−0.11	NA
For young leaves	−0.15	NA
For mature leaves	−0.06	NA
Δ Distance moved (m/3 min) for all food items	−0.36*	0.82**
For young leaves	−0.45*	1.14**
For mature leaves	−0.01	−0.10

DBH diameter at breast height, *NA* not available

* $p < 0.05$, ** $p < 0.01$

feeding gain co-occurred with an increase in feeding effort, indicating patch depletion. When separated by food type, these trends were only significant for young leaves, which is intuitive because young leaves are the preferred food type of red colobus (Snaith and Chapman 2005). Interestingly, red colobus fed in significantly larger trees than guerezas, making their difference in patch depletion behavior more remarkable since larger trees produce more food.

Patch depletion behavior, if present among guerezas, should have been most apparent during the time of the year we sampled, which was during the period of lowest food availability (Fig. 1). However, a potential confound arises from the possibility that only certain groups of guerezas deplete patches in a single visit. Two of the groups we observed (Kasembo and Zikuru) were found to be of high rank among guereza groups by Harris (2006). This could mean that they occupy preferred home ranges with higher food availability or quality; it is possible that lower-ranking groups of guerezas do exhibit patch depletion behavior. Since guereza groups have short daily travel distances, cohesive groups, and typically feed in neighboring trees (Harris et al. 2010), it is unlikely that the decrease in distances moved is due to an increase in visual monitoring to keep group members in sight.

Red colobus may deplete patches simply because their groups are much larger than those in guerezas and will thus have more individuals feeding simultaneously. However, we found that the number of feeders did not affect patch depletion patterns in either species, which is evidence against group size as a driving force behind their difference in patch depletion behavior. This difference may instead have a basis in digestive physiology. Red colobus have an extra chamber in their stomach, called a presaccus, which may function for storage and preliminary digestion of food for more efficient processing (Chivers 1994; Stevens and Hume 1995; Caton 1998; National Research Council 2003; Wright et al. 2008). Guerezas lack this chamber and frequently rest for extensive periods of time in a patch between feeding bouts and before moving to another patch to feed, a behavior that is much less common among red colobus. Thus, guerezas may have a lower energy budget, spending more time resting and digesting their food; red colobus spend less time in each patch and move rapidly to continue feeding, which may be necessary to feed a large group (Snaith and Chapman 2005).

It is interesting to consider why guerezas might leave a patch before depleting it of food. It is possible that their feeding habits may be dictated by physiological thresholds, such as limited nutrient, toxin, or gut capacities (Chapman and Chapman 2002). If they are feeding on a patch high in a certain nutrient, they may relocate to another tree to obtain more of another nutrient before depleting the patch. They may also require long resting periods after bouts of feeding to detoxify specific secondary compounds found in their food or to clear their guts to enable additional food intake.

If guerezas do not deplete food patches, it is puzzling that they do not increase their group sizes to the point at which they do deplete them. Infanticide is sometimes considered a driver for smaller groups and may offer an explanation for this. Thomas' langurs (*Presbytis thomasi*) have been postulated to experience selection for small or mid-sized groups due to infanticide because higher rates of group takeovers by males and higher rates of infanticide occur in larger groups for this species (Steenbeek and van Schaik 2001). A similar effect of infanticide on group size has been suggested for the guereza (Chapman and Pavelka 2005), and this may offer an explanation of the group size difference between guerezas and red colobus, as the former have much higher infanticide rates than the latter (C. A. Chapman, unpublished data).

This study found evidence that within a single visit to a tree, guereza groups do not deplete resources to the extent that feeding effort is increased. Since Snaith and Chapman (2005) found such patch depletion in red colobus, it is likely that there is a fundamental difference in the use of food resources between these two sympatric, folivorous species. Possible explanations for this difference include a lower capacity to intake toxins, nutrients, or food volume in guerezas and/or their lack of a presaccus. A difference in the level of within-group food competition thus remains a candidate driver of the vast difference in group size between these two species, along with divergent infanticide rates. This study highlights the need for a more careful examination of feeding behavior among folivorous primates, which current socioecological models typically consider as one category. The variation we have seen in feeding behavior between the colobines in Kibale shows that even if two folivorous primates share the same habitat and food resources, they may use these resources very differently, and thus may occupy distinct ecological niches. Socioecological models may be refined by assessing folivores with different physiological traits or social organizations separately, once further study clarifies the trends in patch depletion among different folivorous primates.

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