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## Towards an ecological solution to the folivore paradox: patch depletion as an indicator of within-group scramble competition in red colobus monkeys (*Piliocolobus tephrosceles*)

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**Abstract** A number of socioecological models assume that within-group food competition is either weak or absent among folivorous primates. This assumption is made because their food resources are presumed to be superabundant and evenly dispersed. However, recent evidence increasingly suggests that folivore group size is food-limited, that the primates prefer patchily distributed high-quality foods, and display some of the expected responses to within-group scramble competition. To investigate this apparent contradiction between theoretical models and recent empirical data, we examined the foraging behaviour of red colobus monkeys (*Piliocolobus tephrosceles*) in Kibale National Park, Uganda. We found that red colobus monkeys foraged in a manner that suggests they deplete patches of preferred foods: intake rate slowed significantly during patch occupancy while movement rate, an index of foraging effort, increased. Furthermore, patch occupancy was related to the size of the feeding group and the size of the patch. These results suggest that within-group scramble competition occurs, may limit folivore group size, and should be considered in models of folivore behavioural ecology.

**Keywords** Colobines · Kibale · Patch depletion · Red colobus · Scramble competition · Social systems · Socioecological models

### Introduction

Food competition is commonly accepted as an important potential cost of group living, and is among the primary factors invoked to explain variation in social structure and group size (Wrangham 1980; Janson and van Schaik 1988; van Schaik 1989; Isbell 1991; Chapman et al. 1995; Sterck et al. 1997; Isbell and Young 2002). Depending on the distribution and abundance of food resources, individuals in groups will experience either contest or scramble competition, or both. While contest competition refers to direct contests that result in differential access to food, scramble competition occurs more passively as the foraging efficiency of all group members declines as a function of group size (Janson and van Schaik 1988). Larger groups deplete shared food patches more quickly, and must compensate by visiting more patches each day (Janson and van Schaik 1988; Janson and Goldsmith 1995). It is this relationship between scramble competition and group size that our research will address. Although the costs will vary in relation to the nature of the food supply and the relative increase in travel cost due to additional group members (Chapman et al. 1995; Janson and Goldsmith 1995; Chapman and Chapman 2000b), the predicted outcome is that in habitat of constant quality, individuals in larger groups will suffer greater costs.

These predictions form the basis of the ecological constraints model (Chapman et al. 1995; Chapman and Chapman 2000b; Wrangham 2000), and are well supported by empirical data, particularly among frugivorous primates who compete for patchy, high-quality food resources (Leighton and Leighton 1982; Ghiglieri 1984a, b; Strier 1989; Chapman 1990a, b; Wrangham et al. 1993, 1996; Chapman et al. 1995; Chapman and Chapman 2000a). The picture is less clear for folivores: because their food resources are presumed to be superabundant and evenly

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dispersed, it is often assumed that within-group scramble competition is weak or absent (Wrangham 1980; Isbell 1991; Janson and Goldsmith 1995; Sterck et al. 1997; Steenbeek and van Schaik 2001; Isbell and Young 2002). The underlying assumption is that patches of leaves are not depletable; therefore, depletion rate does not increase and additional travel costs are not accrued with increasing group size. Because within-group food competition is thus relaxed, individuals are theoretically free to form larger groups. But many folivores, despite this assumed reduction of within-group feeding competition, often live in relatively small groups (Janson and Goldsmith 1995; Crockett and Janson 2000; Steenbeek and van Schaik 2001; Koenig and Borries 2002). This apparent contradiction is often referred to as the folivore paradox (Steenbeek and van Schaik 2001; Koenig and Borries 2002), and it has been proposed that its resolution may be achieved by invoking social factors, like the risk of infanticide, that could lead to selection for small group size (Isbell 1991; Janson and Goldsmith 1995; Treves and Chapman 1996; Steenbeek and van Schaik 2001; Koenig and Borries 2002).

