Group Size and Food Competition in Red Colobus Monkeys:
Addressing the Folivore Paradox

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of the degree of Ph.D. *Ad Personam*

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THESIS FORMAT AND STYLE

This is a manuscript-based thesis composed of a collection of four papers. Two papers have been previously published, and two are currently in review. Together, the four papers provide a report of my PhD research program. To create a single cohesive text, a general introduction and conclusion are provided, as well as linking statements between chapters.

CONTRIBUTIONS OF CO-AUTHORS

I am the lead author on all papers presented in the thesis; I was responsible for conceptualization of the research problem, building the context, designing the research program, collecting, analyzing and interpreting the data, and writing the manuscripts. Colin Chapman, my thesis advisor, provided support and advice throughout my PhD and made intellectual contributions; as such, he is a co-author on all chapters. Chapter Four involved technical expertise in parasite and hormone data collection and analysis. Jessica Rothman and Michael Wasserman provided advice on how to properly process samples and interpret laboratory results, and were involved in the last stages of manuscript preparation; they are thus co-authors on this chapter.

ORIGINAL CONTRIBUTIONS TO KNOWLEDGE

The “folivore paradox”, that leaf eating monkeys form surprisingly small groups given that they seem to experience little feeding competition, has been acknowledged as a problem for several years. This thesis contributes to *i*) better understanding the nature of the paradox; *ii*) identifying methodological problems that underlie the problem; *iii*) synthesizing the relevant theoretical knowledge and empirical data in a manner that leads to a way forward; *iv*) presenting a new working model for primate socioecologists that addresses some of the problems that led to the paradox; *v*) developing an expanded list of potential behavioural indicators of food competition that will allow methodological clarity and stronger empirical testing of hypotheses; *vi*) developing a novel test for patch depletion which allows an important assumption to be tested; *vii*) conducting a comprehensive, multi-group, ecologically-controlled study of within-group scramble competition in folivores that measures a variety of potential behavioural indicators and physiological outcomes of food competition; *viii*) providing strong and convincing evidence that folivores experience scramble competition; *ix*) suggesting that reproductive success is reduced in larger groups, likely as a result of the costs associated with scramble competition; *x*) demonstrating that red colobus surprisingly show signs of between-group contest competition and that larger groups have an advantage in these contests; however, the expression of contest is subtle and difficult to observe; *xi*) finding that larger groups had surprisingly fewer parasites than smaller groups, and similar cortisol levels, suggesting that stress and parasitism are not among the costs that lead to reduced reproductive success in larger groups; and *xii*) demonstrating that the expected increase in socially-transmitted parasites in larger groups may have been avoided by behavioural changes such as increasing group spread.

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ABSTRACT

Food competition is an expected cost of group living. It is therefore puzzling that there is little evidence for competition among group-living folivorous monkeys. Given the expected advantages of group living, it is even more puzzling that folivores do not form larger groups despite this apparent lack of food competition. This has become known as the folivore paradox, and to date there is no broadly accepted theoretical solution. However, there have been theoretical and methodological problems with previous studies, preventing clear interpretation of results. I synthesized existing theory and data and demonstrated that, when habitat conditions are appropriately accounted for, folivores do show signs of food competition. I provide a broadened list of behavioural indices of food competition, and suggest an expanded working model to better organize and understand primate socioecology.

The notion that folivores experience little or no food competition is based in part on the assumption that their food resources are superabundant and evenly dispersed, and thus non-depletable. I examined the foraging behaviour of red colobus monkeys (*Procolobus rufomitratus*) in Kibale National Park, Uganda and found that intake rate slowed despite increasing feeding effort during patch occupancy. Furthermore, occupancy time was related to the size of the feeding group and to the size of the patch. These results suggest that red colobus depleted patches of preferred foods, and that larger groups deplete patches more quickly. Because food patches are depletable, red colobus likely experience increasing foraging costs in larger groups due to scramble competition.

I conducted a multi-group, ecologically controlled study to determine whether red colobus display any predicted behavioural indicators of food competition. I simultaneously followed 9 groups of red colobus and controlled for spatial and temporal variation in food availability. I found that larger groups occupied larger home ranges than smaller groups, and that group size was related to increased foraging effort (longer daily travel distance), increased group spread, and reduced female reproductive success. These results suggest that folivorous red colobus monkeys experience within-group scramble competition and possess a suite of behavioral responses that may mitigate the cost of competition and represent adaptations for group living. The results offer an ecological solution to the folivore paradox for this species.

Stress and disease impose fitness costs, which may vary with group size. I assessed the relationships between group size, stress, and parasite infections using fecal cortisol as a measure of physiological stress, and fecal egg counts to assess the prevalence and intensity of gastrointestinal helminth infections. I also examined the effect of behaviors that could potentially reduce parasite transmission (e.g., increasing group spread and reducing social contact). I found that cortisol was unrelated to group size, but parasite prevalence was negatively related to group size and group spread. The observed increase in group spread could have reduced the rate of parasite transmission in larger groups. The results suggest that neither gastrointestinal parasitism nor stress directly imposed group-size related fitness costs, and thus are unlikely to be among the mechanisms directly limiting group size in red colobus monkeys.

RÉSUMÉ

La compétition pour la nourriture est considérée coûteuse pour les espèces vivant en groupe. Fait déconcertant; nous avons très peu d'évidences que la compétition affecte les espèces de singes folivores grégaires. Il est donc surprenant que les singes folivores ne forment pas de larges groupes en cette apparente absence de compétition pour les ressources alimentaires. Ces observations sont à la base du «paradoxe des folivores», et jusqu'à maintenant, aucune théorie ne fait l'unanimité. Plusieurs problèmes théoriques et méthodologiques ont été répertoriés dans les études précédentes, et ces problèmes peuvent être à la base de ce paradoxe via une interprétation biaisée des résultats. Suite a un travail de synthèse des théories et bases de données existantes, j'ai finalement démontré que lorsque les conditions de l'habitat sont incluses dans l'analyse, les singes folivores confirment des signes de compétition pour les ressources alimentaires. Dans cet ouvrage, je fourni une liste d'indices comportementaux qui examinent la compétition pour les ressources alimentaires et je suggère un nouveau modèle afin de mieux organiser notre compréhension de la socio-écologie des primates.

La notion sur laquelle les espèces folivores sont sujettes à une faible ou une absence de compétition pour les ressources alimentaires réside en partie sur la supposition que leurs ressources sont inépuisables, c'est-à-dire surabondantes et également distribuées. J'ai examiné le comportement d'alimentation des singes Colobe rousse (*Procolobus rufomitratus*) dans le Parc National de Kibale, Ouganda. J'ai découvert que le taux d'alimentation diminue malgré une augmentation de l'effort durant la quête alimentaire pour une parcelle donnée. De plus, le temps d'occupation de la parcelle était relié à la taille des groupes d'alimentation ainsi qu'à la taille de la parcelle d'alimentation. Ces résultats suggèrent que les Colobe rousse épuisent les parcelles avec de la nourriture préférentielle et que les groupes plus larges épuisent les parcelles plus rapidement. Les Colobe rousse sont soumis à des coûts d'alimentation plus important dans les larges groupes du à la compétition par exploitation car j'ai prouvé que les parcelles d'alimentation sont épuisables.

En contrôlant pour la variation spatiale et temporelle de la disponibilité de nourriture, j'ai conduis une étude avec 9 groupes de singe folivores (les groupes variant en taille) pour déterminer si la compétition pour les ressources pourrait se traduire par des indicateurs comportementaux chez les Colobe rousse. J'ai simultanément suivi les 9 groupes de Colobe rousse. J'ai découvert que les larges groupes occupaient des domaines vitaux plus grands que les petits groupes. J'ai également démontré que la taille des groupes était reliée à l'augmentation de l'effort lors de la quête alimentaire (plus longue distance journalière parcourue), qu'il y avait une augmentation de la dispersion des individus dans le groupe et que les femelles avaient une réduction de leur succès reproducteur. Ces résultats suggèrent que les Colobe rousse sont soumis a une compétition par exploitation à l'intérieur des groupes et qu'ils possèdent un assortiment de réponses comportementales qui peuvent réduire le coût de compétition et donc représenter des adaptations à la vie en groupe. Ces résultats offrent une solution écologique au « paradoxe des folivores » pour cette espèce de singe.

Le stress et les maladies imposent des coûts à la valeur adaptative des individus et ces coûts peuvent varier en fonction de la taille du groupe. J'ai estimé la relation entre la taille des groupes, le stress et le taux d'infection par les parasites en utilisant le cortisol fécal comme mesure du stress physiologique et le décompte des œufs d'helminthes dans les fèces pour estimer la prévalence et l'intensité des infections par les parasites gastro-intestinaux. J'ai aussi examiné les comportements qui peuvent potentiellement réduire la transmission des parasites (ex. : l'augmentation de la dispersion des individus dans un groupe réduit les contacts sociaux). J'ai découvert que le taux de cortisol n'est pas relié à la taille des groupes, mais que la prévalence des parasites était négativement reliée à la taille des groupes et à la dispersion des individus à l'intérieur des groupes. L'augmentation de la dispersion des individus à l'intérieur des groupes pourrait contribuer à réduire le taux de transmission des parasites dans les larges groupes. Ces résultats suggèrent que ni le parasitisme gastro-intestinal, ni le stress imposent des coûts directs reliés à la valeur adaptative et à la taille des groupes. Il est donc peu probable que ces deux facteurs contribuent à limiter la taille des groupes chez les Colobe rousse.

INTRODUCTION

Food competition is an expected cost of group living. It is therefore puzzling that there is little evidence for competition among group-living folivorous monkeys. It is even more puzzling that folivores do not form larger groups despite this apparent lack of food competition and the known benefits of forming groups. This has become known as the folivore paradox, and to date there is no broadly accepted theoretical solution.

In Chapter 1, I provide a comprehensive review of the literature regarding the development of primate socioecological theory, and critically evaluate the empirical evidence supporting the contention that folivores do not experience food competition. I then synthesize existing empirical data to examine whether folivores show signs of food competition. I provide a broadened list of behavioural indices of food competition, and suggest an expanded working model to better organize and understand primate socioecology.

The notion that folivores experience little to no food competition is based in part on the assumption that their food resources are superabundant, evenly dispersed, and thus non-depletable. In Chapter 2, I test the assumption that patches of leaves are not depletable by examining the foraging behaviour of red colobus monkeys (*Procolobus rufomitratus*) in Kibale National Park, Uganda. If food patches are depletable, then red colobus may experience increasing foraging costs in larger groups, and behavioural indicators of food competition should be observed.

In Chapter 3, I conduct a multi-group, ecologically controlled study to determine whether red colobus experience food competition. I simultaneously followed 9 groups of red colobus to examine possible group-size effects on the expected behavioural indicators or consequences of food competition.

Finally, in chapter 4, I assess the relationships between group size, stress, and parasite infections in red colobus, because stress and parasitism have fitness costs, which may be among the fitness consequences of increasing group size.

CHAPTER 1: PRIMATE GROUP SIZE AND SOCIOECOLOGICAL MODELS: DO FOLIVORES REALLY PLAY BY DIFFERENT RULES[1]

Introduction

Because primates display such remarkable diversity, they are an ideal taxon within which to examine the evolutionary significance of group living and the ecological factors responsible for variation in social organization. However, as with any social vertebrate, the ecological determinants of primate social variability are not easily identified because inter-specific variation in group size and social organization results from the compromises required to accommodate the associative and dissociative forces of many factors including predation, (Alexander 1974; Clutton-Brock and Harvey 1977; van Schaik 1989) conspecific harassment and infanticide, (Wrangham 1979; Watts 1996; Steenbeek and van Schaik 2001) foraging competition (Alexander 1974; Vehrencamp and Bradbury 1984) and cooperation, (Emlen and Oring 1977) dominance interactions, (Vehrencamp 1983) reproductive strategies, and socialization (van Schaik 1983; Boesch 1996; van Schaik 1999). Causative explanations have emerged primarily through the construction of theoretical models that organize the observed variation in primate social organization and group size relative to measurable ecological variation (Alexander 1974; Wrangham 1980; Terborgh and Janson 1986; van Schaik 1989; Isbell 1991; Sterck, Watts, and van Schaik 1997). Recently, contradictions have emerged between empirical data and long-standing assumptions about food competition in folivores, which challenge conventional interpretations of their competitive regime. We take a historical perspective to review the development of existing models and examine the manner in which they have been applied to folivores. We focus specifically on ecological variation and the consequent expressions of food competition, and how traditional assumptions have led to what has been called the folivore paradox

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(Steenbeek and van Schaik 2001; Koenig and Borries 2002). We explicitly examine the context within which the folivore paradox was proposed and provide a critical examination of whether folivores experience food competition. While we recognize the importance of predation, infanticide, and social factors, no attempt is made to provide an exhaustive review of these phenomena, or to discuss their effects on social organization and group size. We conclude by making suggestions for future refinements of both empirical enquiry and theoretical models that we hope will improve our ability to adequately characterize the competitive regime and social organization of folivorous primates.

Explanatory Models of Primate Social Organization

Early assessments of primate socioecology relied primarily on correlational analyses to examine the relationships between ecological and behavioral variation, and generally categorized primates according to group size, the number of males per group, or broad ecological categories based on diet, locomotion, and habitat (Crook and Gartlan 1966; Eisenberg, Muckenhirn, and Rudran 1972; Alexander 1974; Clutton-Brock and Harvey 1977). This work provided important insights into the variation in primate behavior and the ecological conditions associated with a number of behavioral traits. The research of behavioral ecologists working on other taxa (Emlen and Oring 1977; Emlen 1978; Vehrencamp and Bradbury 1978; Vehrencamp 1979, 1983) provided a strong theoretical basis for the development of primate-specific qualitative models grounded in evolutionary theory. In a seminal paper, Wrangham (1980) shifted the focus of primate socioecology in two ways. First, he used an evolutionary approach to generate hypotheses about the adaptive significance of social organization rather than relying on correlational analyses. Second, he focused primarily on female relationships as determined by food competition. This brought primate socioecological theory in line with the basic premise that, for most species, female behavior is affected by ecological variables and food competition, while males are primarily affected by mating competition and the distribution of receptive females (Trivers 1972; Emlen and Oring 1977; Vehrencamp and Bradbury 1978). Female food competition, as the ultimate evolutionary force influencing primate social organization, has provided the fundamental starting point for all subsequent models.

Wrangham (1980) proposed an ecological mechanism for the formation of female-bonded primate groups; specifically, females will live in groups when the benefits of cooperative resource defense outweigh the costs of within-group feeding competition. Females will form bonds with their relatives to cooperatively defend access to food resources. Large groups will out-compete smaller groups and obtain greater fitness by excluding neighboring groups from food sources. This requires that high-quality food is distributed in discrete, defensible patches, and that fallback foods (those eaten when preferred high-quality foods are unavailable) occur in large, uniform patches that minimize within-group competition. When feeding sites within food patches are limited or vary in quality, competition within groups will lead to the formation of female dominance hierarchies. For these female-bonded species, between-group competition will select for group formation, and create a selective advantage for larger groups, while within-group competition (in non-territorial species) or the ability to defend a home range of appropriate size (in territorial species) will ultimately constrain group size. Non-female bonded species are classified into two categories: *i.* those that rely almost exclusively on high-quality, patchy resources and display short-term variation in group size so that individuals can respond to fluctuations in food availability and competition intensity (e.g., chimpanzees (*Pan troglodytes*) and spider monkeys (*Ateles spp.*)), and *ii.* those whose preferred foods occur in low-quality uniform patches with a large number of feeding sites (i.e., leaves, particularly mature leaves), and thus live in cohesive groups with little or no feeding competition (e.g., many non-female bonded folivores were placed in this category).

Empirical work has supported the importance of between-group competition, among other factors, in determining group size and social organization in primates (Koenig et al. 1998; Koenig 2000; Stevenson and Castellanos 2000), birds (Emlen 1978), carnivores (Macdonald 1979), and humans (Alexander 1974). By highlighting the social consequences of food competition, Wrangham (1980) refocused the attention of primatologists. Over the next decade, a clearer understanding of food competition was developed, which led to expanded ecological models of primate social organization. Building on the work of population and behavioral ecologists (Nicholson 1954; MacArthur and Pianka 1966; Stephens and Krebs 1986), Janson and van Schaik (1988; van Schaik 1989) defined four types of food competition (Box 1) that provided conceptual clarity in subsequent models. The type and intensity of food competition have important implications for group size, social behaviour, dominance relationships, and dispersal patterns. Depending on the distribution and abundance of food resources, individuals in groups will experience either contest or scramble competition or both. If individuals or groups can exclude others from resources, then contest competition will result in differential access to food, and may ultimately lead to skewed fitness. Scramble competition occurs because all individuals must forage from the same limited resource base, and results in equally reduced feeding opportunities for all individuals. Because the cost of scramble competition intensifies as groups get larger, within-group scramble competition is expected to impose a limit on group size, while contest competition between groups may favor larger groups (Wrangham 1980; Janson and van Schaik 1988).

Various authors built on Wrangham's work to make predictions about the outcome of competition on group size and social relationships (van Schaik 1989; Isbell 1991; Sterck, Watts, and van Schaik 1997; Koenig 2002). van Schaik (1989) modified Wrangham's model and suggested that predation risk was the ultimate factor forcing females to live in groups despite the costs imposed by feeding competition. Building on previous work (Alexander 1974; Wrangham 1980; Terborgh and Janson 1986), van Schaik argued that the costs of within-group competition far outweigh any advantages resulting from communal resource defense, and that resource defense cannot be invoked as the primary selective force for grouping. Rather, the threat of predation puts a lower limit on group size, while within-group food competition sets the upper limit. If food is uniformly distributed in small patches of even quality that cannot be monopolized, or in very large patches where the whole group can feed, then competition will be by scramble. Female fitness will be affected primarily by group size, and individuals will not be able to increase food acquisition through overt behaviors. If food occurs in well-defined, defensible patches that vary in quality and are not large enough for all group members, then contest competition will occur within groups. If high-quality food is clumped, and patches are large enough for all group members, then between-group competition will be important. van Schaik outlined a series of predictions regarding female dispersal and social relationships under various competitive regimes. This model was among the first to draw a sharp distinction between frugivores and folivores in terms of food distribution, competitive regime, and social outcomes. Within groups, folivores are classified as scramblers, and frugivores as contesters, while between-group contests are assumed only to occur among frugivores. This distinction has been maintained in the literature and has become amplified, such that some later models assume that folivores experience no feeding competition at all (Isbell 1991).

Box 1. Types of food competition

Between-group contest (BGC) occurs when territories or food patches can be cooperatively defended by group members. This type of competition should favor larger or more aggressive groups that can supplant or exclude smaller groups from feeding sites.

Between-group scramble (BGS) results from the common use of food resources by all groups/individuals, and increases in intensity with increasing population density. The effects of BGS are presumed to be independent of group size and to have little effect on social behavior.

Within-group contest (WGC) occurs when food is distributed in such a manner that it can be monopolized or defended resulting in the development of dominance hierarchies, differential access to resources, and skewed energy gains. Behavioural consequences include direct contests over access to food and may take the form of aggressive interactions, displacement, or avoidance.

Within-group scramble (WGS) occurs due to the limited nature of the food supply which must be shared among group members. Competition increases in intensity with group size and smaller groups are favoured. As feeding opportunities are reduced equally for all group members, WGS is unrelated to the development of dominance hierarchies and does not lead to skewed resource acquisition.

(Janson and van Schaik 1988, van Schaik 1989)

Sterck et al. (1997) expanded van Schaik's model to explicitly integrate social variables and to more clearly define the possible social outcomes. By incorporating the effects of male behavior (particularly sexual coercion and infanticide), habitat saturation, and the cost of dispersal, along with predation and food distribution, this model seems to explain more of the observed variation in primate grouping patterns and social organization. With respect to folivores, Sterck et al. (1997) suggested that infanticide in particular may have important social consequences for some species.

Isbell and colleagues (Isbell 1991; Isbell and Young 2002) advanced ideas about how the social and ecological cost of dispersal may act as a major determinant of social organization and proposed that when food is clumped, both WGS and WGC occur, and when food is dispersed, neither occurs. In constructing this model, Isbell (1991) provided valuable methodological clarification by explicitly defining five behavioral indicators of food competition (Box 2), which can be used to assess the competitive regime of a species. Interestingly, although separate indicators were proposed for contest and scramble competition, Isbell (Isbell 1991) linked them together by presenting data demonstrating that they covary, i.e., among species whose home range size increases with group size, females are aggressive between groups. Similarly, among species with strong female dominance hierarchies, day range (daily travel distance) increases with group size, while species with weak or no female dominance hierarchies demonstrate no relationship between day range and group size. This is an important point because the model precludes the possibility of scramble competition without contest competition. The model does not allow for the possibility that foods may be limiting but not defensible, or patchy but not monopolizable, and that competition could be by scramble alone, as suggested in earlier models (Wrangham 1980; van Schaik 1989). Furthermore, Isbell (1991) presented empirical data from a wide range of studies to demonstrate that many folivores experience no food competition. Notably however, Isbell raised the possibility that ranging and group size may be poor indicators of competition among folivores, or that previous attempts to measure these variables may have been confounded by food availability. This foresight is now proving to be very important.

Developed alongside these models was one that simply proposed to explain variation in group size. The ecological constraints model (or scramble competition hypothesis) suggests that group size is a function of travel costs (Chapman 1990b; Chapman, Wrangham, and Chapman 1995; Janson and

Goldsmith 1995; Wrangham 2000). Within-group competition is associated with increasing day range because when food is patchy, larger groups will deplete patches more quickly, individuals will obtain less food per patch, and groups will have to visit more patches in a day (Waser 1977; Chapman and Chapman 2000b). The energetic cost of travel between food patches is the mechanism by which scramble competition imposes a cost on individuals and limits group size. The model is well supported by empirical data, particularly among frugivorous primates who compete for patchy, high-quality food resources (Leighton and Leighton 1982; Ghiglieri 1984; Strier 1989; Chapman 1990b; Chapman, Wrangham, and Chapman 1995; Wrangham et al. 1996). Variation in group size is not a simple function of food abundance, however, but is a response to the interaction of the size, density, and distribution of food patches as well as individual differences in energy budget, travel costs, and foraging strategy. Nevertheless, existing evidence clearly demonstrates *i)* the cost of grouping to individuals, *ii)* the limiting effect of food competition on group size, and *iii)* the mechanism behind the relationship between group size and day range. While acknowledging that observed group sizes will be confounded by other variables (e.g., predation risk, resource defense, mating strategies), the ecological constraints model proposes that the upper limit on group size is set by the increasing costs of travel imposed in larger groups. The application of this model

Box 2. Behavioral indicators of food competition

Type of Competition	**Behavioral Indicator**
Between-group contest	Between-group aggression among females
Between-group scramble	Positive relationship between home range size and group size
Within-group contest	Strong female dominance hierarchies
Within-group scramble	Positive relationship between day range (daily travel distance) and group size
	Negative relationship between female reproductive rates and group size

(Isbell 1991)

to folivores has rarely been examined (but see Gillespie and Chapman 2001; Ganas and Robbins 2005).