Because scramble competition cannot be directly observed, and foraging efficiency is difficult to measure, increasing day range with increasing group size has been used as a behavioural indicator of within-group scramble competition (Isbell 1991; Chapman et al. 1995; Janson and Goldsmith 1995; Chapman and Chapman 2000b; Wrangham 2000; Isbell and Young 2002). For this reason, the evidence for the absence of scramble competition among folivores comes primarily from studies that have found no relationship between group size and day range or travel costs (Clutton-Brock and Harvey 1977; Struhsaker and Leland 1987; Isbell 1991; Janson and Goldsmith 1995; Yeager and Kirkpatrick 1998; Yeager and Kool 2000). However, using these studies to infer that there is no scramble competition is problematic because they generally lack sufficient controls for ecological variation among groups or species. Primates may adjust group size in response to ecological conditions, thereby avoiding scramble costs (i.e. large groups could occur in areas with abundant food, negating the need to increase day range). Ecological variation can thus confound correlations between group size and day range when making comparisons across groups, and especially across species.

In this study, we use red colobus (*Piliocolobus tephrosceles*) monkeys in Kibale National Park, Uganda, to examine scramble competition in a folivorous species because six lines of evidence suggest that folivores are food-limited and may experience within-group scramble competition. First, day range may be related to group size. Despite earlier findings to the contrary, Gillespie and Chapman (2001) found that a large group of red colobus had longer day ranges than a small group, and day range increased even further in the large group when food availability decreased. Although the sample size was small, this study confirms the need to re-assess the inferences drawn on the basis of earlier studies that lacked ecological controls. Second, group size can be predicted by habitat variables such as local food tree density, seasonality, forest block size, degree of deciduous-

ness, and degree of disturbance (Chapman and Chapman 2000a; Struhsaker 2000b; Struhsaker et al. 2004). Third, field data suggest that colobine diets are not based simply on superabundant and evenly distributed leaf resources, but that many colobus monkeys preferentially select high-quality young leaves, flowers, unripe fruits, and seeds (Oates 1994; Chapman et al. 2002b). These resources tend to be distributed in patches that are irregularly distributed in space and time, and within which food abundance is limited (Oates 1994; Oates and Davies 1994; Koenig et al. 1998), and thus provide the ecological conditions typically associated with scramble competition. Fourth, a number of studies have found that red colobus exhibit fission–fusion behaviour, where large groups divide into smaller ones, in response to low food availability, particularly in degraded habitat (Skorupa 1988; Oates 1994; Siex and Struhsaker 1999; Chapman and Chapman 2000a; Struhsaker 2000a; Struhsaker et al. 2004). Such short-term variation in group size is a well-documented response to changing ecological conditions among a number of frugivores (Tutin et al. 1983; Goodall 1986; Chapman 1990a; Boesch 1996; van Schaik 1999), and it is possible that some folivores have a similar strategy to minimize the costs of within-group scramble competition when resources become scarce. Fifth, contest competition has recently been documented both within and between folivore groups (Koenig 2000; Korstjens et al. 2002), suggesting that food competition can indeed be important. Last, folivore biomass can be predicted by food availability, particularly high-quality foods (McKey et al. 1981; Waterman et al. 1988; Davies 1994; Fimbel et al. 2001; Chapman and Chapman 2002; Chapman et al. 2002a). Although this does not directly suggest that there will also be constraints on group size, it does provide further support that folivores may be limited in important ways by the availability and distribution of food resources.

Two central assumptions of the ecological constraints model are that food patches are depleted, and that the rate of depletion is related to the size of the group (Chapman 1988). Charnov's marginal value theorem (Charnov 1976) 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. Optimally foraging animals should functionally deplete food patches before traveling to the next patch, and patches will be depleted more quickly by larger groups (Charnov 1976; Pyke 1984). If food patches truly are superabundant, patches will not be depleted and there will be no relationship between patch occupancy time and group size. Thus, patch depletion should provide a measurable behavioural indicator of the presence or absence of within-group scramble competition. Specifically, scramble competition is indicated if the following predictions are met:

1. If group size is limited by the availability of foods that occur in patches, patches will be depleted.
2. In depletable patches, patch occupancy time (feeding time in a single patch) will decrease with increasing group size and decreasing patch size.

We designed this project to empirically test these predictions.