The Folivore Paradox

In applications of socioecological models, many authors have implicitly or explicitly assumed that food competition within folivore groups is inconsequential and that populations and groups are not limited by the availability of food (but see Borries 1993; Koenig et al. 1998). This inference is based primarily on studies that have found no relationship between group size and day range among folivores. For example, Clutton-Brock and Harvey (1977) found that feeding group weight was not related to day range length across diurnal, arboreal folivore genera. Similarly, Yeager and colleagues (Yeager and Kirkpatrick 1998; Yeager and Kool 2000) found that across 17 Asian colobine species, day range did not increase with increasing group size. More specifically, early data for red colobus *(Piliocolobus tephrosceles)* in Kibale, Uganda showed no relationship between group size and day range (Struhsaker and Leland 1987). More recently, Fashing (2001) found no relationship between group size and day range across five groups of black–and-white colobus *(Colobus guereza)*. In general, the flat relationship between group size and day range, in combination with the long-standing assumption that leaf resources are abundant and evenly dispersed, has been used to infer that within-group food competition is weak or absent among folivores (Wrangham 1980; Isbell 1991; Janson and Goldsmith 1995; Sterck, Watts, and van Schaik 1997; Steenbeek and van Schaik 2001; Isbell and Young 2002).

Given this assumed reduction in feeding competition, folivores are theoretically free to form larger groups. If protection from predation is a major aggregative force (Alexander 1974; van Schaik 1983; Terborgh and Janson 1986; van Schaik 1989) then folivores should take advantage of this reduction in feeding competition to form large groups. However, many folivores live in surprisingly small groups relative to similarly sized frugivores who should be more constrained by the patchy distribution of fruit (Janson and Goldsmith 1995; Crockett and Janson 2000). This apparent contradiction has been referred to as the folivore paradox (Steenbeek and van Schaik 2001; Koenig and Borries 2002). Social factors, such as the risk of infanticide, have been invoked to solve the problem. For example, Crockett and Janson (2000) found that the rate of infanticide increased with group size in red howlers (*Alouatta seniculus*), but only until the group was large enough to create paternity confusion, at which point WGS became more costly. They suggested that infanticide avoidance could constrain group size below the level where WGS imposes a cost. Steenbeek and van Schaik (Steenbeek and van Schaik 2001) suggested that among Thomas' langurs (*Presbytis thomasi*) (Steenbeek and van Schaik 2001), group size was limited by the risk of infanticide because larger groups were more at risk of male takeover. Although demonstrable effects of WGS were observed (day range increased with group size, and females in larger groups ate less fruit and more leaves) the authors concluded that WGS was not limiting group size because dietary switching was marginal and there was no effect on activity budget or birth rate. Koenig and Borries (2002) 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. However, Treves and Chapman (1996) found that infanticide avoidance did not limit group size in different populations of hanuman langurs, but that increasing group size may have been a counter-strategy to prevent takeovers and infanticide. The available evidence indicates that in some populations, infanticide may constrain group size, but it might not provide a complete solution to the folivore paradox. Furthermore, the data do not rule out the possibility that ecological factors may also play an important role in limiting folivore group size in some populations.

Do folivores experience within-group scramble competition?

Nine lines of evidence suggest that folivores experience within-group scramble competition and that group size may be ecologically constrained. This evidence implies that *i.* current interpretations of primate socioecology inadequately characterize the competitive regime of folivores, and *ii.* although social factors are no doubt also important, the folivore paradox may be resolved for some species on ecological grounds.

Folivore foods vary in distribution and quality

Folivores have traditionally been defined as those primate taxa with morphological adaptations specialized for the efficient digestion of leaves (Kay and Davies 1994), and a significant proportion of their diets were thought to be composed of leaf matter. Recent evidence suggests that previous assumptions that folivores rely on ubiquitous and evenly distributed food resources that are of relatively low and uniform nutritional quality need to be reassessed. It is now clear that folivores feed selectively, and that their food resources vary in quality, availability, and spatial distribution. Many folivores primarily select high-quality young leaves, seeds, flowers, and unripe fruits (Oates 1994; Oates and Davies 1994; Koenig et al. 1998; Yeager and Kool 2000; Chapman and Chapman 2002). These resources are often patchily distributed in both space and time and vary in nutritional quality (Milton 1980; Glander 1981, 1982; Oates 1994; Chapman et al. 2003), and thus may provide the ecological conditions typically associated with food competition. It is probably only mature leaves that are distributed in a superabundant and continuous manner, and even these vary dramatically in nutritional quality. Koenig and colleagues (Koenig et al. 1998; Koenig 2000) have demonstrated that forest-living hanuman langurs preferentially exploited mature leaves that occurred in low-density clumps that were not large enough for all group members to feed simultaneously, and were higher in protein and soluble sugar than other available foods. Black-and-white colobus (*C. guereza*) in Kibale are among the most highly folivorous primates known and yet they are selective eaters; they more frequently choose young than old leaves, select certain tree species, alter their range use to obtain certain foods, and eat foods of varied nutritional content (Oates 1977; Harris 2005, 2006). Similarly, *C. guereza* and *A. palliata* do not forage continuously as they move through the canopy, but feed only in certain trees, and often travel directly from one source to another (Oates 1977; Milton 1980). For many folivores, mature leaves are heavily consumed only when other foods are scarce (Yeager and Kool 2000). These studies suggest that the simple designation “folivore” is insufficient for characterizing the diet of primate species (Glander 1981; Koenig et al. 1998), or for making behavioral inferences.

Folivores may deplete patches of food

An important assumption underlying current interpretations of competition among folivores is that they do not deplete food patches. This assumption necessarily underlies the idea that folivores do not need to increase day range to compensate for increasing patch depletion rates in larger groups, and thus do not experience scramble competition. However, a recent study found that red colobus monkeys functionally depleted patches of high-quality foods (young leaves) and that patch occupancy time was related to the size of the feeding group and the size of the patch (Snaith and Chapman 2005). Similar patch-size effects have been demonstrated for howling monkeys (Leighton and Leighton 1982; Chapman 1988). If patches are depleted more quickly by larger groups, day range is expected to increase. However, this relationship may not always be simple, and alternate responses may exist. For example, if larger groups cannot compensate for increased depletion rates by increasing travel distance, they may increase group spread to maintain fewer individuals per patch (Leighton and Leighton 1982; Chapman 1988; Snaith and Chapman 2005; Koenig and Borries 2006). Alternatively, individuals may deplete patches further, possibly by feeding on less desirable plant parts. This idea is based on the logic of Charnov's (1976) marginal value theorem, which proposed that giving-up times should occur after more depletion (at a lower intake rate) when the time required to find another food patch is high. There has been no examination of whether folivores use compensatory measures such as this; however, the observations that folivores demonstrably deplete patches and that patch size is related to feeding group size are consistent with the assumptions of the ecological constraints model, and suggest that WGS occurs among folivores.

Group size is related to habitat quality

It has recently been demonstrated that folivore group size can be predicted by habitat variables. For example, across the geographical range of red colobus, group size tended to be larger in rain forests and moist woodlands than in drier seasonal habitats (Struhsaker 2000b, a). Across 10 sites, red colobus group size ranged from 7-83 (n=60) and was affected by tree density, degree of deciduousness, degree of forest disturbance, and forest block size (Struhsaker 2004). Similarly, across 4 study sites in Kibale, group size was larger where food tree density was greater (Chapman and Chapman 2000a; Gillespie and Chapman 2001). Black and white colobus monkeys typically form much smaller groups than often-sympatric red colobus; however, in Nyungwe, black-and-white colobus (*C. angolensis*) form exceptionally large groups of more than 300 individuals (Fimbel et al. 2001). This has been attributed to the almost unrestricted availability of unusually high-quality mature leaves (high in protein, low in fiber; although this result must be interpreted with caution because fiber content was determined using a different technique than those used in other studies). Furthermore, Dunbar (1987) reported that *C. guereza* group size was related to territory quality and that groups permanently fissioned into smaller groups when group size exceeded 10 trees/individual and territory size could not be increased. These results suggest that folivore group size may be ecologically constrained and that large groups form only when food conditions mitigate the costs of within-group competition.

Day range may be related to group size

As described above, 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, and is based on the assumption that folivores rely on ubiquitous and evenly distributed food resources (Clutton-Brock and Harvey 1977; Struhsaker and Leland 1987; Yeager and Kirkpatrick 1998; Yeager and Kool 2000; Fashing 2001). However, using these studies to infer that there is no within-group competition is problematic because they generally lack sufficient controls for ecological variation through time, among study groups, or across species. If group size can be adjusted to ecological conditions, as described above, then scramble costs can be avoided, negating the need to increase day range. Ecological variation can thus confound correlational studies, making previous comparisons across groups, and especially across species, difficult to interpret. Several recent studies that controlled for ecological variation found that day range did increase with group size for some folivores (*Gorilla beringei* (Ganas and Robbins 2005). *P. tephrosceles* (Gillespie and Chapman 2001), *P. thomasi* (Steenbeek and van Schaik 2001)). If folivore day range has the potential to be affected by group size in the manner suggested by the ecological constraints model, there is a need to re-assess inferences drawn on the basis of earlier studies that lacked ecological controls.

Day range may be related to food availability

Several studies have found that folivore groups increase day range during periods of food scarcity or in areas with lower food availability (*G. beringei* (Ganas and Robbins 2005), *C. satanas* (McKey and Waterman 1982), *C. angolensis* (Bocian 1997)), presumably due to the need to increase travel between patches. This can be interpreted as an effect of scramble competition because if group size is constrained by local ecological conditions, then a given group might be expected to respond to temporal fluctuations in food availability by increasing their range when food becomes scarce. However, other studies have documented either no relationship (*C. guereza* (Fashing 2001)), or the reverse pattern (*C. satanas* (Fleury and Gautier-Hion 1999)). Careful examination of the relationship between food abundance, the distribution of food patches, and ranging behavior is required to clarify these patterns. Relationships between food abundance and day range are likely to be confounded by food distribution. For example some groups may travel long distances to reach specific resources (Fashing 2001; Doran-Sheehy et al. 2004; Harris 2005; Pages, Lloyd, and Suarez 2005), or may change their diet to rely on more evenly distributed foods during periods of scarcity (Yeager and Kool 2000).

Fission-fusion occurs

A number of studies have found that some folivore species exhibit fission-fusion behavior, where large groups temporarily divide into smaller foraging groups that vary in size and composition (Moreno-Black and Bent 1982; Oates 1994; Siex and Struhsaker 1999; Yeager and Kool 2000; Fimbel et al. 2001; Struhsaker et al. 2004). Studies suggest that this pattern occurs in response to low food availability associated with low tree density, particularly in degraded habitat. Such short-term variation in group size is a well-documented response to variable ecological conditions among frugivores, including chimpanzees (Ghiglieri 1984; Wrangham et al. 1996), bonobos (*P. paniscus*) (Boesch 1996), orangutans (*Pongo pygmaeus*) (Sugardjito, te Boekhorst, and van Hooff 1987; van Schaik 1999), and spider monkeys (Chapman 1990a;

Symington 1990). This strategy is advantageous for individuals who rely on patchy and unpredictable food resources, because the ability to adjust group size allows greater flexibility in response to ecological conditions and can mitigate the costs of food competition.

Reproductive success is related to group size

There is evidence to suggest that female reproductive success may be compromised as group size increases, presumably because increasing food competition leads to nutritional stress. This reasoning is based on the relationship between female nutritional status and fecundity, birthrate, and early infant survival. There is a very clear causative chain linking energy balance to fecundity in humans and apes (Ellison 1990; Knott 1999), and a documented relationship between female nutritional status (food intake) and both birthrate and early infant survival in many primates (van Schaik 1983; Whitten 1983; Harcourt 1987; Silk 1987; Dunbar 1988). Although careful empirical work is required to separate the effects of compromised fecundity from those of infanticide (Crockett and Janson 2000), there appears to be a group-size effect on birthrate in folivores. Gorillas in larger groups spent more time feeding, suggesting a social foraging cost (Watts 1988). Struhsaker et al. (2004) found that habitat quality was the most important factor affecting birth rate across 19 groups of red colobus. Koenig (2000; 2002) found that as group size increased, female nutritional condition was compromised among hanuman langurs. Dunbar (1987) documented the same relationship across four populations of *C. guereza*, and suggested that stress and competition led to reproductive suppression in larger groups. More generally, van Schaik (1983) demonstrated that folivore birthrate (number of infants/female; however, there is disagreement regarding this use of unadjusted birthrates (Dunbar 1988; Crockett and Janson 2000)) decreased with increasing group size, and that this relationship was stronger for folivores than frugivores.

This effect may be related to the energetics of a folivorous diet. Due to their dietary specialization for the digestion of low-quality foods, folivores must devote a large portion of their time to resting and digesting (Milton 1984; DaSilva 1992). This may prevent individuals from increasing food intake to compensate for increasing energetic costs, which may effectively prevent folivores from increasing day range as group size increases, even if food competition intensifies, ultimately resulting in compromised nutrition, fecundity, and birthrates. Measures of female reproductive success and hormonal markers of fecundity may provide important indices of within-group competition costs when changes in day range are not observed.

Food-related contest competition occurs

Recent research suggests that food-related contest competition occurs both within and between some groups of folivores. We believe that this finding is important for two reasons. First, because it challenges previous notions that folivores generally do not or cannot contest for food, and second, because it raises the possibility that the benefits of BGC compensate for the costs of WGS/WGC in some larger folivore groups (Wrangham 1980; Koenig 2002), which may lead to the appearance of no competition and the apparent absence of a group-size effect. Koenig (1998; 2000) documented linear dominance hierarchies within groups of hanuman langurs that fed on high-quality, clumped resources that were too small for all group members. Higher-ranking females attained higher net energy gain and were in the best physical condition, indicating WGC. Furthermore, between-group differences in condition indicated BGC. Remarkably, the benefits of BGC were shown to compensate to some degree for the demonstrated costs of WGC and WGS, with the result that females in mid-sized groups were in the best physical condition. Some populations of black and white colobus monkeys rely on fruit for some portion of their diet and both males and females may participate in food defense (Korstjens 2001). In more leaf-dependent populations of black-and-white colobus, several authors have concluded that males competitively defend food resources as an indirect means to defend access to females (Oates 1977; Fashing 2001; Sicotte and MacIntosh 2004; Harris 2005). A dominance hierarchy between groups has been demonstrated for *C. guereza* at Kibale (Harris 2005, 2006). Dominant groups roared more, won more fights, were avoided by subordinate groups, and maintained core areas with food resources of greater quantity and quality. This case is particularly interesting because this population is highly folivorous (Oates 1977; Chapman et al. 2002; Harris 2005), suggesting that leaves are indeed worth fighting over. In general, this new evidence indicates that folivore groups may compete to monopolize access to food sources even without overt fighting or displacements, and without strict territoriality. As suggested by Wrangham (1980), avoidance is a possible manifestation of contest competition in primates. Dominant groups or individuals may maintain preferential, if not exclusive, access to the best resources simply because they are avoided by subordinate groups or individuals.

Population density is related to habitat quality/food availability

Folivore biomass can be predicted by the distribution of mature leaves with a high protein-to-fiber ratio (Milton 1979; Waterman et al. 1988; Fimbel et al. 2001; Chapman et al. 2002; Chapman et al. 2004). Although this does not directly suggest there will also be constraints on group size, it does provide further support that folivores may be limited in important ways by the quality, availability, and distribution of food resources, and suggests that the potential for food competition exists. Previous assumptions that folivore food resources are nutritionally uniform and not limiting have formed the basis for general inferences about food competition in folivores.

Discussion

Folivores have traditionally been seen as living without food competition or social stratification within or between groups, but this was largely based on the notion that they exploited ubiquitous and invariable food sources. These assumptions have been implicitly or explicitly incorporated into applications of socioecological models and have led to the folivore paradox. However, recent empirical data are increasingly exposing folivores as competitive and socially variable. Many folivore populations exploit high-quality, patchily distributed, temporally variable food resources, and display many of the expected responses to food competition. The emerging picture is complex, folivore strategies vary across populations and species, indicating adaptive flexibility in response to local conditions. Folivores appear to be subject to the same ecological constraints as frugivores and may respond with similar competitive regimes when food conditions are similar. However, rather than simply increasing day range to compensate for increasing group size, folivores may display alternate responses to the costs imposed by scramble competition or may incur fitness costs in larger groups. Perhaps most surprisingly, folivores contest for food, both within and between groups, challenging the long-standing notion that their diet is not worth fighting over, and raising further questions about the apparent lack of dominance relations in some species. Although further investigation is certainly required, the data reviewed here suggest that group size is probably constrained by ecological factors for some species of folivores, just as has been demonstrated for many frugivores. Undoubtedly, folivore group size is also influenced by social factors like infanticide, and the interaction of social factors and ecological constraints requires further investigation. These data provide important insights into the folivore paradox, and may be used towards refining the assumptions behind current interpretations of the competitive regime of leaf-eating monkeys.

In practical terms, we believe there are two areas where efforts are required to provide theoretical clarification and direction for empirical research. First, the terms used to describe resource characteristics and the methods used to measure them, need to be consistently and explicitly defined (Koenig and Borries 2006; Vogel and Janson 2007), particularly if resource characteristics are used to infer particular competitive regimes. Second, a wider range of indicators (including social, behavioural, and energetic consequences) of food competition needs to be recognized.

The abundance and distribution of food determines the type, intensity, and social outcomes of feeding competition. However, the distribution of food varies in a number of interacting dimensions, and on many scales. Wrangham (1980) wrote that BGC requires that high-quality food is distributed in discrete, defensible patches, and that fallback food occurs in large, uniform patches. This is a complex statement that incorporates five separate issues: food source size, quality, patchiness, defensibility, and variability. Separating these ideas, clarifying the spatial and temporal scales at which they operate, and standardizing measurement methods will go a long way towards clarifying ecological measures and their competitive outcomes in future models. Furthermore, Wrangham drew attention to the need to recognize the difference between preferred and fallback foods and that both may influence social organization. That primates can modify their feeding strategies in response to food availability, and exploit different foods with different nutritional and distributional characteristics at different times, may be one of the major issues affecting our ability to construct realistic models.

In the 1980s and 90s, the work of Wrangham (1980), van Schaik (1989), Isbell (1991), Sterck et. al. (1997), and others was instrumental in defining primate competitive regimes, and highlighting the ultimate importance of ecological factors in determining the adaptive strategies of individuals and the consequent social organization of groups. Perhaps most critically, these authors emphasized the importance of applying clear definitions of the types of food competition experienced by individuals in groups, made predictions regarding the social and behavioural consequences of competition, and identified measurable behavioral indicators by which the competitive regime of a species can be assessed. It is now becoming increasingly apparent that primates possess a suite of responses to food competition, and that any single index may be confounded by a variety of ecological and social factors. In the next sections (and summarized in Box 3), we propose an expanded set of behavioral indicators of competition. The necessity of incorporating multiple indices of competition into both theory and empirical studies was highlighted by our exploration of the folivore paradox, where the failure to document the simple expectation of increasing day range with increasing group size led to premature conclusions about food competition.

The most commonly used evidence of food-related between-group contest competition has been female aggression during between-group encounters (Wrangham 1980; van Schaik 1989; Isbell 1991; van Schaik, Assink, and Salafsky 1992), and was the indicator originally proposed by Isbell (see Box 2) to measure this phenomenon. This follows from sexual selection theory (Trivers 1972) which suggests that because female reproductive success is limited by access to resources, females should compete for and defend food, while males should compete for and defend mates. However, a lack of female participation in between-group encounters should not be used as evidence that BGC is *not* related to food. Males may also participate in BGC in defense of food resources as an indirect means to defend access to females (Emlen and Oring 1977), Furthermore, overt aggressive between-group interactions are not required; avoidance behaviors may also indicate BGC (Wrangham 1980; van Schaik, Assink, and Salafsky 1992).

Between-group scramble competition results from the common use of food resources by all groups/individuals; it can thus occur only when groups occupy overlapping ranges and, in habitat of constant quality, BGS will increase in intensity with increasing population density. Earlier work (Dunbar 1988; Isbell 1991), suggested that an increase in home range size as a result of an increase in group size could be used to indicate BGS. However, because between-group scramble is an effect of population density, and is independent of group size, this is not an appropriate measure. Rather, a positive relationship between population density (cumulative group size) and habitat quality indicates that BGS competition occurs.

Female dominance hierarchies have traditionally been used as the primary indicator of within-group contest competition. Because contest competition results in skewed energy acquisition (Vehrencamp 1983; Janson and van Schaik 1988; van Schaik 1989), inter-individual differences in fitness, as indicated by skew in birthrate, body condition, and other physiological measures, may also indicate WGC. Although such measures must be used with care (because individual differences in fitness will be affected by many factors such as genetic and ontogenetic variation), in cases where overt contests and dominance hierarchies are rare or difficult to observe (e.g., subtle avoidance behavior or the ability to occupy the best feeding sites), they may prove useful. For example, it has been shown that there may be a demonstrable WGC effect on food intake and reproductive success, without the expected agonistic alliances and nepotistic affiliative patterns (Koenig 2000), or without clear behavioral contests over relevant food items (Whitten 1983). Measures of birthrate and body condition have the additional advantage of being more direct indicators of fitness, and if they can be related to differences in rank, they may provide an index of the ultimate effects of food competition on the reproductive success of individuals (Koenig 2000).

A positive relationship between day range and group size has long been used as the primary indicator of within-group scramble competition. However, the relationship between day range and group size can be obscured by ecological

Box 3. Expanded list of behavioral indicators of food competition

Type of Competition	Behavioral Indicator
Between-group contest	• Food-related between-group aggression among females • Food-related between-group aggression among males as an indirect means to defend access to females • Between-group dominance hierarchy • Between-group displacements or avoidance
Between-group scramble	• Positive relationship between habitat quality and population density
Within-group contest	• Female dominance hierarchies • Food related within-group aggression, avoidance or displacements and/or agonistic alliances • Rank-related skew in food acquisition, nutritional status, fecundity, and reproductive success
Within-group scramble	• Positive relationship between group size and day range and/or home range size • Positive relationship between group size and habitat quality • Negative relationship between day range and habitat quality • Fission-fusion related to temporal variation in resource availability • Positive relationship between patch depletion rate and group size, and/or negative relationship between depletion rate and patch size • Positive relationship between group size and normalized group spread, and/or non-positive relationship between total group size and feeding group size • Longer giving-up time in larger groups and/or poorer habitat • Negative relationship between group size and female nutritional status, fecundity, and reproductive success

variation, and increasing day range is not the only possible behavioral response to scramble competition in groups. Group size itself may be constrained by local habitat quality, so that individuals may avoid the need to increase day range. Furthermore, within groups, individuals may compensate for temporal fluctuations in competition intensity caused by ecological variation by adjusting day range through time or by fissioning. Individuals may also avoid the travel costs associated with increasing day range by altering group spread, or patch depletion thresholds and giving-up times. If individuals are unable to compensate for grouping costs, then fitness will decrease in larger groups. Such considerations substantially broaden the list of potentially observable indicators of within-group scramble competition.

Expanding the list of acceptable indicators of food competition provides measurable, quantifiable variables for field studies, and may provide direction for the development of hypotheses that will further our understanding of primate socioecology. Furthermore, by constructing this list we acknowledge that primates may employ a variety of possible responses to food competition, and that univariate analyses will often be insufficient for describing the competitive regime of a species.

Based on the issues addressed in this paper, Figure 1 outlines a working-version model of the potential competitive outcomes of variation in resource characteristics. The logic and predictions of this model are essentially no different from those of van Schaik (van Schaik 1989) or Wrangham (Wrangham 1980). We attempt to build on these models by offering a more detailed tool for addressing the multidimensional nature of ecological variation and possible competitive outcomes. The availability, distribution, size, quality, and contestability of food resources are addressed as separate ecological variables that can vary independently of one another. There are no *a priori* assumptions about the mutual exclusion of different types of competition. For example, WGS may occur alone, or along with BGC and/or WGC. When the empirical evidence presented above regarding the distribution, quality, and abundance of folivore foods is applied to this model (or to previous models), it leads to the prediction that many folivores will compete by scramble and/or contest. Perhaps the most important development presented here, from the perspective of understanding ecological constraints in folivores, is the distinction between patchy (i.e., depletable) and continuous food distribution at the second level of classification. This allows for the possibility of WGS without contest competition, and scramble can still be important when food is neither variable in quality nor defensible, a likely scenario for many folivores. We provide examples of folivore populations on as many branches as possible, including branches representing competitive regimes that have traditionally been reserved for frugivores. Further research is required to determine whether the ideas presented in Figure 1 are a useful and accurate way to depict the ecological pressures influencing the evolution of primate social organization.

The evidence presented here suggests several profitable directions for future field research. First, it is important to understand individual behavioral strategies. Data regarding the activity budgets, nutrient gain, and reproductive success of recognizable individuals in groups of different sizes are required to quantify the fitness costs of food competition. Second, attention should be focused on subtle expressions of contest competition, such as avoidance or the consistent attainment of better feeding sites by certain individuals or groups, and whether these have fitness consequences. Third, to unravel how primate social organization is shaped by ecological conditions, and whether different species and populations respond in the same manner to ecological variation, we need quantitative ecological data, based on carefully defined measures, for a wide range of species. For example, we need comparable descriptions of the spatial and temporal distribution of food resources, variation in food quality within and between patches and through time, patch size relative to group size, and patch attributes such as contestability. Because these factors are presumed to be of primary importance in determining the nature of within- and between-group competition, we need to investigate their social outcomes in hypothesis-driven field studies.

It is unlikely that any model will ever capture the entire range of social variability among primates, and we recognize that our focus on feeding competition captures only part of the puzzle. Many other factors, including predation, infanticide, dispersal costs and social dynamics must also be incorporated. But we hope that the issues brought to light by this ecological examination of the folivore paradox will contribute to the next generation of models by increasing our understanding of the adaptive significance of particular competitive regimes and the selective forces shaping primate food competition and social organization.

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References Cited

Alexander RD. 1974. The evolution of social behavior. Annu Rev Ecol Syst. 5:325-383.

Bocian CM. 1997. Niche separation of black and white colobus monkeys (*Colobus angolensis* and *C. guereza*) in the Ituri forest [dissertation]. New York: The City University of New York; 202 p.

Boesch C. 1996. Social grouping in Tai chimpanzees. In: McGrew WC, Marchant LF, Nishida T, editors. Great ape societies. Cambridge: Cambridge University Press. p. 101-113.

Borries C. 1993. Ecology of female social relationships - Hanuman langurs (*Presbytis entellus*) and the van Schaik model. Folia Primatol. 61:21-30.

Chapman CA. 1988. Patch use and patch depletion by the spider and howling monkeys of Santa Rosa National Park, Costa Rica. Behav Ecol. 105:99-116.

Chapman CA. 1990a. Association patterns of spider monkeys: the influence of ecology and sex on social organization. Beh Ecol Sociobiol. 26:409-414.

Chapman CA. 1990b. Ecological constraints on group size in three species of neotropical primates. Folia Primatol. 55:1-9.

Chapman CA, Chapman LJ. 2000a. Constraints on group size in red colobus and red-tailed guenons: examining the generality of the ecological constraints model. Int J Primatol. 21:565-585.

Chapman CA, Chapman LJ. 2000b. Determinants of group size in primates: the importance of travel costs. In: Boinski S, Garber PA, editors. On the move: how and why animals travel in groups. Chicago: University of Chicago Press. p. 24-41.

Chapman CA, Chapman LJ. 2002. Foraging challenges of red colobus monkeys: influence of nutrients and secondary compounds. Comp Biochem Physiol A Physiol. 133:861-875.

Chapman CA, Chapman LJ, Bjorndal KA, Onderdonk DA. 2002. Application of protein-to-fiber ratios to predict colobine abundance on difference spatial scales. Int J Primatol. 23:283-310.

Chapman CA, Chapman LJ, Naughton-Treves L, Lawes MJ, McDowell LR. 2004. Predicting folivorous primate abundance: Validation of a nutritional model. Am J Primatol. 62:55-69.

Chapman CA, Chapman LJ, Rode KD, Hauck EM, McDowell LR. 2003. Variation in the nutritional value of primate foods: among trees, time periods and areas. Int J Primatol. 24:317-333.

Chapman CA, Wrangham RW, Chapman LJ. 1995. Ecological constraints on group size: an analysis of spider monkey and chimpanzee subgroups. Beh Ecol Sociobiol. 36:59-70.

Charnov EL. 1976. Optimal foraging, the marginal value theorem. Theor Popul Biol. 9:129-136.

Clutton-Brock TH, Harvey PH. 1977. Primate ecology and social organization. J Zool Soc Lon. 183:1-39.

Crockett CM, Janson CH. 2000. Infanticide in red howlers: female group size, group composition, and a possible link to folivory. In: van Schaik CP, Janson CH, editors. Infanticide by males and its implications. Cambridge: Cambridge University Press. p. 75-98.

Crook JH, Gartlan JS. 1966. Evolution of primate societies. Nature. 210:1200-1203.

DaSilva GL. 1992. The western black and white colobus as a low energy strategist: activity budget, energy expenditure and energy intake. J Anim Ecol. 61:79-91.

Doran-Sheehy DM, Greer D, Mongo P, Schwindt D. 2004. Impact of ecological and social factors on ranging in western gorillas. Am J Primatol. 64:207-222.

Dunbar RIM. 1988. Primate social systems. New York: Cornell University Press.

Dunbar RLM. 1987. Habitat quality, population dynamics and group composition in colobus monkeys (*Colobus guereza*). Int J Primatol. 8:299-329.

Eisenberg JF, Muckenhirn NA, Rudran R. 1972. The relation between ecology and social structure in primates. Science. 176:863-874.

Ellison PT. 1990. Human ovarian function and reproductive ecology - new hypotheses. Amer Anthropol. 92:933-952.

Emlen ST. 1978. Cooperative breeding in birds and mammals. In: Krebs JR, Davies NB, editors. Behavioural Ecology: An Evolutionary Approach 2nd ed. London: Sinauer and Associates. p. 305-339.

Emlen ST, Oring LW. 1977. Ecology, sexual selection, and the evolution of mating systems. Science. 197:215-223.

Fashing PJ. 2001. Activity and ranging patterns of guerezas in the Kakamega forest: intergroup variation and implications for intragroup feeding competition. Int J Primatol. 22:549-577.

Fimbel C, Vedder A, Dierenfeld E, Mulindahabi F. 2001. An ecological basis for large group size in *Colobus angolensis* in the Nyungwe Forest, Rwanda. Afr J Ecol. 39:83-92.

Fleury MC, Gautier-Hion A. 1999. Seminomadic ranging in a population of black colobus (Colobus satanas) in Gabon and its ecological correlates. Int J Primatol. 20:491-509.

Ganas J, Robbins MM. 2005. Ranging behavior of the mountain gorillas (*Gorilla beringei beringei*) in Bwindi Impenetrable National Park, Uganda: a test of the ecological constraints model. Beh Ecol Sociobiol. 58:277-288.

Ghiglieri MP. 1984. Feeding ecology and sociality of chimpanzees in Kibale Forest, Uganda. In: Rodman PS, Cant JGH, editors. Adaptations for foraging in nonhuman primates: contributions to organismal biology of prosimians, monkeys, and apes. New York: Columbia University Press. p. 161-194.

Gillespie TR, Chapman CA. 2001. Determinants of group size in the red colobus monkey (*Procolobus badius*): an evaluation of the generality of the ecological-constraints model. Beh Ecol Sociobiol. 50:329-338.

Glander KE. 1981. Feeding patterns in mantled howling monkeys. In: Kamil AC, Sargent TD, editors. Foraging behavior. New York: Garland Press. p. 231-257.

Glander KE. 1982. The impact of plant secondary compounds on primate feeding behavior. Yearbook Phys Anthrop. 25:1-18.

Harcourt A. 1987. Dominance and fertility among female primates. J Zool Soc Lon. 213:471-487.

Harris TR. 2005. Roaring, intergroup aggression, and feeding competition in black and white colobus monkeys (*Colobus guereza*) at Kanyawara, Kibale National Park, Uganda [dissertation]. New Haven, CT: Yale University; 253 p.

Harris TR. 2006. Between-group contest competition for food in a highly folivorous population of black and white colobus monkeys (*Colobus guereza*). Beh Ecol Sociobiol. 61:317-329.

Isbell LA. 1991. Contest and scramble competition: patterns of female aggression and ranging behaviour among primates. Behav Ecol. 2:143-155.

Isbell LA, Young TP. 2002. Ecological models of female social relationships in primates: similarities, disparities and some directions for future clarity. Behaviour. 139:177-202.

Janson CH, Goldsmith ML. 1995. Predicting group size in primates: foraging costs and predation risks. Behav Ecol. 6:326-336.

Janson CH, van Schaik CP. 1988. Recognizing the many faces of primate food competition: methods. Behaviour. 105:165-186.

Kay RNB, Davies AG. 1994. Digestive physiology. In: Davies AG, Oates JF, editors. Colobine monkeys: their ecology, behaviour and evolution. Cambridge: Cambridge University Press. p. 229-250.

Knott CD. 1999. Reproductive, physiological and behavioral responses of orangutans in Borneo to fluctuations in food availability [dissertation]. Cambridge: Harvard University; 355 p.

Koenig A. 2000. Competitive regimes in forest-dwelling Hanuman langur females (*Semnopithecus entellus*). Beh Ecol Sociobiol. 48:93-109.

Koenig A. 2002. Competition for resources and its behavioral consequences among female primates. Int J Primatol. 23:759-783.

Koenig A, Beise J, Chalise MK, Ganzhorn JU. 1998. When females should contest for food - testing hypotheses about resource density, distribution, size and quality with Hanuman langurs (*Presbytis entellus*). Beh Ecol Sociobiol. 42:225-237.

Koenig A, Borries C. 2002. Feeding competition and infanticide constrain group size in wild hanuman langurs. Am J Primatol. 57:33-34.

Koenig A, Borries C. 2006. The predictive power of socioecological models: a reconsideration of resource characteristics, agonism, and dominance hierarchies. In: Hohmann G, Robbins M, Boesch C, editors. Feeding ecology in apes and other primates. Cambridge: Cambridge University Press. p. 263-284.

Korstjens AH. 2001. The mob, the secret sorority, and the phantoms, PhD thesis [dissertation]. Utrecht: Utrecht University; 173 p.

Leighton M, Leighton DR. 1982. The relationship of size of feeding aggregate to size of food patch: howler monkeys (*Alouatta palliata)* feeding in *Trichilia cipo* fruit trees on Barro Colorado Island. Biotropica. 14:81-90.

MacArthur RH, Pianka ER. 1966. On the optimal use of a patchy environment. Am Nat. 100:603-609.

Macdonald DW. 1979. Flexible social system of the golden jackal, *Canis-Aureus*. Beh Ecol Sociobiol. 5:17-38.

McKey D, Waterman PG. 1982. Ranging behavior of a group of black colobus (*Colobus satanas*) in the Douala-Edea Reserve, Cameroon. Folia Primatol. 39:264-304.

Milton K. 1979. Factors influencing leaf choice by howler monkeys: a test of some hypotheses of food selection by generalist herbivores. Am Nat. 114:363-378.

Milton K. 1980. The foraging strategy of howler monkeys. New York: Columbia University Press.

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

Moreno-Black GS, Bent EF. 1982. Secondary compounds in the diet of *Colobus angolensis*. Afr J Ecol. 20:29-36.

Nicholson AJ. 1954. An outline of the dynamics of animal populations Aust J Zool. 2:9-65.

Oates JF. 1977. The guereza and its food. In: Clutton-Brock TH, editor. Primate ecology: studies of feeding and ranging behaviour in lemurs, monkeys and apes. London: Academic Press. p. 275-321.

Oates JF. 1994. The natural history of African colobines. In: Davies AG, Oates JF, editors. Colobine monkeys: their ecology, behaviour and evolution. Cambridge: Cambridge University Press. p. 75-128.

Oates JF, Davies AG. 1994. What are the colobines. In: Oates JF, Davies AG, editors. Colobine monkeys: their ecology, behaviour and evolution. Cambridge: Cambridge University Press. p. 1-10.

Pages G, Lloyd E, Suarez SA. 2005. The impact of geophagy on ranging behaviour in Phayre's leaf monkeys (*Trachypithecus phayrei*). Folia Primatol. 76:342-346.

Sicotte P, MacIntosh AJ. 2004. Inter-group encounters and male incursions in *Colobus vellerosus* in Central Ghana. Behaviour. 141:533-553.

Siex K, Struhsaker TT. 1999. Ecology of the Zanzibar red colobus monkey: demography variability and habitat stability. Int J Primatol. 20:163-192.

Silk JB. 1987. Social behavior in evolutionary perspective. In: Cheney DL, Seyfarth RM, Wrangham RW, Struhsaker TT, editors. Primate societies. Chicago: University of Chicago Press. p. 318-329.

Snaith TV, Chapman CA. 2005. Towards an ecological solution to the folivore paradox: patch depletion as an indicator of within-group scramble competition in red colobus. Beh Ecol Sociobiol. 59:185-190.

Steenbeek R, van Schaik CP. 2001. Competition and group size in Thomas's langurs (*Presbytis thomasi*): the folivore paradox revisited. Beh Ecol Sociobiol. 49:100-110.

Stephens DW, Krebs JR. 1986. Foraging theory. Princeton: Princeton University Press.

Sterck EHM, Watts DP, van Schaik CP. 1997. The evolution of female social relationships in nonhuman primates. Beh Ecol Sociobiol. 41:291-309.

Stevenson PR, Castellanos MC. 2000. Feeding rates and daily path range of the Colombian wooly monkeys as evidence for between- and within-group competition. Folia Primatol. 71:399-408.

Strier KB. 1989. Effects of patch size on feeding associations in Muriquis (*Brachyteles arachnoides*). Folia Primatol. 52:70-77.

Struhsaker TT. 2000a. The effects of predation and habitat quality on the socioecology of African monkeys: lessons from the islands of Bioko and Zanzibar. In: Whitehead PF, Jolly CJ, editors. Old world monkeys. Cambridge: Cambridge University Press. p. 393-430.

Struhsaker TT. 2000b. Variation in adult sex ratios of red colobus monkey social groups: implications for interspecific comparisons. In: Kappeler PM, editor. Primate males: causes and consequences of variation in group composition. Cambridge: Cambridge University Press. p. 108-119.

Struhsaker TT, Leland L. 1987. Colobines: infanticide by adult males. In: Smuts BB, Cheney DL, Seyfarth RM, Wrangham RW, Struhsaker TT, editors. Primate societies. Chicago: University of Chicago Press. p. 83-97.

Struhsaker TT, Marshall AR, Detwiler K, Siex K, Ehardt C, Lisbjerg DD, Butynski TM. 2004. Demographic variation among Udzungwa red colobus in relation to gross ecological and sociological parameters. Int J Primatol. 25:615-658.

Sugardjito J, te Boekhorst IJA, van Hooff JARAM. 1987. Ecological constraints on the grouping of wild orang-utans (*Pongo pygmaeus*) in the Gunung Leuser National Park, Sumatra, Indonesia. Int J Primatol. 8:17-41.

Symington MM. 1990. Fission-fusion social organization in *Ateles* and *Pan*. Int J Primatol. 11:47-61.

Terborgh J, Janson CH. 1986. The socioecology of primate groups. Annu Rev Ecol Syst. 17:111-135.

Treves A, Chapman CA. 1996. Conspecific threat, predation avoidance, and resource defense: implications for grouping in langurs. Beh Ecol Sociobiol. 39:43-53.

Trivers RL. 1972. Parental investment and sexual selection. In: Campbell B, editor. Sexual selection and the descent of man 1871-1971. New York: Aldine Publishing. p. 136-175.

van Schaik CP. 1983. Why are diurnal primates living in groups? Behaviour:120-144.

van Schaik CP. 1999. The socioecology of fission-fusion sociality in orangutans. Primates. 40:69-86.

van Schaik CP, Assink PR, Salafsky N. 1992. Territorial behavior in Southeast Asian langurs: resource defense or mate defense. Am J Primatol. 26:233-242.

van Schaik CP. 1989. The ecology of social relationships amongst female primates. In: Standen V, Foley RA, editors. Comparative socioecology: The behavioural ecology of humans and other mammals. Boston: Blackwell Scientific Publications. p. 195-218.

Vehrencamp SL. 1979. The roles of individual, kin, and group selection in the evolution of sociality. In: Marler P, Vandenbergh JG, editors. Handbook of behavioral neurobiology. New York: Plenum Press. p. 351-389.

Vehrencamp SL. 1983. A model for the evolution of despotic versus egalitarian societies. Anim Behav. 31:667-682.

Vehrencamp SL, Bradbury JW. 1978. Mating systems and Ecology. In: Krebs JR, Davies NB, editors. Behavioural Ecology: An Evolutionary Approach 2nd ed. London: Sinauer and Associates. p. 251-278.

Vehrencamp SL, Bradbury JW. 1984. Mating systems and ecology. In: Krebs JR, Davies NB, editors. Behavioural ecology: an evolutionary approach 2nd ed. London: Sinauer and Associates. p. 251-278.

Vogel E, Janson CH. 2007. Predicting the frequency of food-related agonism in white-faced capuchin monkeys (*Cebus capucinus*) using a novel focal-tree method. Am J Primatol. 69:1-18.

Waser PM. 1977. Feeding, ranging and group size in the mangabey *Cercopithecus albigena*. In: Clutton-Brock TH, editor. Primate ecology: studies of feeding and ranging behaviour in lemurs, monkeys and apes. New York: Academic Press. p. 183-222.

Waterman PG, Ross JAM, Bennet EL, Davies AG. 1988. A comparison of the floristics and leaf chemistry of the tree flora in two Malaysian rain forests and the influence of leaf chemistry on populations of colobine monkeys in the old world. Biol J Linn Soc. 34:1-32.

Watts DP. 1988. Environmental influences on mountain gorilla time budgets. Am J Primatol. 15:195-211.

Watts DP. 1996. Comparative socio-ecology of gorillas. In: McGrew WC, Marchant LF, Nishida T, editors. Great ape societies. Cambridge: Cambridge University Press. p. 16-28.

Whitten PL. 1983. Diet and dominance among female vervet monkeys (*Cercopithecus aethiops*). Am J Primatol. 5:139-159.

Wrangham RW. 1979. On the evolution of ape social systems. Soc Sci Inform. 18:335-368.

Wrangham RW. 1980. An ecological model of female-bonded primate groups. Behaviour. 75:262-300.

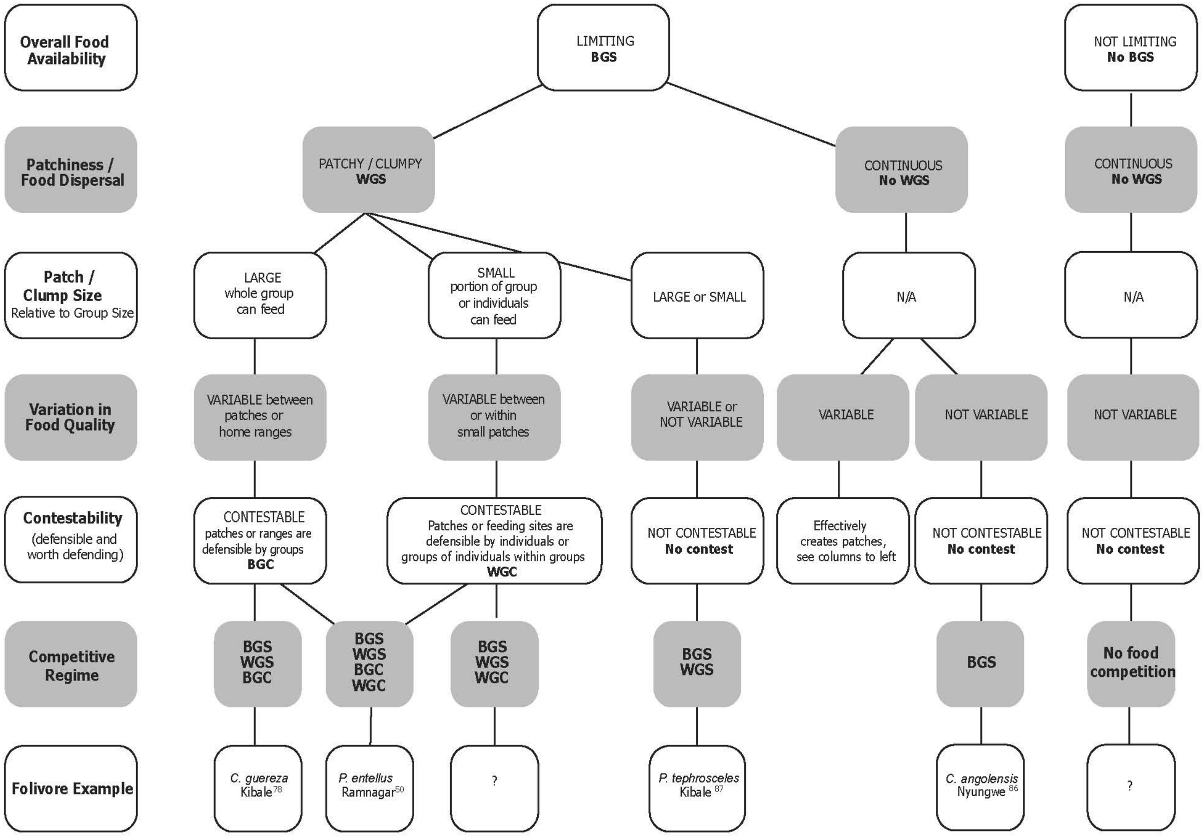
Wrangham RW. 2000. Why are male chimpanzees more gregarious than mothers? A scramble competition hypothesis. In: Kappeler PM, editor. Primate males: causes and consequences of variation in group composition. Cambridge: Cambridge University Press. p. 248-258.