## Methods

We studied red colobus monkeys in Kibale National Park, western Uganda (795 km<sup>2</sup>; 0°13′–0°41′N and 30°19′–30°32′E) (Chapman et al. 1997; Chapman and Lambert 1999). Kibale is a mid-altitude moist-evergreen forest with a relatively species-poor flora (68 tree species were identified in 4.8 ha of vegetation sampling; Chapman et al. 1997). The area receives approximately 1749 mm of rainfall annually (1990–2001) that peaks during two rainy seasons. We collected data from May 1995 to July 2004, with focused effort to collect patch depletion and occupancy data between May and July, 2004. We selected well-habituated red colobus groups in the Kanyawara area of the park (compartment K-30 and K14 Mikana, ~1500 m elevation) for study.

We observed the feeding behaviour of red colobus groups using a focal patch method that allowed collection of data from a feeding group, where each observation period represented the full occupancy period of a single food patch (defined as a single feeding tree). Focal patches were selected on an opportunistic basis whenever monkeys were observed entering a patch to feed. Data collection began when the first member of a group entered a patch and continued until all individuals vacated the patch. Minimum patch occupancy time was measured as the amount of time spent feeding in a patch, from the time the first individual began to eat until all individuals stopped eating. Group size (number of animals in the patch) and feeding group size (number of animals feeding) were recorded every 5 min. Data concerning the size and composition of the entire social group were not collected. Food type, tree species, and diameter at breast height (dbh) were recorded for each patch.

Throughout each focal occupancy period, intake rate was measured as the number of bites (putting food item(s) into the mouth) in 1 min intervals. Feeding effort was indexed as the rate of movement and measured as the distance (m) moved in 3 min intervals. These data were collected in turn from as many adult members of a feeding group as possible during each patch occupancy period. Individuals were selected for observation of intake rates and feeding effort in an ad hoc manner, moving from one clearly visible feeding individual to another. The data thus represent intake and effort rates for the feeding group as a whole.

Patch depletion was tested in two ways; first, feeding costs and gains were examined within each patch throughout the duration of occupancy. Intake rate (bites/min) was used as an index of feeding gain, and movement (m/3 min) within the patch as an index of effort or cost. If intake rate slows within a patch, this may indicate that the patch is becoming depleted, or it may indicate that the animals are becoming satiated. However, if intake rate slows while feeding effort remains constant or increases, satiation seems unlikely, and this provides evidence that the patch is be-

coming depleted. Measuring both intake rates and feeding effort also allows us to control for individual differences in motivation to feed, for example some individuals may be less motivated to feed, which would confound measures of intake in a similar manner to the satiation problem. However, by measuring effort we have an index of feeding motivation which allows us to control for this.

Intake rate and movement rate values from the first quarter of each patch occupancy were compared with values from the last quarter using a paired *t*-test. This test allows for differential feeding rates across different food species and types. Because biological data frequently violate some of the assumptions of parametric statistical tests, we tested our data for normality and found no violations, but to be conservative, we also ran non-parametric tests (Wilcoxon signed ranks), which produced very similar results to the paired *t*-test. The data were analysed for all food patches together, and then were separated by food type to look at young and mature leaf patches separately because depletion was expected only in patches of limiting/preferred foods i.e. young leaves (preference determined by Oates 1994; Oates and Davies 1994; Chapman and Chapman 2002).