Wrangham RW, Chapman CA, Clark-Arcadi AP, Isabirye-Basuta G. 1996. Social ecology of Kanyawara chimpanzees: implications for understanding the costs of great ape groups. In: McGrew WC, Marchant LF, Nishida T, editors. Great ape societies. Cambridge: Cambridge University Press. p. 45-57.

Yeager CP, Kirkpatrick CR. 1998. Asian colobine social structure: ecological and evolutionary constraints. Primates. 39:147-155.

Yeager CP, Kool K. 2000. The behavioral ecology of Asian colobines. In: Whitehead PF, Jolly CJ, editors. Old world monkeys. Cambridge: Cambridge University Press. p. 496-521.

Figure 1. Working model of how resource abundance and distribution may affect competitive regime



Legend: BGS=Between-group scramble competition; BGC=Between-group contest competition; WGS=Within-group scramble competition; WGC=Within-group contest competition

LINKING STATEMENT 1

In Chapter 1, I found evidence to suggest that folivores likely experience scramble competition, but that comprehensive ecologically controlled studies are required to further test this hypothesis. The notion that folivores experience little to no food competition is based in part on the assumption that their food resources are superabundant and evenly dispersed, and thus non-depletable. Before seeking behavioural evidence of food competition in a species, it would be prudent to test this assumption; if patches are in fact depletable, then scramble competition is ecologically possible.

In Chapter 2, I test the assumption that patches of leaves are not depletable by examining the foraging behaviour of red colobus monkeys (*Procolobus rufomitratus*) in Kibale National Park, Uganda. I developed a novel method for examining patch depletion, based on the assumption that if food is becoming depleted, it will take more effort to acquire near the end of the time spent feeding in a patch. I thus compared the intake rate and foraging effort at the start to those at the end of the patch occupancy period. If food patches are depletable, then red colobus likely experience increasing foraging costs in larger groups due to scramble competition, and further study will be required to determine whether there are observable behavioural mechanisms and physiological costs of competition in these species.

CHAPTER 2: TOWARDS AN ECOLOGICAL SOLUTION TO THE FOLIVORE PARADOX: PATCH DEPLETION AS AN INDICATOR OF WITHIN-GROUP SCRAMBLE COMPETITION IN RED COLOBUS[2]

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 they 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 can limit folivore group size, and should be considered in models of folivore behavioural ecology.

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;

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van Schaik 1989; Isbell 1991; Chapman, Wrangham, and Chapman 1995; Sterck, Watts, and van Schaik 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 we are concerned with in this paper. 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, Wrangham, and Chapman 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, Wrangham, and Chapman 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, Gittleman, and Chapman 1993; Chapman, Wrangham, and Chapman 1995; Wrangham et al. 1996; Chapman and Chapman 2000a). The picture is less clear for folivores: because their food resources are presumed to be superabundant and evenly dispersed, it is often assumed that within-group scramble competition is weak or absent (Wrangham 1980; Isbell 1991; Janson and Goldsmith 1995; Sterck, Watts, and van Schaik 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, Wrangham, and Chapman 1995; Janson and Goldsmith 1995; Chapman and Chapman 2000b; Wrangham 2000; Isbell and Young 2002). 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; Isbell and Young 2002). However, using these studies to infer that there is no scramble competition is problematic because they generally lack sufficient controls for ecological variation among study 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 deciduousness, 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, Chapman, and Gillespie 2002) 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, McGrew, and Baldwin 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, Sterck, and Noe 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. 2002). Although this does not directly suggest 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 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 preferred foods that occur in patches, patches will be depleted.
2. In depletable patches, patch occupancy (feeding time in a single patch) will decrease with increasing group size (when patch size is held constant), and/or with decreasing patch size (when group size is held constant).

We designed this project to empirically test these predictions.

Methods

We studied red colobus monkeys of Kibale National Park, western Uganda (795 km^2; 0^o 13' - 0^o 41' N and 30^o 19' - 30^o 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 members 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 five minutes. 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 one minute intervals. Feeding effort was indexed as the rate of movement and measured as the number of times the animal changed location and the distance (meters) moved in three minute 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/minute) was used as an index of feeding gain, and movement (meters/3 minutes) 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 becoming 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 problem.

Intake rate and movement rate values from the first quarter of each patch occupancy period 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. 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 (this food preference as 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. Monkeys consumed primarily 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=5.76, 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 minutes (range 15-74 minutes, sd=12.43, n=45).

Intake rate slowed significantly during patch occupancy (n=68, start rate x=16.05 bites/minute, end rate x=13.67, paired t=5.022, p<0.0001), while movement rate increased (n=45, start rate x=0.33 meters/3 minutes, end rate x=1.15, paired t=-3.89, p<0.0001) when all patches were analyzed 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 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) (Figure 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 correlation coefficient=0.002, p=0.989, n=44), suggesting that occupancy time is 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, Kotler, and Mitchell 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 folivore 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 Hooff 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 were 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, Palombit, and Rodman 1992; Korstjens, Sterck, and Noe 2002), but we know of no 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 be used as a behavioural indicator of the *presence* of within-group scramble competition**,** and 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. 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 increased. 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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References Cited

Boesch C. 1996. Social grouping in Tai chimpanzees. In: McGrew WC, Marchant LF, Nishida T, editors. Great ape societies. Cambridge: Cambridge University Press. p. 101-113.

Brown JS. 1988. Patch use as an indicator of habitat preference, predation risk, and competition. Beh Ecol Sociobiol. 22:37-47.

Brown JS. 1989. Desert rodent community structure: a test of four mechanisms of coexistence. Ecol Monogr. 59:1-20.

Brown JS, Kotler BP, Mitchell WA. 1994. Foraging threory, patch use, and the structure of a Negev desert granivore community. Ecology. 75:2286-2300.

Chapman CA. 1988. Patch use and patch depletion by the spider and howling monkeys of Santa Rosa National Park, Costa Rica. Behav Ecol. 105:99-116.

Chapman CA. 1990a. Association patterns of spider monkeys: the influence of ecology and sex on social organization. Beh Ecol Sociobiol. 26:409-414.

Chapman CA. 1990b. Ecological constraints on group size in three species of neotropical primates. Folia Primatol. 55:1-9.

Chapman CA, Chapman LJ. 2000a. Constraints on group size in red colobus and red-tailed guenons: examining the generality of the ecological constraints model. Int J Primatol. 21:565-585.

Chapman CA, Chapman LJ. 2000b. Determinants of group size in primates: the importance of travel costs. In: Boinski S, Garber PA, editors. On the move: how and why animals travel in groups. Chicago: University of Chicago Press. p. 24-41.

Chapman CA, Chapman LJ. 2002. Foraging challenges of red colobus monkeys: influence of nutrients and secondary compounds. Comp Biochem Physiol A Physiol. 133:861-875.

Chapman CA, Chapman LJ, Bjorndal KA, Onderdonk DA. 2002. Application of protein-to-fiber ratios to predict colobine abundance on difference spatial scales. Int J Primatol. 23:283-310.

Chapman CA, Chapman LJ, Gillespie TR. 2002. Scale issues in the study of primate foraging: red colobus of Kibale National Park. American Journal of Physical Anthropology. 117:349-363.

Chapman CA, Chapman LJ, Wrangham RW, Isabirye-Basuta G, Ben-David K. 1997. Spatial and temporal variability in the structure of a tropical forest. Afr J Ecol. 35:287-302.

Chapman CA, Lambert JE. 1999. Habitat alteration and the conservation of African primates: a case study of Kibale National Park, Uganda. Am J Primatol. 50:169-186.

Chapman CA, Wrangham RW, Chapman LJ. 1995. Ecological constraints on group size: an analysis of spider monkey and chimpanzee subgroups. Beh Ecol Sociobiol. 36:59-70.

Charnov EL. 1976. Optimal foraging, the marginal value theorem. Theor Popul Biol. 9:129-136.

Clutton-Brock TH, Harvey PH. 1977. Primate ecology and social organization. J Zool Soc Lon. 183:1-39.

Crockett CM, Janson CH. 2000. Infanticide in red howlers: female group size, group composition, and a possible link to folivory. In: van Schaik CP, Janson CH, editors. Infanticide by males and its implications. Cambridge: Cambridge University Press. p. 75-98.

Davies AG. 1994. Colobine populations. In: Davies AG, Oates JF, editors. Colobine monkeys: their ecology, behaviour and evolution. Cambridge: Cambridge University Press.

Fimbel C, Vedder A, Dierenfeld E, Mulindahabi F. 2001. An ecological basis for large group size in *Colobus angolensis* in the Nyungwe Forest, Rwanda. Afr J Ecol. 39:83-92.

Ghiglieri MP. 1984a. The chimpanzees of Kibale Forest. New York: Columbia University Press.

Ghiglieri MP. 1984b. Feeding ecology and sociality of chimpanzees in Kibale Forest, Uganda. In: Rodman PS, Cant JGH, editors. Adaptations for foraging in nonhuman primates: contributions to organismal biology of prosimians, monkeys, and apes. New York: Columbia University Press. p. 161-194.

Gillespie TR, Chapman CA. 2001. Determinants of group size in the red colobus monkey (*Procolobus badius*): an evaluation of the generality of the ecological-constraints model. Beh Ecol Sociobiol. 50:329-338.

Goodall J. 1986. The Chimpanzees of Gombe: Patterns of Behaviour. London: Harvard University Press.

Grether GF, Palombit RA, Rodman PS. 1992. Gibbon foraging decisions and the marginal value model. Int J Primatol. 13:1-17.

Isbell LA. 1991. Contest and scramble competition: patterns of female aggression and ranging behaviour among primates. Behav Ecol. 2:143-155.

Isbell LA, Young TP. 2002. Ecological models of female social relationships in primates: similarities, disparities and some directions for future clarity. Behaviour. 139:177-202.

Janson CH, Goldsmith ML. 1995. Predicting group size in primates: foraging costs and predation risks. Behav Ecol. 6:326-336.

Janson CH, van Schaik CP. 1988. Recognizing the many faces of primate food competition: methods. Behaviour. 105:165-186.

Koenig A. 2000. Competitive regimes in forest-dwelling Hanuman langur females (*Semnopithecus entellus*). Beh Ecol Sociobiol. 48:93-109.

Koenig A, Beise J, Chalise MK, Ganzhorn JU. 1998. When females should contest for food - testing hypotheses about resource density, distribution, size and quality with Hanuman langurs (*Presbytis entellus*). Beh Ecol Sociobiol. 42:225-237.

Koenig A, Borries C. 2002. Feeding competition and infanticide constrain group size in wild hanuman langurs. Am J Primatol. 57:33-34.

Korstjens AH, Sterck EHM, Noe R. 2002. How adaptive or phylogenetically inert is primate social behaviour? A test with two sympatric colobines. Behaviour. 139:203-225.

Kotler BP, Brown JS. 1988. Environmental heterogeneity and the coexistence of desert rodents. Annu Rev Ecol Syst. 19:281-307.

Leighton M, Leighton DR. 1982. The relationship of size of feeding aggregate to size of food patch: howler monkeys (*Alouatta palliata)* feeding in *Trichilia cipo* fruit trees on Barro Colorado Island. Biotropica. 14:81-90.

McKey DB, Gartlan JS, Waterman PG, Choo GM. 1981. Food selection by black colobus monkeys (*Colobus satanas*) in relation to plant chemistry. Biol J Linn Soc. 16:115-146.

Oates JF. 1994. The natural history of African colobines. In: Davies AG, Oates JF, editors. Colobine monkeys: their ecology, behaviour and evolution. Cambridge: Cambridge University Press. p. 75-128.

Oates JF, Davies AG. 1994. What are the colobines. In: Oates JF, Davies AG, editors. Colobine monkeys: their ecology, behaviour and evolution. Cambridge: Cambridge University Press. p. 1-10.

Pyke GH. 1984. Optimal foraging theory: a critical review. Annu Rev Ecol Syst. 15:523-575.

Siex K, Struhsaker TT. 1999. Ecology of the Zanzibar red colobus monkey: demography variability and habitat stability. Int J Primatol. 20:163-192.

Skorupa JP. 1988. The effect of selective timber harvesting on rain forest primates in Kibale Forest, Uganda. PhD Thesis. University of California, Davis.

Steenbeek R, van Schaik CP. 2001. Competition and group size in Thomas's langurs (*Presbytis thomasi*): the folivore paradox revisited. Beh Ecol Sociobiol. 49:100-110.

Sterck EHM, Watts DP, van Schaik CP. 1997. The evolution of female social relationships in nonhuman primates. Beh Ecol Sociobiol. 41:291-309.

Strier KB. 1989. Effects of patch size on feeding associations in Muriquis (*Brachyteles arachnoides*). Folia Primatol. 52:70-77.

Struhsaker TT. 2000a. The effects of predation and habitat quality on the socioecology of African monkeys: lessons from the islands of Bioko and Zanzibar. In: Whitehead PF, Jolly CJ, editors. Old world monkeys. Cambridge: Cambridge University Press. p. 393-430.

Struhsaker TT. 2000b. Variation in adult sex ratios of red colobus monkey social groups: implications for interspecific comparisons. In: Kappeler PM, editor. Primate males: causes and consequences of variation in group composition. Cambridge: Cambridge University Press. p. 108-119.

Struhsaker TT, Leland L. 1987. Colobines: infanticide by adult males. In: Smuts BB, Cheney DL, Seyfarth RM, Wrangham RW, Struhsaker TT, editors. Primate societies. Chicago: University of Chicago Press. p. 83-97.

Struhsaker TT, Marshall AR, Detwiler K, Siex K, Ehardt C, Lisbjerg DD, Butynski TM. 2004. Demographic variation among Udzungwa red colobus in relation to gross ecological and sociological parameters. Int J Primatol. 25:615-658.

Treves A, Chapman CA. 1996. Conspecific threat, predation avoidance, and resource defense: implications for grouping in langurs. Beh Ecol Sociobiol. 39:43-53.

Tutin CG, McGrew WC, Baldwin PJ. 1983. Social organization of savanna-dwelling chimpanzees, *Pan troglodytes verus*, at Mt. Assirik, Senegal. Primates. 24:154-173.

van Schaik CP. 1999. The socioecology of fission-fusion sociality in orangutans. Primates. 40:69-86.

van Schaik CP, van Hooff JARAM. 1983. On the ultimate causes of primate social systems. Behaviour. 85:91-117.

van Schaik CP. 1989. The ecology of social relationships amongst female primates. In: Standen V, Foley RA, editors. Comparative socioecology: The behavioural ecology of humans and other mammals. Boston: Blackwell Scientific Publications. p. 195-218.

Waterman PG, Ross JAM, Bennet EL, Davies AG. 1988. A comparison of the floristics and leaf chemistry of the tree flora in two Malaysian rain forests and the influence of leaf chemistry on populations of colobine monkeys in the old world. Biol J Linn Soc. 34:1-32.

Wrangham RW. 1980. An ecological model of female-bonded primate groups. Behaviour. 75:262-300.

Wrangham RW. 2000. Why are male chimpanzees more gregarious than mothers? A scramble competition hypothesis. In: Kappeler PM, editor. Primate males: causes and consequences of variation in group composition. Cambridge: Cambridge University Press. p. 248-258.

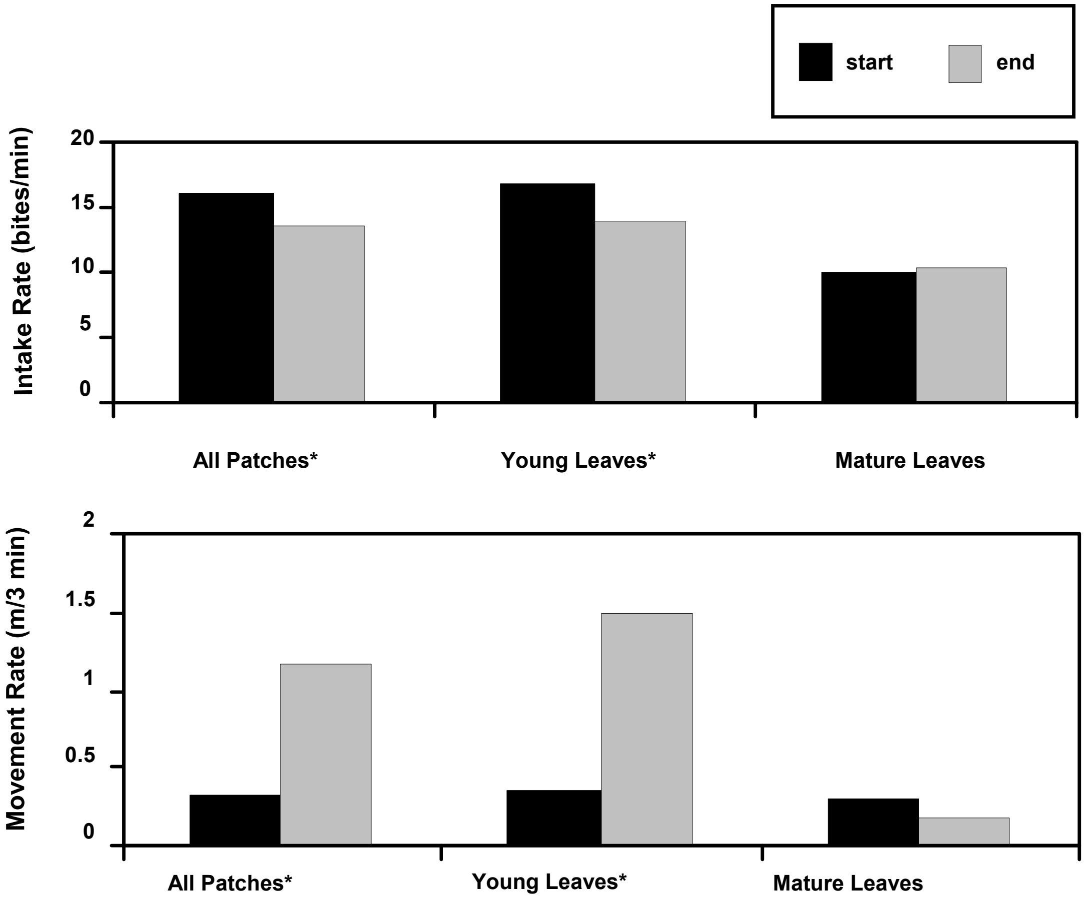
Wrangham RW, Chapman CA, Clark-Arcadi AP, Isabirye-Basuta G. 1996. Social ecology of Kanyawara chimpanzees: implications for understanding the costs of great ape groups. In: McGrew WC, Marchant LF, Nishida T, editors. Great ape societies. Cambridge: Cambridge University Press. p. 45-57.

Wrangham RW, Gittleman JL, Chapman CA. 1993. Constraints on group size in primates and carnivores: population density estimates and day-range as assays of exploitation competition. Beh Ecol Sociobiol. 32:199-209.

Yeager CP, Kirkpatrick CR. 1998. Asian colobine social structure: ecological and evolutionary constraints. Primates. 39:147-155.

Yeager CP, Kool K. 2000. The behavioral ecology of Asian colobines. In: Whitehead PF, Jolly CJ, editors. Old world monkeys. Cambridge: Cambridge University Press. p. 496-521.

Figure 2. Patch depletion by red colobus monkeys



Changes in (a) intake rate (bites / minute) and (b) movement rates (m / 3 meters) of red colobus (*Piliocolobus tephrosceles*) in Kibale National Park, Uganda. * indicates a statistically significant difference between start and end.

LINKING STATEMENT 2

Chapter 2 demonstrated that red colobus monkeys deplete patches of preferred foods, and that larger groups deplete patches more quickly than smaller groups. This result suggests that within-group scramble competition, and ecological constraints on group size, are possible in this species. In Chapter 3, I conduct a multi-group, ecologically controlled study to determine whether red colobus experience food competition. I simultaneously followed nine groups of red colobus to examine possible group-size effects on the expected behavioural indicators or consequences of food competition.

CHAPTER 3: RED COLOBUS MONKEYS DISPLAY ALTERNATIVE BEHAVIORAL RESPONSES TO THE COSTS OF SCRAMBLE COMPETITION

Abstract

Food competition is an expected cost of group living. It is therefore puzzling that there is little evidence for competition among group-living folivorous monkeys; for example, daily travel distance does not seem to increase with group size. It is even more puzzling that folivores do not form larger groups despite this apparent lack of food competition. This has become known as the folivore paradox, and to date there is no broadly accepted theoretical solution. However, there have been no multi-group studies that have controlled for the potentially confounding effects of variation in habitat quality. We studied 9 groups of red colobus monkeys (*Procolobus rufomitratus*) in Kibale National Park, Uganda and controlled for spatial and temporal variation in food availability. We found that larger groups occupied larger home ranges than smaller groups, and that group size was related to increased foraging effort (longer daily travel distance), increased group spread, and reduced female reproductive success. Our results also suggest that monkeys in larger groups spent more time feeding and less time engaged in social behaviour. These results suggest that folivorous red colobus monkeys experience within-group scramble competition and possess a suite of behavioral responses that may mitigate the cost of competition and represent adaptations for group living. The results insight into the folivore paradox and the evolutionary ecology of group size.

Introduction

Food competition is commonly accepted as an inescapable consequence of group living, and is among the primary factors invoked to explain variation in social structure and group size among social mammals (Alexander 1974; Wrangham 1980; Jarman and Southwell 1986; Rubenstein 1986; van Schaik 1989). Within-group scramble, or exploitation, competition is defined as the collective depletion of limited resources and results in reduced foraging efficiency for all group members (Nicholson 1954; Janson and van Schaik 1988). Scramble competition intensifies as groups get larger and imposes a limit on group size because there will be a threshold below which further reductions in foraging efficiency cannot be tolerated. The energetic cost of travel is the presumed mechanism by which scramble limits group size; as groups get larger, food patches are depleted more quickly, individuals obtain less food from a given patch, and must travel further to find sufficient food resources (Milton 1984; Janson 1988; Chapman and Chapman 2000b; Wrangham 2000). The predicted outcome is that there will be a positive relationship between group size and day journey length. Group size should also be positively related to home range size because a larger group will need to occupy a larger area that contains enough food for all members.

Two intriguing observations about the social-ecology of folivorous monkeys raise questions about our theoretical understanding of food competition. First, field data suggest that large groups of folivores do not travel further in a day than small groups (Clutton-Brock and Harvey 1977; Struhsaker and Leland 1987; Isbell 1991; Janson and Goldsmith 1995), which is puzzling because it suggests that food competition within groups is inconsequential, which in turn suggests that group size should not be limited by the availability of food. Second, given this apparent lack of feeding competition, it is paradoxical that these monkeys do not typically form larger groups (Janson and Goldsmith 1995; Crockett and Janson 2000; Steenbeek and van Schaik 2001; Koenig and Borries 2002), particularly because larger groups are thought to provide better protection from predators (Alexander 1974). This has been called the folivore paradox, and although social explanations related to infanticide avoidance have been proposed (Janson and Goldsmith 1995; Steenbeek and van Schaik 2001; Koenig and Borries 2002), there is currently no broadly applicable theoretical solution.

We recently reviewed the literature and found evidence to suggest that folivores may experience scramble competition, and that it may limit group size (Snaith and Chapman 2007). However, to effectively address the relationship between day range and group size, multi-group, ecologically-controlled studies are required.

Controlling for ecological variation in resource availability is critical, as it remains the most likely confounding factor preventing clear interpretation of previous results. Studies that found no relationship between group size and day range (Clutton-Brock and Harvey 1977; Struhsaker and Leland 1987; Isbell 1991; Yeager and Kirkpatrick 1998) are problematic because they generally did not account for ecological variation in food resources, and if group size is adjusted in response to habitat quality, then there may be no need to increase day range (i.e., larger groups can exist in richer habitat without incurring greater scramble costs).

Furthermore, increasing day range may not be the only behavioural indicator of scramble competition (reviewed in Snaith and Chapman 2007). For example, reduced foraging efficiency may be indicated by increasing feeding and/or travel time, and such reductions may be compensated for with decreasing resting and/or social time (Caraco 1979; Altmann 1980; Dunbar and Dunbar 1988). As trees fill up with competitors, some individuals may have less opportunity to feed in the upper portion of the tree crowns where food quality may be best (nitrogen, and thus protein, availability improves with greater exposure to sunlight (Ellsworth and Reich 1993; Hollinger 1996)). In addition, individuals may increase group spread (occupy more trees) to reduce the effects of communal depletion, which may reduce the need to increase day range (Clutton-Brock and Harvey 1977; Janson and Goldsmith 1995). Alternatively, large groups may adopt a fissioning strategy where subgroups travel and forage independently of each other. Finally, if behavioural responses are insufficient to compensate for increasing foraging costs, the energetic costs of food competition may lead to nutritional stress and compromised reproductive success in larger groups (e.g., reduced fecundity and/or infant survival) (van Schaik 1983; Whitten 1983; Dunbar 1988; Knott 1999). However, this cost may be difficult to observe if large groups have a competitive advantage in between-group contest competition, which may offset the costs of within-group competition (Wrangham 1980; Clark and Mangel 1986; Dunbar 1988; Janson and van Schaik 1988; Janson 1992; Koenig 2000).

To our knowledge, there have been no multi-group, ecologically-controlled, studies that have measured a range of possible responses to scramble competition in folivorous primates. Here we measure and control for spatial and temporal variation in food availability and examine several alternative behavioural responses to food competition in red colobus monkeys (*Procolobus rufomitratus*) in Kibale National Park, Uganda. If red colobus experience within-group scramble competition, then we predict that larger groups will have longer day ranges and larger home ranges, will spread out more, feed less frequently in the upper canopy, spend more time feeding and traveling and less time resting and/or engaged in social behavior, and will be more likely to fission temporarily into smaller foraging groups. If there is a fitness cost associated with within-group competition, then reproductive success may be reduced in larger groups. If larger group size confers a competitive advantage, we predict that larger groups will occupy better quality habitat and will displace or be avoided by smaller groups.

Methods

We studied folivorous red colobus monkeys at Kanyawara in Kibale National Park, Uganda (795 km2; 0^{o} 13' - 0^{o} 41' N and 30^{o} 19' - 30^{o} 32' E) between May, 2005 and August, 2006. The research site is described by Chapman et al. (1997) and Struhsaker (1997). Although Kibale forest has two wet and dry seasons each year, there is a large degree of variability both within and between years, and there is no strong predictable seasonality in vegetation phenology or food availability (Struhsaker 1997). Red colobus are an ideal subject because they are highly folivorous and show extreme variation in group size (9 to >120 individuals, from Struhsaker 2000b and this study). Red colobus group composition is generally multi-male, multi-female with both sexes (but primarily females) dispersing, there is no peak in birth seasonality, and inter-birth intervals vary widely with an average of about 23 months (Struhsaker 1975; Struhsaker and Leland 1987). Red colobus are well studied at Kibale (Struhsaker 1975; Chapman and Chapman 1999). However, the small-scale ecological correlates of group size and the effects of group size on ranging behavior and fitness are not well understood.

We followed 9 groups of monkeys and controlled for ecological variability in two ways. First, we selected groups that occupied overlapping home ranges, and followed them simultaneously (5 groups during May and 4 groups during June, 2006). Second, we quantified the food available to each group using vegetation transects and phenological data. Data were collected by TVS and 15 field assistants. We conducted an intense training period to standardize data collection techniques and to minimize inter-observer error.

We followed 9 groups of monkeys for 215 complete follow days (2586 hours of data, 22 980 scan samples; Table 1). Each group was followed from 6:30 am to 7:00 pm each day for at least 25 consecutive days. Although all groups were well-habituated to humans (all groups occupied areas heavily used by researchers and most groups had previously been followed), the first 5 follow days for each group were considered habituation, and the data were discarded.

Group size and composition were determined by taking frequent counts of all individuals and identifying their age/sex class (adult female with infant, adult female no infant, adult male, sub-adult, juvenile, infant, and unknown). Group counts were conducted opportunistically whenever conditions were favorable (e.g., crossing openings), but at least once a day. Reported group size and composition data were derived from a compilation of these counts, taking into consideration the visibility and context of each count.

Subgroups were defined as a portion of the group that was separated by more than 300 m from the rest of the group, with no group members scattered in between. Whenever possible, we followed all subgroups simultaneously. Subgroup data and subgroup counts were collected in the same manner as for whole groups, but are considered separately in analyses.

Behavior and Ranging

Behavioral data were collected using scan sampling. The behavior of 5 adult or sub-adult individuals was recorded every 30 min from 7:00 am to 6:30 pm or later if the group had not settled for the night. At the beginning of each scan, the first monkey seen was used, but we waited 5 seconds before recording its behaviour to avoid biasing our data in favor of eye-catching behaviors. We then moved to the next monkey to the right of the first, until the behaviour of 5 monkeys was recorded. Data recorded were age/sex class; activity (feed, rest, travel, social); feeding height (upper, middle, or lower third of tree crown), food tree species, plant part, and diameter at breast height (dbh). Diet was determined from these scan data, and staple tree species were defined as any tree (and staple foods as any species-part combination) consumed for >1% of the feeding observations of any group (following Rothman et al. 2007).

Inter-group encounters were recorded whenever observed. When possible, we recorded the size and identity of all groups involved and measured the closest inter-group distance achieved. Interactions were classified as mutual avoidance, directional avoidance, or aggressive displacement involving fights and/or chases.

Ranging behavior was recorded by marking the location of the center of the group at 30-minute intervals on a detailed map showing the trail network and a grid of 10 x 10 m cells. The distance traveled in each half-hour was recorded, along with group spread (calculated as the area of an ellipse defined by the distance between the most distantly separated monkeys along two perpendicular axes) and the number of trees occupied by the group. Day range was calculated by summing all half-hourly distances. Previous research on this species suggests that 20 days are sufficient to obtain stable average day range estimates (Gillespie and Chapman 2001 and unpub. data, after 20 days of data collection, cumulative average day range estimates stabilized). Home range was calculated by plotting all day ranges onto a map of the study area with a 100 m grid and including all grid cells entered. This coarse-scale short-term measure of home range should not be taken to represent year-round red colobus home range size in comparative studies.

Habitat Quality

To estimate variation in habitat quality, we developed an index that incorporated spatial variation in food availability (total leaf biomass in a given area), temporal variation in food availability (phenological availability of food items), and food quality (based on a preference index).

Available habitat was quantified from vegetation transects sampled between May 2005 and August 2006. A grid of 100 x 100 m cells was overlain on a 496 ha area that captured the observed home ranges of all groups. A 100 m transect was placed within each grid cell, normally starting from a trail intersection near the edge of the cell, and all trees >10 cm dbh within 5 m of either side of the transect were identified and measured. The 10 cm threshold was selected because red colobus rarely feed in smaller trees (Gillespie and Chapman 2001).

Food availability is often calculated using stem density or the cumulative dbh or basal area of food species. However, stem density does not account for the size of each tree, and the sum of dbh or basal area will not scale in the same manner as the sum of crown volume or leaf biomass. We thus calculated an index of leaf biomass for each tree based on studies of tree allometry and resource allocation, which have demonstrated that leaf biomass scales as $M^{3/4}$, and dbh scales as $M^{3/8}$, where M= total mass of the tree (Enquist, Brown, and West 1998; Enquist and Niklas 2001). Enquist et al. found both theoretical and empirical support for these relationships, and found them to be robust across tree species and ecosystems. We transformed the equations provided by Enquist et al. to find leaf biomass = dbh^2. We validated this index for 6 of the most common red colobus food trees in Kibale. We selected these tree species based on 4 years of independent red colobus feeding data from Kibale (Chapman, unpublished data). We measured the dbh and crown volume of 10 individuals of each species (we use crown volume as an index of leaf biomass). Crown volume was calculated from the estimated height and width of the crown, assuming cylindrical crown shape. We found that the relationship between dbh^2 and crown volume was significant for all trees combined and was significant for all but one species individually, and for that species a positive trend was demonstrated (all trees, r=0.697, p.0.001, n=60; *Celtis africana* r=0.811, p=0.004, n=10; *C. durandii* r=0.839, p=0.002; *Funtumia africana* r=0.940, p<0.001; *Markhamia lutea* r=0.858, p=0.001; *Prunus africana* r=0.766, p=0.010; *Strombosia scheffleri* r=0.555, p=0.096). Based on these scaling relationships, we use dbh2 as an index of the leaf biomass of an individual tree, and summed across trees to obtain the cumulative leaf biomass for each species in an area.

Three kilometers of phenology trails were established in 1998 to track 309 trees of 37 species (Chapman et al. 2004). Since that time, each tree has been surveyed each month to determine phenophase. Following Struhsaker (1975), the proportional abundance of each plant part was scored using a scale of 0-4 (where 0=0%, 1=1-25%, 2=26-50%, 3=51-75%, 4=76-100% crown). An index of monthly availability was obtained by calculating an average score for each species-part combination each month (following Peres 1994). We used a paired t-test (with the May and June scores of a single tree as the pair) to determine whether there were temporal differences in food availability between months. We control for differences across months by including a phenology term in our habitat quality equation below.

Preferred foods are eaten more frequently than would be expected on the basis of their relative availability in the environment, and a variety of indices exist for calculating food preferences on this basis (Lechowicz 1982; Krebs 1989). We used Manly's α for constant prey populations (Manly, Miller, and Cook 1972; Chesson 1978; Krebs 1989), calculated as

$$\alpha_i = (r_i/p_i) / \sum_{i \ldots n} (r_i/p_i)$$

where α_i represents the preference index of food type *i*, r_i represents its proportion in the diet, p_i represents its proportional availability in the environment (proportion of total leaf biomass), and *n* represents all available food types. Because Johnson (1980) demonstrated that calculations of preference are strongly affected by the inclusion of common but rarely eaten foods, we included only those foods that represented 1% or more of the diet (staple foods). We pooled feeding data from all groups to obtain r_i, and used the entire area used by all groups to obtain p_i. Manly's α is normalized so that the sum of all α values is 1. Food types with $\alpha > 1/n$ are preferred, and $\alpha < 1/n$ are avoided. Foods with greater α values are assumed to be of higher quality to red colobus than those with lower values.

We combined these datasets to calculate an index of habitat quality as

$$HQ = \Sigma_{i \ldots n} (s_i t_i \alpha_i)$$

where HQ represents the relative quality of the home range of a group, s_i represents the spatial availability (cumulative leaf biomass) of food species i, t_i represents its temporal availability (phenology score for the most-eaten plant part of species i for the appropriate month), and α i represents its preference index. Because phenology data were not available for all species, we substituted the mean value of the appropriate plant-part (i.e., if there were no phenology data for species x and the most-eaten part of this species was young leaves, then the average young leaf score of all species was used). The habitat quality index is reported as both an overall value reflecting all available food in the home range of each group, and on a per ha basis to normalize for differences in home range size.

Group-Size Effects

We examined whether group size was related to day range length, home range size and quality, group spread, number of trees occupied, feeding height, feeding tree size, and activity budget using non-parametric partial correlation tests that controlled for the effect of habitat quality per ha (rk is the partial correlation coefficient for ranked data). All group-wise tests were conducted using mean group values of behavioral and habitat measures (n=9). Because we ran multiple comparisons, we reduced α from 0.05 using the Benjamini and Yekutieli modified False Discovery Rate method, which has been shown to be a meaningful experiment-wise correction for multiple pairwise tests that reduces Type I error while maintaining statistical power (Narum 2006). For 12 pairwise tests, the appropriate critical value is 0.016 (Narum 2006). Because directional predictions were made, these tests were one-tailed. Sub-group-size effects were measured for Group 10 by comparing sub-group size to day range length and group spread using Spearman correlation tests (rs). For these comparisons, n=5 (4 subgroups with 3 or more follow days, plus the whole group) and α =0.033 for two pairwise tests, one-tailed.

We used the number of offspring (infants + juveniles) relative to the number of adult females in a group as an index of female reproductive success. Because we do not know the reproductive history of the females in each group, this ratio was determined using group count data, and represents a snapshot index of reproductive success. We used a Spearman correlation to compare the ratio of offspring/female to the number of adult females in a group. Such analyses have been debated in the literature because it is often thought that plotting a ratio against its own denominator will lead to a spurious negative correlation. This is not the case, however, as has been convincingly argued by Smith (2005) and empirically demonstrated by Jungers et al. (1995). A spurious correlation between y/x and x will only occur when x and y are independent of one another and randomly distributed (Jungers, Falsetti, and Wall 1995). In the context of examining group composition (y/x) relative to group size (x), x and y are positively correlated (non-random, non-independent); therefore, a negative correlation between offspring/female and number of females is a meaningful indication of decreasing female reproductive success with increasing group size. An alternative demonstration of the same result can be achieved without the use of a ratio by plotting the number of offspring against the number of females in a group and examining the intercept. A non-zero intercept (regardless of slope) signifies an allometric relationship between x and y because the ratio of y/x must change as a function of x (Jungers, Falsetti, and Wall 1995).

Results

Behavior and Ranging

Group size varied from 25 to 127 individuals. Average day range length varied among groups from 418 to 953 m. Home range size varied from 23 to 66 ha and home ranges overlapped extensively among groups. Average group spread varied from 298 to 10,746 m^2 overall, and the average number of trees occupied varied from 4 to 35 trees.

All groups spent the greatest proportion of their time feeding (mean 40-51% across groups), followed by resting (25-30%), then traveling (16-29%), and engaged in social activities (5-10%). Individuals in all groups spent more time feeding in the upper tree crowns (mean 42-84% of feeding observations) than the lower crowns (1%-8%).

Red colobus ate 268 identifiable food items (species-part combination) from 95 tree species. Young leaves made up the largest portion of the diet (77.2% of feeding observations), followed by petioles (11.6%), fruit (3.4%), mature leaves (2.7%), seeds (1.9%), and flowers (1.4%). Bark, dead wood, soil, and insects were eaten infrequently. Diet composition varied widely from group to group. Fifty-six items from 40 species were eaten for >1% of the feeding observations of any group. These were defined as staple foods and were used to calculate Manly's α and HQ.

We observed 42 inter-group interactions between groups of known relative size (study groups and groups for which we obtained a count sufficient to determine whether it was larger or smaller than the focal group). Of the interactions, 13 were mutual avoidances, 20 were directional avoidances, and 9 were aggressive displacements. Eleven of 20 directional avoidances occurred at more than 50 m.

Habitat Quality

We identified and measured 17,381 trees along 496 vegetation transects. We thus sampled 49.6 ha to characterize an area of 496 ha that captured all areas used by the study groups. The phenology dataset included data for 309 trees of 33 species. The only significant temporal change in plant part availability was that young leaves were more available during May than during June (n=309 trees, May average score 1.54, June average score 1.24, paired-t=4.689, p<0.001), making the phenology term in the calculation of HQ important. We calculated Manly's α, for all staple food species; 12 of the 40 staple food trees were preferred. Several of the most-eaten foods were not considered preferred because they were abundant. Habitat quality varied from 20,375 to 61,596, or 453/ha to 1100/ha, across groups.

Group-Size Effects

When statistically controlling for habitat quality per ha, group size was positively related to home range size (r_k=0.851, p=0.004), day range length (r_k=0.854, p=0.004; Figure 3), group spread (r_k=0.885, p=0.002), and the number of trees occupied (r_k=0.939, p<0.001; Table 2). There was no significant relationship between group size and time spent feeding in the upper crown (r_k=-0.612, p=0.053). There were no significant relationships between group size and time budget variables when habitat quality was controlled. However, there were non-significant trends suggesting that feeding time increased (r_k=0.584, p=0.044) and social time decreased (r_k=-0.680, p=0.032) in larger groups. The p values do not meet our conservatively corrected critical value of 0.016, but as they are less than 0.05, we believe the trends are noteworthy and that we simply may not have had sufficient power to detect significant relationships. There was a similar trend suggesting that group size was positively related to overall habitat quality (r_s=0.617, p=0.038), but not to habitat quality/ha (r_s=0.150, p=0.350).

Two of the largest groups occasionally fissioned into subgroups. Group 10 (74 members) frequently fissioned into two or more subgroups, which varied in size from 30 to 54 individuals. Subgroups remained separate for periods lasting from six hours to three days. Although group 10 displayed the longest average day range on days when the whole group was together (953m for whole group vs. 311, 560, 691 and 852 for subgroups followed for at least three full days each), there was no significant relationship between subgroup size and day range (r_s=0.205, p=0.370) or group spread (r_s=0.564, p=0.161; Figure 4). Group LM (127 members) fissioned near the end of the study, but we did not obtain reliable subgroup counts or enough full day follows of subgroups to characterize their behavior.

The number of offspring per adult female varied across groups from 0.55 to 1.31. The offspring/female ratio was negatively related to the number of adult females in a group (r_s= -0.900, p<0.001, n=9). This allometric relationship is further demonstrated by the non-zero intercept when the number of adult females is plotted against the number of offspring in a group (intercept 6.537, significantly different from 0; t=3.469, p=0.010; Figure 5).

Group size seemed to be an important factor determining the outcome of inter-group interactions. We observed 29 directional inter-group encounters, 24 of which (83%) were won by the largest group involved. Of the 20 directional avoidances, smaller groups avoided larger groups in 16 cases. All nine decided interactions involving fights or chases were won by the larger group and resulted in the smaller group retreating.

Discussion

Many previous studies found that there was no relationship between group size and day range or travel costs in folivorous monkeys (Clutton-Brock and Harvey 1977; Isbell 1991; Janson and Goldsmith 1995; Yeager and Kirkpatrick 1998; Yeager and Kool 2000; Isbell and Young 2002). Specifically, early work on red colobus monkeys at Kibale suggested that despite considerable variation in group size (9- 68), there was little variation in day journey length (Struhsaker and Leland 1987). The absence of a group-size effect on day range, in combination with the assumption that folivores rely on evenly distributed foods, led to the assumption that folivores experience little to no within-group scramble competition (reviewed in Snaith and Chapman 2007). However, these early studies made comparisons between groups during different time periods, in different areas, and even across species without controlling for ecological variation, which is expected to affect both group size and day range length. Recent work has indeed begun to suggest that red colobus may experience scramble competition. For example, a large group had longer day ranges than a smaller group (Gillespie and Chapman 2001), the day range of one group increased when food was less available (Gillespie and Chapman 2001), group sizes were larger in richer habitats (Chapman and Chapman 2000a; Struhsaker 2000a; Struhsaker et al. 2004), and larger groups depleted food patches more quickly than smaller groups (a necessary condition for food competition to impose an ecological constraint on group size) (Snaith and Chapman 2005). Although this evidence suggests that folivores experience scramble competition, and that it may limit group size, it is not broadly accepted as a solution to the folivore paradox.

Here we present the results of the first multi-group study that measures several behavioural indicators of scramble competition in folivorous primates while systematically controlling for spatial and temporal variation in food availability. Our results suggest that red colobus display many of the predicted behavioural responses to scramble competition. As group size increased, groups traveled farther each day, spread out more, occupied more trees, and were likely to fission into smaller foraging groups. We also found trends indicating that individuals in larger groups may have spent more time feeding and less time engaged in social behavior.

The three largest groups appeared to have adopted remarkably different ranging strategies. Group 3 ranged in a manner consistent with the general pattern across groups (relatively long day range length as expected for their large group size). Group 10 used a fissioning strategy; they traveled very long distances when the whole group ranged together, but when they fissioned, the subgroups did not travel as far. In contrast, LM remained cohesive most of the time, and while their day range was surprisingly short, their group spread was dramatically larger than any other group.

Our results suggest that red colobus possess a suite of possible behavioral responses to within-group scramble competition, which may complement or mitigate the typical day range response. These behavioural changes may represent mechanisms by which scramble competition imposes fitness costs because the observed changes suggest increased foraging effort, which may be associated with nutritional stress, which in turn is known to affect fecundity and infant survival in some species (van Schaik 1983; Whitten 1983; Harcourt 1987; Dunbar 1988; Ellison 1990; Knott 1999). Our finding that females in larger groups had fewer offspring supports the suggestion that female fitness was compromised with increasing group size, possibly as a consequence of increasing food competition.

Habitat quality is expected to co-vary with group size, home range size, and day range length, and should interact with the group-size related costs of scramble. Larger groups occupied larger home ranges than smaller groups, which were of higher quality overall, but not per ha, which suggests that group size and/or home range size are adjusted in response to habitat quality. The differences in habitat quality in this study were not sufficient to offset the need to increase day range in response to within-group competition (likely because we purposely reduced inter-group variation in habitat quality by simultaneously following groups in overlapping areas). When comparing across study sites or groups, there is a much greater risk that unmeasured ecological variation will confound group-size effects on day range and activity budgets. Thus, measuring and controlling spatial and temporal variation in habitat quality will be even more important in uncovering such relationships.

There may be a fitness advantage available to larger groups if they are more successful in between-group competition, which may partially compensate for the costs of within-group competition. We found some evidence that increasing group size conferred a competitive advantage; more than 80% of decided interactions were in favor of the larger group. Although we can draw no conclusions about whether inter-group competition was food-related, these interactions suggest that there may be some benefits associated with larger group size. The finding that larger groups occupy better quality habitat may or may not support this hypothesis because further work is required to test the direction of this relationship (i.e., do larger groups monopolize better areas, or do better areas simply support larger groups?). Furthermore, because we found that female reproductive success declined as the number of females in a group increased, we have no evidence that competitive advantages gained in larger groups translate into fitness gains. The subtle nature of these interactions (only 31% involved highly visible chases or fights; the rest were quiet avoidances) and the distances over which avoidances occurred (most at more than 50 m, and several at as far as 200 m) suggest that between-group competition is subtle and difficult to observe in red colobus.