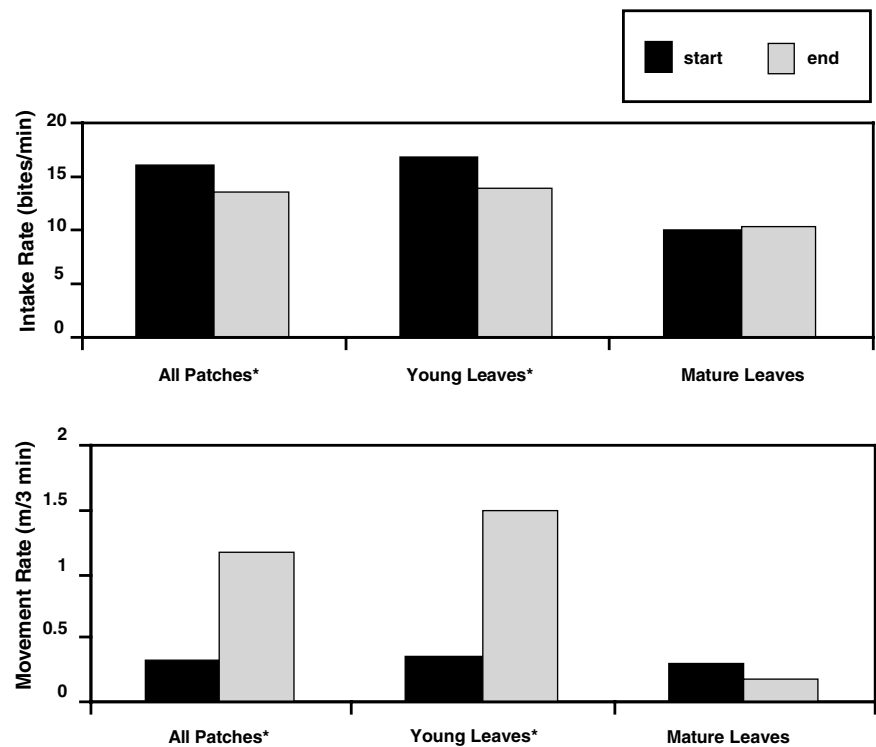
Second, the effects of group size and patch size on patch occupancy time were examined. If scramble competition is absent, then patch occupancy should be unaffected by variation in group size or patch size. However, if group size is limited by within-group scramble competition, then occupancy time should increase with increasing patch size and/or decreasing group size. Multiple linear regression was used to test whether patch occupancy was affected by dbh and feeding group size. All statistical tests were two-tailed with  $\alpha=0.05$ .

## Results

Data were collected on groups feeding in 45 focal patches during May–July, 2004 and from an additional 23 patches collected between 1995 and 1998. The 1995–1998 dataset includes feeding rate data only, while the 2004 dataset also includes movement rates and patch occupancy data. Red colobus consumed young leaves in 63% ( $n=43$ ) of patches, mature leaves in 24% ( $n=16$ ), young leaves and buds in 6% ( $n=4$ ), petioles in 4% ( $n=3$ ), and leaf buds in 3% ( $n=2$ ). Group size ranged from 1 to 18 individuals ( $x=.76$ ,  $SD=3.95$ ,  $n=67$ ), while the feeding group size ranged from 1 to 15 ( $x=3.63$ ,  $SD=2.94$ ,  $n=67$ ). Mean patch occupancy was 36 min (range 15–74 min,  $SD=12.43$ ,  $n=45$ ).

Intake rate slowed significantly during patch occupancy ( $n=68$ , start rate  $x=16.05$  bites/min, end rate  $x=13.67$ , paired  $t=5.022$ ,  $p<0.0001$ ), while movement rate increased ( $n=45$ , start rate  $x=0.33$  m/3 min, end rate  $x=1.15$ , paired  $t=-3.89$ ,  $p<0.0001$ ) when all patches were analysed together. As predicted, when analyses were run separately for young and mature leaves, this effect was evident only in young leaf patches (young leaves intake rate:  $n=43$ , start rate  $x=16.87$  end rate  $x=13.96$ , paired  $t=5.33$ ,  $p<0.0001$ ; young leaves movement rate:  $n=26$ , start rate  $x=0.36$  end

**Fig. 1** Changes in (a) intake rate (bites/min) and (b) movement rates (m/3 min) of red colobus (*Piliocolobus tephrosceles*) in Kibale National Park, Uganda. \* indicates a statistically significant difference between start and end (see text for more details)



rate  $x=1.50$ , paired  $t=-4.01$ ,  $p<0.0001$ ; mature leaves intake rate:  $n=16$ , start rate  $x=9.99$  end rate  $x=10.31$ , paired  $t=-1.25$ ,  $p=0.23$ ; mature leaves movement rate:  $n=14$ , start rate  $x=0.30$  end rate  $x=0.19$ , paired  $t=0.61$ ,  $p=0.55$ ; Fig. 1).

As predicted, patch occupancy time was significantly affected by the size of the patch (dbh) and the number of animals feeding in it ( $R^2=0.145$ ,  $p=0.037$ ,  $n=44$ ). Dbh and feeding group size were not correlated (Pearson  $r=0.002$ ,  $p=0.989$ ,  $n=44$ ), suggesting that occupancy time is simultaneously affected by both factors. The effect of this relationship is weak, likely reflecting the fact that other factors, in addition to foraging efficiency, influence patch occupancy. For example, experimental work using desert rodents to test various predictions of optimal foraging theory have found that giving-up time is affected by a number of factors including predation risks/costs and missed opportunity costs (Brown 1988; Kotler and Brown 1988; Brown 1989; Brown et al. 1994).