Dunbar (1996) suggested that ecological constraints on group size could be understood in terms of the need to balance the time budget; resting time should be reallocated when foraging demands increase, and group size will be limited by the point at which all spare resting time has been used. However, there has been considerable debate in the literature regarding the flexibility of social and resting time, and which of the two will be compromised (Altmann 1980; Foley 1987; Dunbar and Dunbar 1988; Dunbar 1992b; Bronikowski and Altmann 1996;

Dunbar 1996). Our results suggested that with increasing group size, feeding time increased, resting time remained unchanged, and social time decreased.

This response may be related to the digestive constraints of a folivorous strategy that requires considerable resting time for digestion (van Schaik 1983; Milton 1984; DaSilva 1992; Janson and Goldsmith 1995), as well as to the concurrent increase in group spread that we observed in larger groups. In baboons, seasonal reductions in social time have been attributed to increased group spread and reduced social contacts due to seasonally-high within-group competition for scarce food resources (Alberts et al. 2005). Our findings may provide an analogous situation, whereby an increasing number of conspecifics results, perhaps counter-intuitively, in reduced social behaviour.

The time budget tradeoff also raises interesting questions regarding the evolutionary relationships among group size, brain size, dietary strategy, and sociality. Among primates, frugivores tend to have larger brains, more complex social systems, and more complex foraging skills than folivores (Clutton-Brock and Harvey 1980; Dunbar 1992a). Dunbar (1992a) has suggested that brain size may limit group size by limiting the ability of individuals to manage social relationships. When this idea is considered together with the expensive tissue hypothesis (Aiello and Wheeler 1995), which suggests that there is a trade-off between gut size and brain size, it looks like folivores must overcome two challenges to increase social capacity/group size. First, their large and expensive digestive system prevents energy allocation to developing brain size, which may in turn limit group size and social capacity. Second, because resting/digesting time cannot be compromised (Milton 1984), social time will be compromised to compensate for increased foraging time in larger groups, which may prevent the development of complex social relationships and/or limit group size. This logic provides interesting insight into the folivore paradox, because even if the solution is ecologically based, there may be social and physiological mediating factors involved.

The observed relationships between group size, home range size, and habitat quality should be considered in light of population distribution theory. If group size varies simply as a result of habitat quality, and individuals are free to select the most ideal group, then group choice by individuals may be considered analogous to habitat selection in an ideal free distribution (Fretwell 1972). However, if home range size and quality vary as a function of group size and dominance, then group size dynamics may be analogous to the ideal despotic distribution (Fretwell 1972). We found that although group size was related to increased habitat quality and a between-group competitive advantage, it was also related to increased foraging effort and reduced female reproductive success. This muddies the suggestion of an ideal free and/or ideal despotic distribution, because according to theory, all individuals in an ideal free distribution should achieve equal fitness, while in an ideal despotic distribution, individuals able to occupy richer habitat (in this case, larger groups) should achieve greater reproductive success (Fretwell 1972).

That there were reproductive costs associated with increasing group size raises the question of why red colobus females, who disperse and can theoretically select groups of appropriate size (Struhsaker 1975), would accept a fitness cost in large groups. Many components of fitness vary with group size; for example, the social and safety benefits of grouping are generally well-accepted (Alexander 1974). An optimal group size should theoretically exist, and above and below this optimal size, individuals will experience reduced fitness (Pulliam and Caraco 1984). However, even when optimal group size is exceeded, individuals may still benefit from joining (vs. remaining alone) and thus observed group size for many species exceeds the predicted optimal and there can be no single group size that is optimal for all individuals (Pulliam and Caraco 1984). In this context, it is perhaps not surprising that red colobus experience increasing fitness costs as group size increases.

Our study has several limitations. First, because our focus was primarily limited to within-group scramble competition, we have only addressed a subset of possible modes of competition; the relationships we documented here may be influenced by between-group and between-species scramble competition. Second, we only followed nine groups. While this is a large number for a study of wild primates, it is still fairly small, and statistical power would be improved with a larger sample size. Third, by designing our research to control ecological variation, we may have reduced our ability to detect the role of such variation in determining primate group size and behaviour. Despite these limitations, we found clear evidence that red colobus experience food competition, and that its costs increased with group size.

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References Cited

Aiello LC, Wheeler P. 1995. The expensive tissue hypothesis. Curr Anthrop. 36:199-221.

Alberts SC, Hollister-Smith JA, Mututua RS, Sayialel SN, Muruthi PM, Warutere K, Altmann J. 2005. Seasonality and long-term change in a savanna environment. In: Brockman DK, van Schaik CP, editors. Seasonality in primates. Cambridge: Cambridge University Press. p. 157-198.

Alexander RD. 1974. The evolution of social behavior. Annu Rev Ecol Syst. 5:325-383.

Altmann J. 1980. Baboon mothers and infants. Cambridge, MA: Harvard University Press.

Bronikowski AM, Altmann J. 1996. Foraging in a variable environment: Weather patterns and the behavioral ecology of baboons. Beh Ecol Sociobiol. 39:11-25.

Caraco T. 1979. Time budgeting and group size: a test of theory. Ecology. 60:618-627.

Chapman CA, Chapman LJ. 1999. Implications of small scale variation in ecological conditions for the diet and density of red colobus monkeys. Primates. 40:215-231.

Chapman CA, Chapman LJ. 2000a. Constraints on group size in red colobus and red-tailed guenons: examining the generality of the ecological constraints model. Int J Primatol. 21:565-585.

Chapman CA, Chapman LJ. 2000b. Determinants of group size in primates: the importance of travel costs. In: Boinski S, Garber PA, editors. On the move: how and why animals travel in groups. Chicago: University of Chicago Press. p. 24-41.

Chapman CA, Chapman LJ, Struhsaker TT, Zanne AE, Clark CJ, Poulsen JR. 2004. A long-term evaluation of fruit phenology: importance of climate change. J Trop Ecol. 21:1-14.

Chapman CA, Chapman LJ, Wrangham RW, Isabirye-Basuta G, Ben-David K. 1997. Spatial and temporal variability in the structure of a tropical forest. Afr J Ecol. 35:287-302.

Chesson J. 1978. Measuring preference in selective predation. Ecology. 59:211-215.

Clark CW, Mangel M. 1986. The evolutionary advantages of group foraging. Theor Popul Biol. 30:45-75.

Clutton-Brock TH, Harvey PH. 1977. Primate ecology and social organization. J Zool Soc Lon. 183:1-39.

Clutton-Brock TH, Harvey PH. 1980. Primates, brains and ecology. J Zool Soc Lon. 190:309-323.

Crockett CM, Janson CH. 2000. Infanticide in red howlers: female group size, group composition, and a possible link to folivory. In: van Schaik CP, Janson CH, editors. Infanticide by males and its implications. Cambridge: Cambridge University Press. p. 75-98.

DaSilva GL. 1992. The western black and white colobus as a low energy strategist: activity budget, energy expenditure and energy intake. J Anim Ecol. 61:79-91.

Dunbar RIM. 1988. Primate social systems. New York: Cornell University Press.

Dunbar RIM. 1992a. Neocortex size as a constraint on group size in primates. J Hum Evol. 20:469-493.

Dunbar RIM. 1992b. Time - a hidden constraint on the behavioral ecology of baboons. Beh Ecol Sociobiol. 31:35-49.

Dunbar RIM. 1996. Determinants of group size in primates: a general model. In: Runciman WG, Maynard Smith JM, Dunbar RIM, editors. Evolution of social behaviour patterns in primates and man. Oxford: Oxford University Press. p. 33-57.

Dunbar RIM, Dunbar P. 1988. Maternal time budgets of gelada baboons. Anim Behav. 36:970-980.

Ellison PT. 1990. Human ovarian function and reproductive ecology - new hypotheses. Amer Anthropol. 92:933-952.

Ellsworth DS, Reich PB. 1993. Canopy structure and vertical patterns of photosynthesis and related leaf traits in a deciduous forest. Oecologia. 96:169-178.

Enquist BJ, Brown JH, West GB. 1998. Allometric scaling of plant energetics and population density. Nature. 395:163-165.

Enquist BJ, Niklas KJ. 2001. Invariant scaling relations across tree-dominated communities. Nature. 410:655-660.

Foley R. 1987. Another unique species. New York: John Wiley and Sons, Inc.

Fretwell SD. 1972. Populations in a seasonal environment. Princeton: Princeton University Press.

Gillespie TR, Chapman CA. 2001. Determinants of group size in the red colobus monkey (*Procolobus badius*): an evaluation of the generality of the ecological-constraints model. Beh Ecol Sociobiol. 50:329-338.

Harcourt A. 1987. Dominance and fertility among female primates. J Zool Soc Lon. 213:471-487.

Hollinger DY. 1996. Optimality and nitrogen allocation in a tree canopy. Tree Physiology. 16:627-634.

Isbell LA. 1991. Contest and scramble competition: patterns of female aggression and ranging behaviour among primates. Behav Ecol. 2:143-155.

Isbell LA, Young TP. 2002. Ecological models of female social relationships in primates: similarities, disparities and some directions for future clarity. Behaviour. 139:177-202.

Janson CH. 1988. Intra-specific food competition and primate social structure: a synthesis. Behaviour. 105:1-17.

Janson CH. 1992. Evolutionary ecology of primates social structure. In: Smith EA, Winterhalder B, editors. Evolutionary ecology and human behaviour. New York: Aldine de Gruyter. p. 95-130.

Janson CH, Goldsmith ML. 1995. Predicting group size in primates: foraging costs and predation risks. Behav Ecol. 6:326-336.

Janson CH, van Schaik CP. 1988. Recognizing the many faces of primate food competition: methods. Behaviour. 105:165-186.

Jarman PJ, Southwell CJ. 1986. Grouping, associations and reproductive strategies in eastern grey kangaroos. In: Rubenstein DI, Wrangham RW, editors. Ecological aspects of social evolution: birds and mammals. Princeton: Princeton University Press. p. 399-429.

Johnson DH. 1980. The comparison of usage and availability measurements for evaluating resource preference. Ecology. 61:65-71.

Jungers WL, Falsetti AB, Wall CE. 1995. Shape, relative size and size-adjustments in morphometrics. Yearbook Phys Anthrop. 38:137-161.

Knott CD. 1999. Reproductive, physiological and behavioral responses of orangutans in Borneo to fluctuations in food availability [dissertation]. Cambridge: Harvard University; 355 p.

Koenig A. 2000. Competitive regimes in forest-dwelling Hanuman langur females (*Semnopithecus entellus*). Beh Ecol Sociobiol. 48:93-109.

Koenig A, Borries C. 2002. Feeding competition and infanticide constrain group size in wild hanuman langurs. Am J Primatol. 57:33-34.

Krebs JR. 1989. Ecological Methodology. New York: Harper Collins.

Lechowicz MJ. 1982. The Sampling Characteristics of Electivity Indexes. Oecologia. 52:22-30.

Manly BFJ, Miller P, Cook LM. 1972. Analysis of a Selective Predation Experiment. Am Nat. 106:719-&.

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

Narum S. 2006. Beyond Bonferroni: less conservative analyses for conservation genetics. Conserv Genet. 7:783-787.

Nicholson AJ. 1954. An outline of the dynamics of animal populations Aust J Zool. 2:9-65.

Peres CA. 1994. Primate Responses to Phenological Changes in an Amazonian Terra-Firme Forest. Biotropica. 26:98-112.

Pulliam HR, Caraco T. 1984. Living in groups: is there an optimal group size. In: Krebs JR, Davies NB, editors. Behavioural ecology: an evolutionary approach 2nd ed. London: Sinauer and Associates.

Rothman JM, Plumptre AJ, Dierenfeld E, Pell AN. 2007. Nutritional composition of the diet of the gorilla (*Gorilla beringei*): a comparison between two montane habitats. J Trop Ecol. 23:673-682.

Rubenstein DI. 1986. Ecology and sociality in horses and zebras. In: Rubenstein DI, Wrangham RW, editors. Ecological aspects of social evolution: birds and mammals. Princeton: Princeton University Press. p. 282-302.

Smith RJ. 2005. Relative size versus controlling for size: Interpretation of ratios in research on sexual dimorphism in the human corpus callosum. Curr Anthrop. 46:249-273.

Snaith TV, Chapman CA. 2005. Towards an ecological solution to the folivore paradox: patch depletion as an indicator of within-group scramble competition in red colobus. Beh Ecol Sociobiol. 59:185-190.

Snaith TV, Chapman CA. 2007. Primate group size and interpreting socioecological models: do folivores really play by different rules? Evol Anthrop. 16:94-106.

Steenbeek R, van Schaik CP. 2001. Competition and group size in Thomas's langurs (*Presbytis thomasi*): the folivore paradox revisited. Beh Ecol Sociobiol. 49:100-110.

Struhsaker TT. 1975. The red colobus monkey. Chicago: University of Chicago Press.

Struhsaker TT. 1997. Ecology of an African rain forest: logging in Kibale and the conflict between conservation and exploitation. Gainesville: University of Florida Press.

Struhsaker TT. 2000a. The effects of predation and habitat quality on the socioecology of African monkeys: lessons from the islands of Bioko and Zanzibar. In: Whitehead PF, Jolly CJ, editors. Old world monkeys. Cambridge: Cambridge University Press. p. 393-430.

Struhsaker TT. 2000b. Variation in adult sex ratios of red colobus monkey social groups: implications for interspecific comparisons. In: Kappeler PM, editor. Primate males: causes and consequences of variation in group composition. Cambridge: Cambridge University Press. p. 108-119.

Struhsaker TT, Leland L. 1987. Colobines: infanticide by adult males. In: Smuts BB, Cheney DL, Seyfarth RM, Wrangham RW, Struhsaker TT, editors. Primate societies. Chicago: University of Chicago Press. p. 83-97.

Struhsaker TT, Marshall AR, Detwiler K, Siex K, Ehardt C, Lisbjerg DD, Butynski TM. 2004. Demographic variation among Udzungwa red colobus in relation to gross ecological and sociological parameters. Int J Primatol. 25:615-658.

van Schaik CP. 1983. Why are diurnal primates living in groups? Behaviour:120-144.

van Schaik CP. 1989. The ecology of social relationships amongst female primates. In: Standen V, Foley RA, editors. Comparative socioecology:

The behavioural ecology of humans and other mammals. Boston: Blackwell Scientific Publications. p. 195-218.

Whitten PL. 1983. Diet and dominance among female vervet monkeys (*Cercopithecus aethiops*). Am J Primatol. 5:139-159.

Wrangham RW. 1980. An ecological model of female-bonded primate groups. Behaviour. 75:262-300.

Wrangham RW. 2000. Why are male chimpanzees more gregarious than mothers? A scramble competition hypothesis. In: Kappeler PM, editor. Primate males: causes and consequences of variation in group composition. Cambridge: Cambridge University Press. p. 248-258.

Yeager CP, Kirkpatrick CR. 1998. Asian colobine social structure: ecological and evolutionary constraints. Primates. 39:147-155.

Yeager CP, Kool K. 2000. The behavioral ecology of Asian colobines. In: Whitehead PF, Jolly CJ, editors. Old world monkeys. Cambridge: Cambridge University Press. p. 496-521.

Table 1. Nine groups of red colobus monkeys followed in Kibale National Park, Uganda

Group Name	Group Size	Month	Full Contact Days	Days Discarded[1]	Full-Group Follows[2]	Days Fissioned	Subgroup Name[3]	Subgroup Size	Subgroup Full-Day Follows
1	70	May	27	5	22				
2	25	May	27	5	22				
3	84	May	29	5	24				
SM	45	May	27	5	22				
LM	127	May/ June	33	5	22	7	LM sub 1	27	*2*
							LM sub 2	Unknown	*2*
							LM sub 3	Unknown	*1*
5	51	June	27	5	22				
6	40	June	27	5	22				
10	74	June	27	5	16	6	10 sub 1	39	*6*
							10 sub 2	32	*6*
							10 sub 3	43	*3*
							10 sub 4	32	*3*
11	71	June	25	5	20				
					Total: 192				***Total: 23***

Grand total full-day follows: 215

[1] The first five days of observation were discarded for every group for habituation
[2] Only full-group, full-day follows (n=192) were included in calculating group-level variables
[3] Subgroups were followed simultaneously when possible, table includes only subgroups for which full-day follows were obtained

Table 2. Summary of group-wise comparisons

Behavioral Responses to Scramble Competition in Larger Groups		
	r_k	**p**
Day range increases	**0.854**	**0.004**
Home range size increases	**0.851**	**0.004**
Group spread increases	**0.885**	**0.002**
# trees occupied increases	**0.939**	**<0.001**
Feeding time increases	***0.584***	***0.044***
Travel time increases	-0.198	0.319
Resting time decreases	-0.270	0.259
Social time decreases	***-0.680***	***0.032***
Feed less in upper tree crown	-0.612	0.053
Fitness Cost of Scramble Competition in Larger Groups		
Fewer offspring/female	**-0.900**	**<0.001**
Group-Size Habitat Co-Variation		
Overall habitat quality increases with group size	***0.617***	***0.038***
Habitat quality per hectare increases with group size	0.150	0.350

For all tests, n=9 groups, r_k is the non-parametric partial correlation coefficient when habitat quality/ha is controlled, and α = 0.016 (experiment-wise error correction for 12 tests), one tailed
Significant results (<0.016) are **bolded** and trends (<0.05) are ***bold italicized***

Figure 3. Group-size effects on day range and group spread across 9 groups of red colobus monkeys

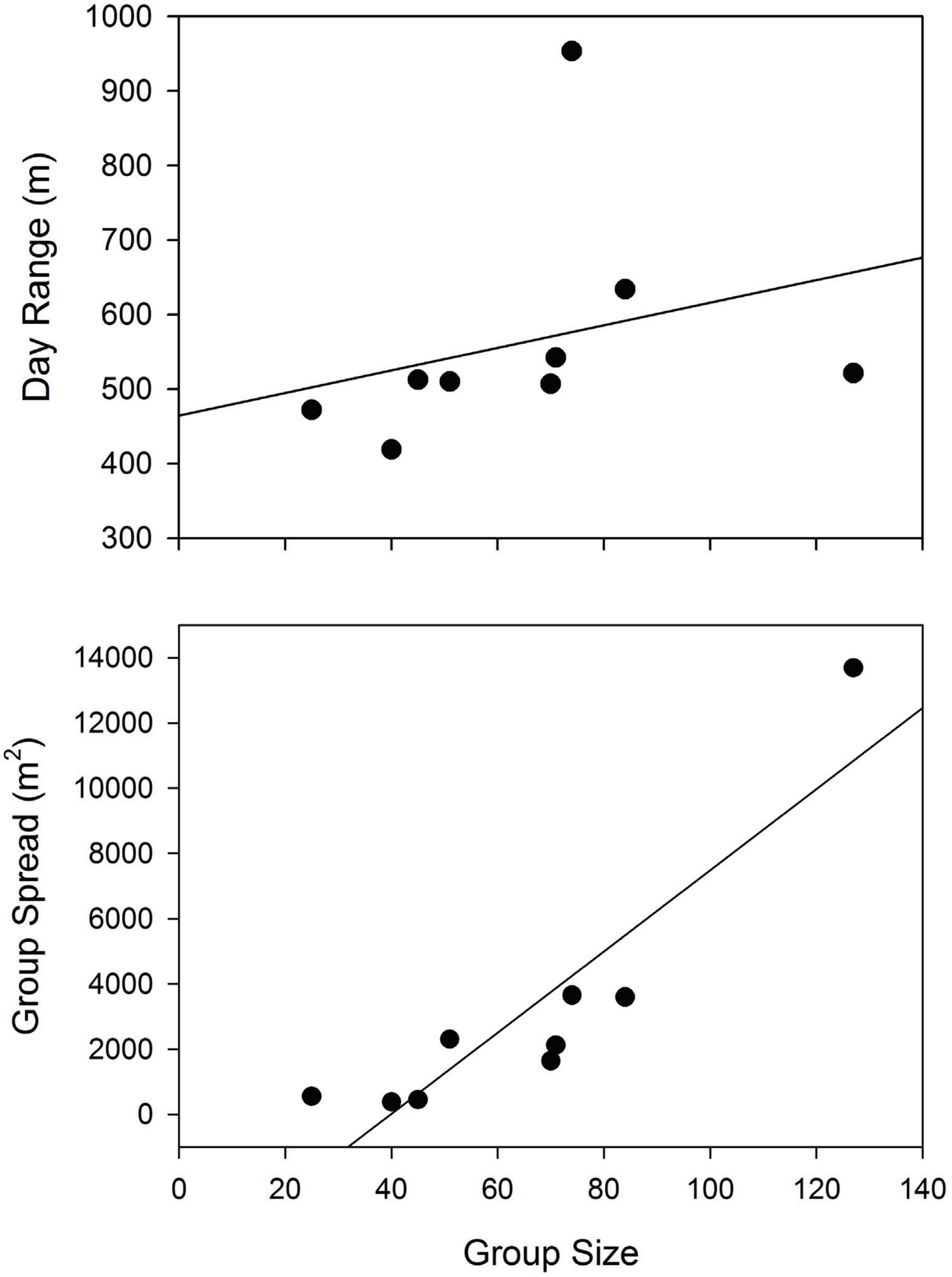


Figure 4. Group-size effects on day range and group spread across Group 10 subgroups

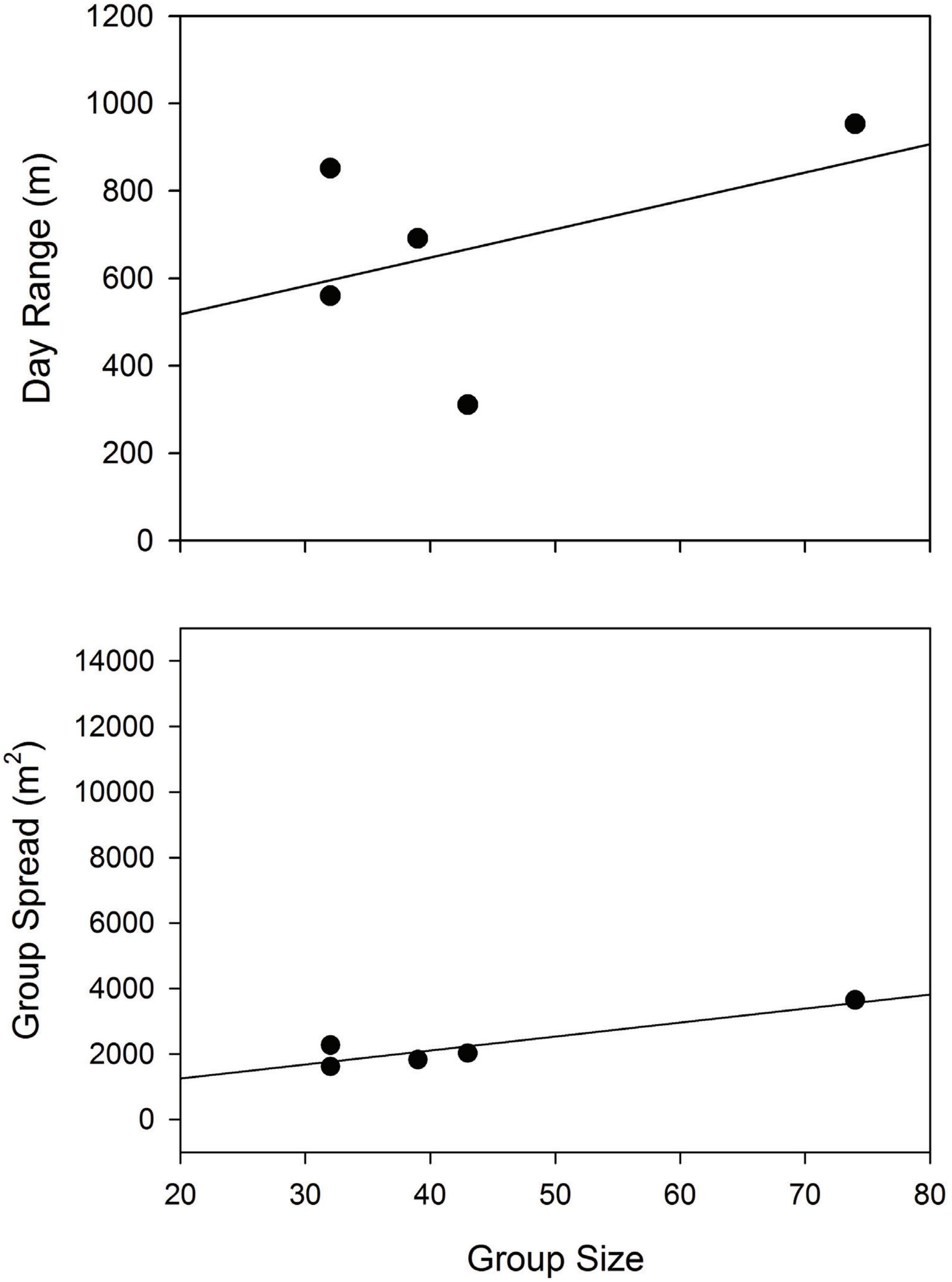
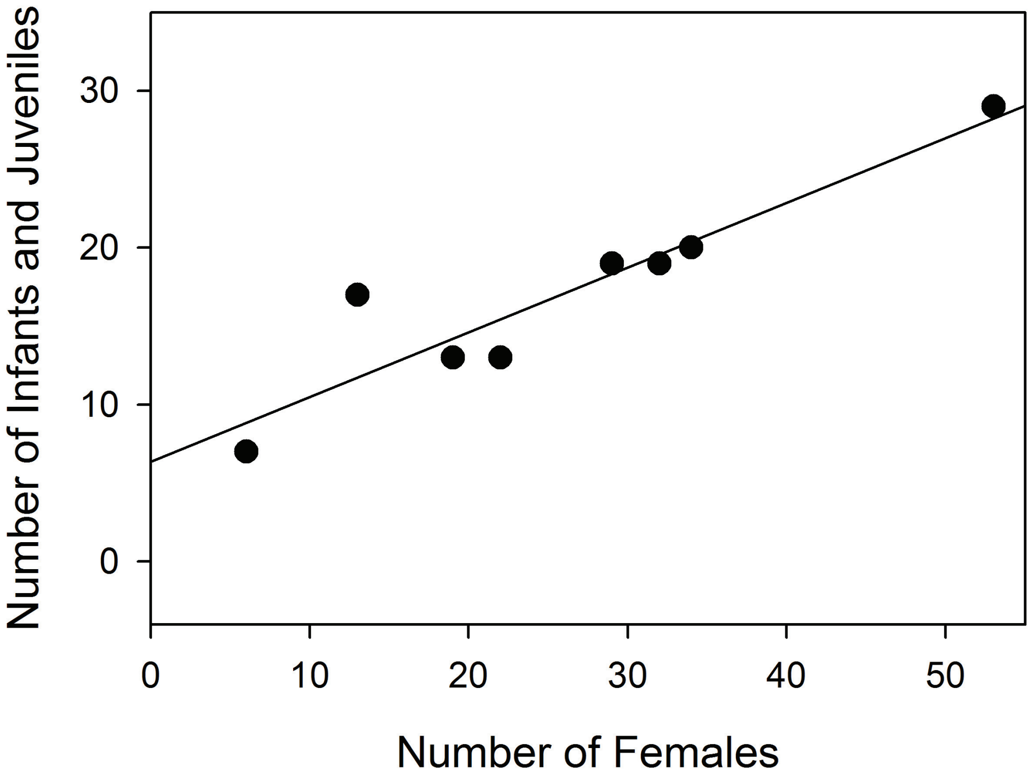


Figure 5. Number of females vs. offspring showing non-zero intercept



LINKING STATEMENT 3

In chapter 3, I found that red colobus display many of the predicted behavioural responses to food competition. I also found that there were fewer infants per female in larger groups, suggesting a reproductive cost of increasing group size. In chapter 4, I assess the relationships between group size, stress, and parasite infections, because stress and parasitism have physiological costs which may vary with group size and may be among the factors leading to reduced reproductive success in larger groups.

CHAPTER 4: BIGGER GROUPS HAVE FEWER PARASITES AND SIMILAR CORTISOL LEVELS: A MULTI-GROUP ANALYSIS IN RED COLOBUS

Abstract

If stress and disease impose fitness costs, and if those costs vary as a function of group size, then stress and disease should exert selection pressures on group size. We assessed the relationships between group size, stress, and parasite infections across nine groups of red colobus monkeys (*Procolobus rufomitratus*) in Kibale National Park, Uganda. We used fecal cortisol as a measure of physiological stress and examined fecal samples to assess the prevalence and intensity of gastrointestinal helminth infections. We also examined the effect of behaviors that could potentially reduce parasite transmission (e.g., increasing group spread and reducing social contact). We found that cortisol was unrelated to group size, but parasite prevalence was negatively related to group size and group spread. The observed increase in group spread could have reduced the rate of parasite transmission in larger groups; however, it is not clear whether this was a density dependent behavioral counter-strategy to infection, or a response to food competition that also reduced parasite transmission. The results suggest that neither gastrointestinal parasitism nor stress directly imposed group-size related fitness costs, and thus are unlikely to be among the mechanisms limiting group size in red colobus monkeys.

Introduction

Among social animals, group size results from a complex set of interacting factors including predation pressure, food competition, and social considerations, many of which are well-studied, particularly among primates. Other factors, such as endocrine responses and infectious diseases, may also be important but comparatively little empirical work has been done on their relationship to group size in primates (Alexander 1974; Anderson and May 1979; Pride 2005b; Nunn and Altizer 2006) (but see Freeland 1976, 1979; Pride 2005b). As a result, our understanding of the determinants and effects of group size among primates is incomplete.

Stress: fitness effects and relationship to group size

A stressor is anything that disrupts an individual's allostatic balance, such as injury, illness, or the threat of predation (Sapolsky 1994). To restore balance, the body initiates a stress response that involves the central nervous and endocrine systems (Selye 1979; Sapolsky 1994). This response mobilizes energy for immediate use, and is a highly effective means of coping with acute stressors; however, under chronic stress, this natural response can lead to fitness costs, because as energy is diverted elsewhere, essential functions such as growth, reproduction, and immunity are compromised (Sapolsky 1994).

Cortisol, a steroid produced in the adrenal cortex, is a key hormone involved in the stress response (Selye 1979; Sapolsky 1994; Wingfield and Romero 2001). Blood serum and fecal cortisol levels have often been used as a measure of stress, and it has been well demonstrated that prolonged stress, as indicated by cortisol levels, has negative effects on fitness and is associated with reduced survival, fecundity, and immunity (Moberg 1985; Boonstra and Singleton 1993; Ferin 1999; Romero and Wikelski 2001; Bercovitch and Ziegler 2002; Creel et al. 2002; Pride 2005a). Because cortisol is part of the body's general stress response (Selye 1979; Sapolsky 1994), it reflects the combined effects of all causes of stress, including social, nutritional, disease-related, and reproductive stress (Sapolsky 1994; Pollard 1995).

Because many stressors are known to vary with group size, cortisol may provide a general index of overall stress levels in groups of different sizes, and thus of the fitness costs associated with variation in group size (Pride 2005b). Indeed, cortisol has been shown to be related to group size, food availability, and feeding effort in mammals (Boonstra and Singleton 1993; Cavigelli 1999; Foley, Papageorge, and Wasser 2001; Chapman, Saj, and Snaith 2007), birds (Wasser et al. 1997; Raouf et al. 2006) and reptiles (Romero and Wikelski 2001). For example, Pride (2005b) found that ringtailed lemurs (*Lemur catta*) experienced the least stress in medium-sized groups, compared to larger or smaller groups. Pride concluded that there was an optimal group size, but that the optimum varied with habitat type and food availability, which suggests that food competition (which may lead to social and nutritional stress) is among the mechanisms by which group size imposes a stress cost.

Parasite infections: fitness effects and relationship to group size

There is a large body of empirical evidence demonstrating the negative fitness consequences of parasitic infections (reviewed in Nunn and Altizer 2006), which include sickness, compromised nutritional status, suppressed immunity, decreased fecundity, and death. Although mild infections may have little effect on the host, negative effects increase with the intensity of infection or with parasite species richness (Nunn and Altizer 2006). Here we focus on gastrointestinal helminths (worms) because they can be non-invasively studied in fecal samples. The most commonly observed helminths in wild primates are nematodes (roundworms), which include species of *Enterobius* (pinworms, superfamily *Oxyuroidea*), *Trichuris* (whipworms, superfamily *Trichuroidea*), *Strongyloides* (threadworms, superfamily *Rhabditoidea*), and other strongyles (superfamily *Strongyloidea*) (Nunn and Altizer 2006).

Freeland (1979) considered parasite population dynamics relative to host group size in terms of island biogeography theory (MacArthur and Wilson 1967; Simberloff 1974). He suggested that host social groups are analogous to biological islands, and that parasite population size and diversity should be affected by host group size and by the rate of migration of parasites between groups (through inter-group contact and host dispersal). In short, larger more connected groups of hosts should support larger and more diverse parasite populations than smaller more isolated groups.

However, understanding the relationship between parasite infections and group size is complicated by a number of confounding factors. First, parasite infections and stress levels are inter-dependent. Parasite burdens, species richness, and pathogenic effects may be amplified when infections co-occur with nutritional, social, or reproductive stress because energy deficiencies and chronic stress can depress immune function and weaken the host’s ability to fight infection (Hausfater and Watson 1976; Appleton and Henzi 1993; Koski, Su, and Scott 1999; Bush et al. 2001; Padgett and Glaser 2003; Nunn and Altizer 2006).

In turn, the nutrient-demands of the parasite and the energetic cost of mounting an immune response to infection, can further compromise nutritional status and can cause or increase stress (Anderson and May 1979; Sheldon and Verhulst 1996; Bush et al. 2001; Koski and Scott 2001).

Second, depending on their life cycle and transmission mode, parasites may create selection pressure for either larger or smaller groups (Freeland 1976; Nunn and Altizer 2006). For example, ectoparasites and parasites transmitted by mobile hosts (e.g., malaria) may decrease in prevalence or intensity with increasing group size due to a dilution effect and/or grooming behaviors (Freeland 1976; Mooring and Hart 1992; Nunn and Altizer 2006; Bordes, Blumstein, and Morand 2007). Conversely, both intrinsic disease risk and infection rates for many parasites that are directly transmitted or transmitted via an intermediate host or an infected substrate (e.g., intestinal helminths, viruses, and protozoa) should increase with group size due to increasing proximity and contact rates among individuals and the increased probability of contact with contaminated substrates (Freeland 1976; Anderson and May 1979; Freeland 1979; Arneberg et al. 1998; Brown et al. 2001; Arneberg 2002; Altizer et al. 2003). Indeed, empirical data largely support this relationship in within-species (but not necessarily between-species) comparisons for birds and mammals; the prevalence, diversity, and severity of helminth, viral, and protozoan infections have been shown to increase with population density or group size, particularly in host species with stable groups (Freeland 1979; Shields and Crook 1987; Cote and Poulin 1995; Brown et al. 2001; Altizer et al. 2003; Nunn et al. 2003; Ezenwa 2004; Chapman, Gillespie, and Speirs 2005).

Third, the fitness costs of infection should create selective pressure for the evolution of immunological and behavioral counter-infection adaptations (Freeland 1976; Nunn and Altizer 2006). Behavioral strategies, such as reducing contact rates and increasing inter-individual spacing, may reduce the likelihood of infection, and may obscure the expected relationships between group size and infections (Freeland 1976; Nunn and Altizer 2006).

Fourth, the social and ranging behaviors of the host species must be considered (Ezenwa 2004; Nunn and Dokey 2006). The degree of home range overlap, the type and frequency of between-group contact, and immigration events may all influence the transmission of parasites between groups, and may reduce inter-group differences (Freeland 1979; Freeland 1980; Altizer et al. 2003). However, unless levels of between-group contact are very high, the effect of group size should not be obscured because smaller group sizes will impose limits on parasite population growth (Freeland 1979). Similarly, differences in the intensity of range use may affect transmission risk by altering the duration of contact with contaminated substrates, and/or the likelihood of exposure to novel pathogens from other groups (Nunn and Dokey 2006).

Finally, spatial and temporal variation in environmental factors may affect the transmissibility, intensity, and pathogenicity of parasite infections. Resource distribution and availability will affect the nutritional status of hosts and thus their immune response, and climatic conditions (temperature, humidity, rainfall) will affect egg survival and thus the probability of transmission via contaminated substrates (Freeland 1976; Stoner 1996; Roepstorff et al. 2001; Nunn and Altizer 2006).

Objectives

We conducted a multi-group study of the costs of increasing group size in folivorous red colobus monkeys (*Procolobus rufomitratus*) in Kibale National Park, Uganda. We assess the relationships between group size, stress, and parasite infections. We use fecal cortisol as a measure of physiological stress, and fecal egg counts as a measure of intestinal helminth infections. We expect that increasing group size will be associated with increased stress levels and increased parasite infections. By measuring both parasite infections and stress levels, we can assess the degree to which they interact. We also examine the relationship between parasite infections and social behavior because changes in group spread or social contact will affect transmission rates. We control for ecological variation by comparing groups that occupied overlapping home ranges and by collecting simultaneous data.

In a separate paper (Snaith and Chapman in review), we presented evidence suggesting that as group size increases, within-group food competition leads to increased foraging effort. This may lead to compromised nutrition and may be associated with increased stress and reduced immunity to parasitism. We also found that larger groups spread out more and spent less time engaged in social interactions. These behavioral differences may be attributable to food competition, but may also represent counter-strategies to parasite transmission. In addition, we found that there were fewer offspring relative to the number of adult females in larger groups, which may simply be due to the effect of food competition, but may also be related to the physiological costs associated with stress and infectious disease.

Methods

Nine groups of red colobus monkeys were followed in Kibale National Park, Uganda during May and June 2006. Group size and composition were determined based on daily counts of group members. To reduce potential confounds associated with temporal and spatial ecological variation, all groups occupied overlapping home-ranges, and all groups were observed during a two-month period. Five groups were followed simultaneously during May, and four groups were followed during June. Each group was followed for at least 22 complete consecutive days (6:30 am until at least 7:00pm; mean 27 days; maximum 33 days) for a total of 215 complete follow days. Behavioral variables were collected using scan sampling and range mapping as described in Snaith and Chapman (in review). Group spread (m^2/individual; calculated as the area of an ellipse defined by the distance between the most distantly separated monkeys along two perpendicular axes, divided by the number of individuals in a group) and the percent of time engaged in social behavior are used as indices of social contact.

Fecal samples were collected to assess fecal cortisol levels and parasite infections. We aimed to collect samples from 5 individuals per group per day, but daily sampling varied from 0-5 per group. Individuals from which samples were collected were identified to age-sex class by observing defecation, but individual recognition was not possible. To avoid confounds associated with age, sex, and reproductive status (Hausfater and Watson 1976; Lloyd 1983; Festa-Bianchet 1989; Bercovitch and Clarke 1995; Klein and Nelson 1999) and diurnal variation in hormone clearance (Sousa and Ziegler 1998), samples were collected before 10:00 am and only from adult males and females with infants.

Samples were collected immediately after defecation, placed into individual vials, and frozen within 5 hours. Half a gram of each sample was prepared for cortisol analysis in the field using the citrate buffer and ethanol technique (Gould, Ziegler, and Wittwer 2005; Chapman et al. 2006). Samples were then sent to the National Primate Research Center at the University of Wisconsin-Madison for measurement of cortisol and metabolites using the methods outlined in Ziegler et al. (1995). Fecal cortisol levels are presented as ng cortisol and metabolites /g dry feces. Dry weights were determined for each sample in the field by oven-drying half a gram of each sample to a constant weight and subtracting the dry weight from the wet weight to determine percent water content.

A portion of each sample was removed and stored in formalin for parasite analysis at McGill University. Half a gram of sample was processed using the formalin-ethyl acetate sedimentation concentration procedure (Garcia 1999). Parasite eggs were counted, photographed, and identified based on their size, shape, color, and content. We were able to identify eggs to the level of superfamily and sometimes genus. Infections were described in terms of prevalence (the proportion of samples infected), density (the number of eggs per sample), average density (mean density across all samples), richness (the number of unique parasite species in a sample) (terms following Bush et al. 1997; Nunn and Altizer 2006). Because we could not identify individual monkeys, our measure of prevalence represents the proportion of *samples* infected, rather than the proportion of *individuals* infected as it is normally defined (Bush et al. 1997; Nunn and Altizer 2006). This measure of prevalence may produce either inflated (if sampling is biased by repeated sampling of infected individuals) or deflated (because infected individuals may not shed eggs in every defecation) estimates

(Huffman 1997; Rothman in press). Although fecal analysis the only non-invasive approach available for the study of gastrointestinal parasitism in wild primates (Gillespie 2006), fecal egg counts may not provide a reliable measure of the actual worm burden, because variation in egg counts may be affected by a variety of factors including parasite oviposition patterns, host fecal output and water content, and clustering of eggs in feces (Hall 1981; Anderson and Schad 1985; Rothman in press). Thus, while extreme variation in fecal egg counts may indicate different parasite burdens, small differences are not likely meaningful, and while we present egg density values by group, we do not include measures of density in our statistical analyses. Furthermore, our egg counts may also be low because we froze our samples which may destroy some eggs (Roepstorff et al. 2001). This limitation will prevent direct comparisons with other studies, but should not introduce bias into between-group comparisons of density or prevalence, because all samples were treated in the same manner. Measures of species richness, however, may be biased if some egg species occurred only in some groups and were more likely to be destroyed by freezing than others; however, we were able to detect the diagnostic stages of parasite species found in similar studies of red colobus in Kibale where feces were not frozen (Chapman, Gillespie, and Speirs 2005; Gillespie, Greiner, and Chapman 2005).

Average values were calculated to characterize the parasite infections and stress levels of each group, and results are presented as group-level measures (n=9). We used Spearman correlations to test whether group size was related to cortisol levels parasite prevalence, parasite richness, and whether parasite prevalence was related to group spread, or percent time social. All tests were conducted using group-level mean measures (n=9). Because we ran multiple comparisons, we reduced α using the Benjamini and Yekutieli modified False Discovery Rate method, which has been shown to be a meaningful experiment-wise correction for multiple pairwise tests that reduces Type I error while maintaining statistical power (Narum 2006). Three pairwise comparisons were made involving group size, and three were made against parasite prevalence, calling for $\alpha=0.027$ in all cases (Narum 2006). In addition, because we found no difference in cortisol levels across groups, we did not statistically control for its effect when examining parasite relationships.

All field and laboratory methods were approved by the McGill Animal Care and Safety Ethics, the Uganda Wildlife Authority and the Uganda National Council for Science and Technology

Results

Group size ranged from 25 to 127 individuals (mean=65). We analyzed 477 samples for fecal cortisol (mean=53 per group, range 36-92). Average group cortisol levels ranged from 93 to 208 ng/g dry feces (mean=162 ng/g), and was unrelated to group size (r_s=0.333, p=0.762) (Figure 6).

We analyzed 442 samples for parasite infection (mean=49 per group, range 38-65). We found eggs of *Trichuris sp.*, *Strongyloides sp.*, *Colobenterobius sp.*, *Enterobius colobi*, and other unidentified strongyles (Strongylida) (Table 3). There were 206 infected samples, giving an overall infection prevalence of 47%. Across groups, infection prevalence varied from 12 to 68% (mean=42%), and was negatively related to group size (r_s=-0.933, p<0.001). This relationship was primarily driven by the variation in *Trichuris* prevalence (Table 1). Overall, maximum species richness was 3 (mean=0.50, range 0-3), and was unrelated to group size (r_s=-0.293, p=0.444). Density ranged from 0 to 97 eggs per sample. Overall average density was 3.58, and average density across groups ranged 1.3 to 7.1 eggs per sample.

Across groups, average group spread varied from 7 to 85 m/individual (mean=30m^2/individual), and percent time social varied from 5.1 to 10.2% (mean=7.2%). Parasite infection prevalence was negatively related to group spread (r_s=-0.733, p=0.024), but was not related to percent time engaged in social activity (r_s=0.617, p=0.076).

Discussion

Physiological stress, as indicated by fecal cortisol, was unrelated to group size, which is puzzling because we previously demonstrated that larger groups experienced more food competition (increased day range/reduced foraging efficiency) and had fewer offspring per female than smaller groups (Snaith and Chapman in review), which led to the expectation that we would observe greater stress in larger groups. This result suggests that larger groups do not necessarily experience higher stress levels, and that physiological stress is not necessarily among the mechanisms limiting group size, or affecting the reproductive success of females in larger groups. However, it is possible that stress is more important during periods of food shortage, and that females may suffer group size-related increases in cortisol (and reductions in fecundity) that were not captured during this study.

Social and density-dependent transmission should lead to higher intestinal helminth infection rates in larger groups unless behavioral counter-strategies exist to reduce transmission rates (Freeland 1976; Moller, Dufva, and Allander 1993; Loehle 1995; Altizer et al. 2003; Nunn and Altizer 2006). Surprisingly, we found a very strong negative relationship between parasite infection prevalence and group size in red colobus monkeys. Freeland (1976) reasoned that behavioral adaptations may obscure the relationship between group size and infection levels. Taking this logic further, if inter-individual contact rates change as a function of group size, then a negative relationship between group size and infection rates may be observed. Our results provide some support for this contention; although there was no effect of the amount of time spent socializing, group spread was negatively related to parasite infection prevalence, which may explain the unexpected negative relationship between group size and parasite infections.