## Discussion

We found that red colobus monkeys in Kibale deplete food patches when feeding on young leaves, as indicated by decreasing gains (intake rate) despite increasing feeding effort (movement while feeding). Furthermore, patch occupancy time was affected by patch size and feeding group size. This provides evidence of a group size-effect, where larger groups deplete patches more quickly, are forced to visit more patches, and will thereby accrue greater travel

costs than smaller groups. These results suggest that red colobus do experience within-group scramble competition, and that this type of competition may be an important factor determining group size. Further studies are required to document the intensity of scramble competition by directly examining the effect of group size on travel costs by measuring inter-patch distance and day range, while controlling for variation in food availability.

The results of this study, in combination with the evidence outlined in the introduction, suggest that our current understanding of folivore food competition is inadequate. Existing applications of socioecological theory to the variation in primate social behaviour are based on the assumption that within-group scramble competition is either weak or absent among folivores (Clutton-Brock and Harvey 1977; van Schaik and van Hooft 1983; van Schaik 1989; Isbell 1991; Janson and Goldsmith 1995). This assumption is based primarily on studies that found no relationship between group size and day range length. However, based on the accumulating evidence, it is possible that these studies were confounded by habitat variation, and that day range would be related to group size if food availability could be accurately measured and held constant. It may be that folivores avoid or mitigate the costs of scramble competition by adjusting group size to food conditions at broad temporal and spatial scales, or more immediately by fission–fusion behaviour. This hypothesis is supported by the studies presented above that have documented a relationship between red colobus group size and habitat quality, group size and day range, and/or fission–fusion in response to food availability. If folivores experience significant within-group scramble costs, a shift in the interpretation of the competitive regime of

folivorous monkeys is required, and may lead to resolution of the folivore paradox on ecological grounds.

We used patch depletion as a novel tool to examine scramble competition among folivorous group-living primates. Previous studies have used similar measures of intake rates within a patch to address questions related to contest competition or foraging theory (Isbell 1991; Grether et al. 1992; Korstjens et al. 2002), but we do not know of any studies that have used a measure of feeding effort to control for the possibly confounding issue of satiation, and none that have applied patch depletion to determine the presence of scramble costs.

Isbell (1991) suggested that increasing day range with increasing group size be used as the behavioural indicator of scramble competition. Based on the results of this study, we propose that patch depletion may also be used as a behavioural indicator of the *presence* of within-group scramble competition. This measure can provide a simple alternative to measuring variation in day range relative to group size because it does not require complex ecological controls across different conditions of food availability. When patch depletion is demonstrated, then further investigations could be conducted to examine the *intensity* of scramble competition by investigating its effects on day range and group size; however, such studies must carefully control for ecological variation across both time and space.

Our methods may have further application in refining our understanding of foraging decisions. Complex foraging strategies are difficult to quantify, and optimality models are difficult to apply. For example, in an attempt to test whether the marginal value model (Charnov 1976) could be applied to gibbon foraging decisions, Grether et al. (1992) measured food intake and found that intake rate declined across time spent in a patch. However, their study did not measure feeding effort and could not reliably distinguish between the effects of patch depletion and satiation. This methodological problem effectively undermines the assumption that patches are being depleted; an assumption that is central to most theories of primate socioecology, yet remains largely untested. Our methods provide a possible solution to such methodological difficulties.

The methods used here also present another opportunity to test the predictions of optimal foraging theory. Charnov (1976) suggested that giving-up time should occur sooner (at a higher gain rate) in richer environments because the chances of finding another food patch are good, and supported this prediction with some evidence from birds. If primates are foraging optimally, then they should give-up later (and deplete patches further) in poor or degraded habitat where the inter-patch distance is greater. This can be empirically tested by comparing depletion thresholds across habitats. Although no evidence for differential patch depletion was found in logged areas in the current study, we did not have sufficient data to compare depletion and giving-up thresholds for individual food species across habitats. This type of research will be useful for conservation efforts because it will help clarify the manner and degree to which individuals and groups are affected by habitat degradation.

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