Elsewhere (Snaith and Chapman in review) we suggested that increased group spread was a behavioral response to increasing food competition in larger groups (c.f. Clutton-Brock and Harvey 1977; Dunbar and Dunbar 1988; Janson and Goldsmith 1995), and here we suggest that it may be a behavioral counter-strategy to parasite infection (c.f.Freeland 1976). We cannot determine the direction of causation here; it is possible that group spread increases due to food competition, and, as a by-product, reduces parasite transmission rates in larger groups, or, transmission risk could directly create selective pressure for density-dependent adjustment of group spread. Careful studies are required to test these alternative explanations, and to examine whether infection risk and food competition exert complementary selection pressures on social behavior and group size in primates. Nonetheless, the strong negative relationship between group size and parasite infection prevalence suggests that parasite infections do not directly impose group-size related costs that may limit group size in this species. However, if group spread is adjusted to reduce parasite transmission, and if increasing group spread is associated with fitness costs, then parasite disease risk may impose an indirect cost by creating selection pressure for a costly behaviour.

However, parasite infections and stress levels are inter-dependent. Increasing stress can cause increasing susceptibility to infection due to compromised immunity, while infections can simultaneously increase stress levels by compromising nutrition and imposing costs associated with the immune response (Sapolsky 1994; Koski and Scott 2001; Nunn and Altizer 2006). Our finding that cortisol was unrelated to group size may thus be related to the reduced parasite infection prevalence observed in larger groups. Less parasite-related stress may have counteracted the effect of other stressors in larger groups, resulting in lower cortisol levels; alternately, if stress was lower in larger groups for some other reason, the reduced parasite levels may have been due to better immune function resulting from lower cortisol levels. The causative direction of this relationship requires further investigation. Furthermore, the cortisol results must be considered relative to the behavioural measures, because if group spread increased as a behavioural mechanism to reduce stress associated food competition in large groups, this may help explain why cortisol does not increase with group size.

We previously demonstrated that larger groups of red colobus experienced reduced foraging efficiency due to increased within-group scramble competition, and we found that female reproductive success, as indicated by the number of offspring relative to the number of females in a group, was lower in larger groups (Snaith and Chapman in review). We further suggested that this ecological mechanism may exert selection pressure to limit group size in some folivorous monkeys. Here we evaluated whether parasite infections and physiological stress may exert similar pressures. Our results suggest that costs associated with parasite infections and stress do not increase with group size. We thus cannot conclude that they contributed to the observed reductions in reproductive success in larger groups, or that they were among the factors limiting group size in red colobus monkeys. Longer-term studies that measure cortisol, disease, and fecundity of individual females (and including periods of food shortage) are required before this conclusion can be reached.

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References Cited

Alexander RD. 1974. The evolution of social behavior. Annu Rev Ecol Syst. 5:325-383.

Altizer S, Nunn CL, Thrall PH, Gittleman JL, Antonovics J, Cunningham AA, Dobson AP, Ezenwa V, Jones KE, Pedersen AB, Poss M, Pulliam JRC. 2003. Social organization and parasite risk in mammals: Integrating theory and empirical studies. Annu Rev Ecol Evol Syst. 34:517-547.

Anderson R, Schad G. 1985. Hookworm burdens and fecal egg counts: an analysis of the biological basis of variation. Trans R Soc Trop Med Hyg. 79:812-825.

Anderson RM, May RM. 1979. Population biology of infectious-fiseases.1. Nature. 280:361-367.

Appleton CC, Henzi SP. 1993. Environmental correlates of gastrointestinal parasitism in montane and lowland baboons in Natal, South-Africa. Int J Primatol. 14:623-635.

Arneberg P. 2002. Host population density and body mass as determinants of species richness in parasite communities: comparative analyses of directly transmitted nematodes of mammals. Ecography. 25:88-94.

Arneberg P, Skorping A, Grenfell B, Read AF. 1998. Host densities as determinants of abundance in parasite communities. Proc R Soc Lond B Biol Sci. 265:1283-1289.

Bercovitch FB, Clarke AS. 1995. Dominance ranks, cortisol concentrations, and reproductive maturation in male rhesus macaques. Physiol Behav. 58:215-221.

Bercovitch FB, Ziegler TE. 2002. Current topics in primate socioendocrinology. Annu Rev Anthropol. 31:45-67.

Boonstra R, Singleton GR. 1993. Population declines in the snowshoe hare and the role of stress. Gen Comp Endocrinol. 91:126-143.

Bordes F, Blumstein DT, Morand S. 2007. Rodent sociality and parasite diversity. Biol Lett. 3:692-694.

Brown CR, Komar N, Quick SB, Sethi RA, Panella NA, Brown MB, Pfeffer M. 2001. Arbovirus infection increases with group size. Proc R Soc Lond B Biol Sci. 268:1833-1840.

Bush AO, Fernandez J, Esch GW, Seed JR. 2001. Parasitism: the diversity and ecology of animal parasites. Cambridge: Cambridge University Press.

Bush AO, Lafferty KD, Lotz JM, Shostak AW. 1997. Parasitology meets ecology on its own terms: Margolis *et al.* revisited. J Parasitol. 83:575-583.

Cavigelli SA. 1999. Behavioural patterns associated with faecal cortisol levels in free-ranging female ring-tailed femurs, Lemur catta. Anim Behav. 57:935-944.

Chapman CA, Gillespie TR, Speirs ML. 2005. Parasite prevalence and richness in sympatric colobines: Effects of host density. Am J Primatol. 67:259-266.

Chapman CA, Saj TL, Snaith TV. 2007. Temporal dynamics of nutrition, parasitism, and stress in Colobus monkeys: Implications for population regulation and conservation. Am J Phys Anthropol. 134:240-250.

Chapman CA, Wasserman MD, Gillespie TR, Speirs ML, Lawes MJ, Saj TL, Ziegler TE. 2006. Do food availability, parasitism, and stress have synergistic effects on red colobus populations living in forest fragments? Am J Phys Anthropol. 131:525-534.

Clutton-Brock TH, Harvey PH. 1977. Primate ecology and social organization. J Zool Soc Lon. 183:1-39.

Cote IM, Poulin R. 1995. Parasitism and group-size in social animals - a metaanalysis. Behav Ecol. 6:159-165.

Creel S, Fox JE, Hardy A, Sands J, Garrott B, Peterson RO. 2002. Snowmobile activity and glucocorticoid stress responses in wolves and elk. Conserv Biol. 16:809-814.

Dunbar RIM, Dunbar P. 1988. Maternal time budgets of gelada baboons. Anim Behav. 36:970-980.

Ezenwa VO. 2004. Host social behavior and parasitic infection: a multifactorial approach. Behav Ecol. 15:446-454.

Ferin M. 1999. Stress and the reproductive cycle. J Clin Endocrinol Metab. 84:1768-1774.

Festa-Bianchet M. 1989. Individual-differences, parasites, and the costs of reproduction for bighorn ewes (*Ovis canadensis*). J Anim Ecol. 58:785-795.

Foley CAH, Papageorge S, Wasser SK. 2001. Noninvasive stress and reproductive measures of social and ecological pressures in free-ranging African elephants. Conserv Biol. 15:1134-1142.

Freeland WJ. 1976. Pathogens and the evolution of primate sociality. Biotropica. 8:12-24.

Freeland WJ. 1979. Primate social groups as biological islands. Ecology. 60:719-728.

Freeland WJ. 1980. Mangabey (*Cercocebus albigena*) movement patterns in relation to food availability and fecal contamination. Ecology. 61:1297-1303.

Garcia LC. 1999. Practical guide to diagnostic parasitology. Washington, DC: ASM Press.

Gillespie TR. 2006. Noninvasive assessment of gastrointestinal parasite infections in free-ranging primates. Int J Primatol. 27:1129-1143.

Gillespie TR, Greiner EC, Chapman CA. 2005. Gastrointestinal parasites of the colobus monkeys of Uganda. J Parasitol. 91:569-573.

Gould L, Ziegler TE, Wittwer DJ. 2005. Effects of reproductive and social variables on fecal glucocorticoid levels in a sample of adult male ring-tailed lemurs (*Lemur catta*) at the Beza Mahafaly Reserve, Madagascar. Am J Primatol. 67:5-23.

Hall A. 1981. Quantitative variability of nematode egg counts in feces: a study among rural Kenyans. Trans R Soc Trop Med Hyg. 75:682-687.

Hausfater G, Watson D. 1976. Social and reproductive correlates of parasite ova emissions by baboons. Nature. 262:688-689.

Huffman MA. 1997. Seasonal trends in intestinal nematode infection and medicinal plant use among chimpanzees in the Mahale Mountains, Tanzania. Primates. 38:111-125.

Janson CH, Goldsmith ML. 1995. Predicting group size in primates: foraging costs and predation risks. Behav Ecol. 6:326-336.

Klein SL, Nelson RJ. 1999. Influence of social factors on immune function and reproduction. Rev Reprod. 4:168-178.

Koski KG, Scott ME. 2001. Gastrointestinal nematodes, nutrition and immunity: Breaking the negative spiral. Annu Rev Nutr. 21:297-321.

Koski KG, Su Z, Scott ME. 1999. Energy deficits suppress both systemic and gut immunity during infection. Biochem Biophys Res Commun. 264:796-801.

Lloyd SS. 1983. Immunosuppression during pregnancy and lactation. Irish Veterinary Journal. 37:64-70.

Loehle C. 1995. Social barriers to pathogen transmission in wild animal populations. Ecology. 76:326-335.

MacArthur RH, Wilson EO. 1967. The theory of island biogeography. Princeton, NJ: Princeton University Press.

Moberg GP. 1985. Influence of stress on reproduction: measure of well-being. In: Moberg GP, editor. Animal Stress. Bethesda, Maryland: American Physiological Society. p. 245-267.

Moller AP, Dufva R, Allander K. 1993. Parasites and the evolution of host social-behavior. Advances in the Study of Behavior, Vol 22. p. 65-102.

Mooring MS, Hart BL. 1992. Animal Grouping for Protection from Parasites - Selfish Herd and Encounter-Dilution Effects. Behaviour. 123:173-193.

Narum S. 2006. Beyond Bonferroni: less conservative analyses for conservation genetics. Conserv Genet. 7:783-787.

Nunn CL, Altizer S. 2006. Infectious diseases in primates: behavior, ecology and evolution. New York: Oxford University Press.

Nunn CL, Altizer S, Jones KE, Sechrest W. 2003. Comparative tests of parasite species richness in primates. Am Nat. 162:597-614.

Nunn CL, Dokey ATW. 2006. Ranging patterns and parasitism in primates. Biol Lett. 2:351-354.

Padgett DA, Glaser R. 2003. How stress influences the immune response. Trends Immunol. 24:444-448.

Pollard TM. 1995. Use of cortisol as a stress marker - practical and theoretical problems. Am J Hum Biol. 7:265-274.

Pride RE. 2005a. High faecal glucocorticoid levels predict mortality in ring-tailed lemurs (*Lemur catta*). Biol Lett. 1:60-63.

Pride RE. 2005b. Optimal group size and seasonal stress in ring-tailed lemurs (*Lemur catta*). Behav Ecol. 16:550-560.

Raouf S, Smith L, Brown M, Wingfield J, Brown C. 2006. Glucocorticoid hormone levels increase with group size and parasite load in cliff swallows. Anim Behav. 71:39-48.

Roepstorff A, Murrell KD, Boes J, Petkevicius S. 2001. Ecological influences on transmission rates of *Ascaris suum* to pigs on pastures. Vet Parasitol. 101:143-153.

Romero LM, Wikelski M. 2001. Corticosterone levels predict survival probabilities of Galapagos marine iguanas during El Nino events. Proc Natl Acad Sci U S A. 98:7366-7370.

Rothman JM. in press. Host-parasite ecology of the helminths in mountain gorillas. J Parasitol.

Sapolsky RM. 1994. Why Zebras Don't Get Ulcers. New York: W.H. Freeman and Company.

Selye H. 1979. The stress of my life. New York: Van Nostrand.

Sheldon BC, Verhulst S. 1996. Ecological immunology: Costly parasite defences and trade-offs in evolutionary ecology. Trends in Ecology & Evolution. 11:317-321.

Shields WM, Crook JR. 1987. Barn swallow coloniality - a net cost for group breeding in the Adirondacks. Ecology. 68:1373-1386.

Simberloff D. 1974. Equilibrium theory of island biogeography and ecology. Annu Rev Ecol Syst. 5:161-182.

Snaith TV, Chapman CA. in review. Red colobus monkeys display alternative behavioral responses to the costs of scramble competition. Behav Ecol.

Sousa MBC, Ziegler TE. 1998. Diurnal variation on the excretion patterns of fecal steroids in common marmoset (*Callithrix jacchus*) females. Am J Primatol. 46:105-117.

Stoner KE. 1996. Prevalence and intensity of intestinal parasites in mantled howling monkeys (*Alouatta palliata*) in northeastern Costa Rica: Implications for conservation biology. Conserv Biol. 10:539-546.

Wasser SK, Bevis K, King G, Hanson E. 1997. Noninvasive physiological measures of disturbance in the Northern Spotted Owl. Conserv Biol. 11:1019-1022.

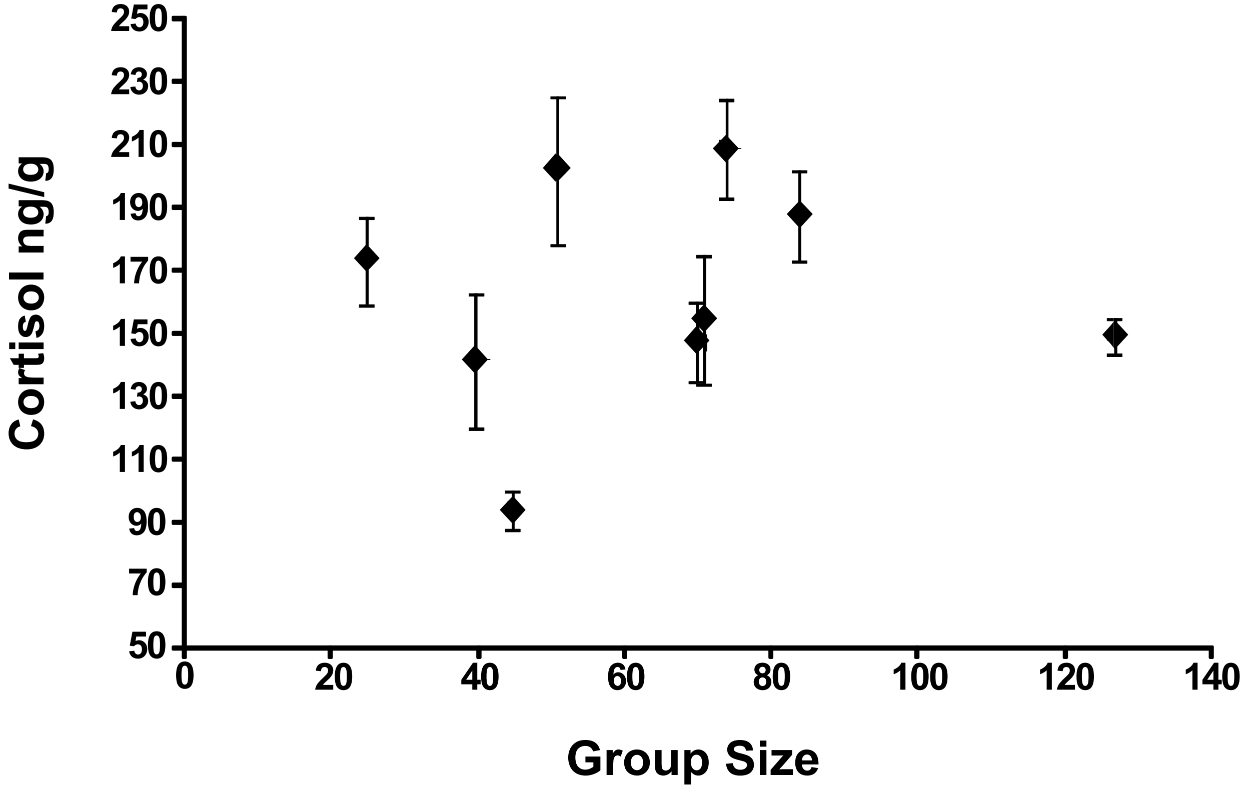
Wingfield J, Romero LM. 2001. Adrenocortical responses to stress and their modulation in free-living vertebrates. In: McEwan B, Goodman H, editors. Handbook of physiology: the endocrine system. New York: Oxford University Press. p. 211-234.

Ziegler TE, Scheffler G, Snowdon C. 1995. The relationship of cortisol levels to social environment and reproductive function in female cotton-top tamarins *Saguinus oedipus*. Horm Behav. 29:407-424.

Table 3. Parasite infection prevalence and densities across nine groups of red colobus

		Trichuris		**Strongyles**		***Strongyloides***		***Colobenterobius***		***Enterobius***	
Group Size	**N Samples**	**Prevalence**	**Mean Density**	**Prevalence**	**Mean Density**	**Prevalence**	**Mean Density**	**Prevalence**	**Mean Density**	**Prevalence**	**Mean Density**
127	47	0.11	3.26 (0-97)	0.02	0.04 (0-1)	0.00	0.00 (n/a)	0.00	0.00 (n/a)	0.01	0.02 (0-1)
84	48	0.21	1.38 (0-10)	0.01	0.02 (0-1)	0.01	0.02 (0-1)	0.00	0.00 (n/a)	0.00	0.00 (n/a)
74	65	0.42	4.38 (0-37)	0.01	0.03 (0-2)	0.01	0.01 (0-1)	0.00	0.00 (n/a)	0.00	0.00 (n/a)
71	38	0.31	4.08 (0-28)	0.03	0.05 (0-1)	0.00	0.00 (n/a)	0.01	0.08 (0-3)	0.00	0.00 (n/a)
70	50	0.37	4.00 (0-32)	0.04	0.06 (0-1)	0.00	0.00 (n/a)	0.00	0.00 (n/a)	0.00	0.00 (n/a)
51	47	0.45	3.02 (0-27)	0.04	0.04 (0-1)	0.00	0.00 (n/a)	0.00	0.00 (n/a)	0.00	0.00 (n/a)
45	48	0.56	3.35 (0-41)	0.02	0.02 (0-1)	0.00	0.00 (n/a)	0.00	0.00 (n/a)	0.00	0.00 (n/a)
40	50	0.65	7.02 (0-89)	0.08	0.06 (0-1)	0.00	0.00 (n/a)	0.00	0.00 (n/a)	0.00	0.00 (n/a)
25	49	0.60	1.22 (0-24)	0.04	0.02 (0-1)	0.08	0.04 (0-1)	0.00	0.00 (n/a)	0.00	0.00 (n/a)

Figure 6. Cortisol levels (mean and standard deviation) across nine groups of red colobus



CONCLUSION

Group living animals are expected to experience food competition, and the costs of competition are expected to increase with group size, and, ultimately, to put an upper limit on the size of social groups (van Schaik 1989). It is therefore puzzling that group-living folivorous monkeys show little evidence of food competition, and that they do not consistently form larger groups despite this apparent lack of food competition (Steenbeek and van Schaik 2001). This has become known as the folivore paradox (Steenbeek and van Schaik 2001).

An important mechanism by which food competition may limit group size is thought to be the cost of travel between food patches, because larger groups will have to visit more patches to feed all group members (Chapman and Chapman 2000; Wrangham 2000). Larger groups are therefore expected to have longer daily ranging distances than smaller groups; however, early studies of folivores found no evidence of this pattern (Clutton-Brock and Harvey 1977; Struhsaker and Leland 1987; Yeager and Kirkpatrick 1998; Yeager and Kool 2000). This evidence formed the basis of the notion that folivores experience little or no food competition within groups (Wrangham 1980; Isbell 1991; Janson and Goldsmith 1995; Sterck, Watts, and van Schaik 1997).

However, there have been theoretical and methodological problems with previous studies that have prevented clear interpretation of results. In Chapter 1, I synthesized existing literature and suggested that ecological controls are necessary to properly assess food competition, and I provided a broadened list of behavioural indices of food competition. In this context, the literature contains many signs of food competition among folivores that had not been appreciated. In Chapter 1, I also reviewed the historical development of primate socioecology, and the development of organizational models, particularly as they relate to folivores. I found that existing models were not detailed enough to adequately characterize the social ecology of folivores and suggested a new working model that I hope will lead to hypothesis-driven studies of food distribution and behaviour and to further model refinement.

The notion that folivores experience little to no food competition necessarily implies that their food resources are superabundant, evenly dispersed, and non-depletable (and thus cannot lead to increasing travel costs for larger groups). In Chapter 2, I tested this assumption by examining the foraging behaviour of red colobus monkeys in Kibale National Park, Uganda. I found evidence that red colobus deplete patches of preferred foods, and that larger groups deplete patches more quickly than smaller groups. This result invalidates the assumption of superabundance, and suggests the possibility of increasing foraging costs in larger groups due to scramble competition.

In Chapter 3, I looked directly for evidence of food competition. I conducted a multi-group, ecologically controlled study to determine whether red colobus display any predicted behavioural indicators of food competition. I simultaneously followed 9 groups of red colobus and controlled for spatial and temporal variation in food availability. My results suggest that red colobus monkeys possess a suite of behavioral strategies that likely represent adaptive responses to feeding competition in groups, that red colobus experience costs associated with scramble competition, and that these costs intensify as group size increases. Our results offer an ecological solution to the folivore paradox, and although the conclusions are so far valid only for red colobus at Kibale, they offer clear direction for addressing the paradox elsewhere. Similar patterns may be revealed in other systems where they have not previously been detected due to confounds associated with unmeasured ecological covariates of group size and alternative behavioural responses.

In Chapter 4, I looked directly at possible physiological costs of food competition in groups. Stress and disease are known to impose fitness costs, and those costs are generally predicted to increase with group size (Nunn and Altizer 2006). Surprisingly, I found that stress was unrelated to group size, and parasite prevalence was negatively related to group size. Nonetheless, females in larger groups seemed to have lower reproductive success than those in smaller groups. The results suggest that neither gastrointestinal parasitism nor stress directly imposed group-size related fitness costs, and thus are unlikely to be among the mechanisms reducing reproductive success or limiting group size in red colobus monkeys. Rather, it is more likely that food competition more directly limits group size and fitness due to the energetic costs associated with reduced foraging efficiency, specifically increased travel costs.

Although my sample size was small, I had a large range of group sizes (25-127), and it is possible that different strategies are used at different group sizes to deal with food competition. With a sample size of 9 groups, I did not have the statistical power to conduct multivariate statistics, but an examination of all behavioural measures plotted against group size does not reveal any obvious differences in strategy between smaller and larger groups. However, the ranging strategies of the three largest groups were startlingly different from one another and suggest that three strategies exist to deal with increasing competition costs: increase daily travel distance, increase group spread, or fission into subgroups. This reaffirms the need to measure a range of possible behavioural responses to food competition, because simply measuring daily ranging distance will not be sufficient to capture all expressions of competition.

While there is ample literature discussing the relationship between group size and food resources for frugivorous and carnivorous taxa, and even for humans, there is much less available regarding folivores. Many browsers and grazers are known to form large herds, suggesting little food competition. However, two studies suggest that there is evidence that ecology constrains group size in folivores. For example, there is variation in social structure among *Equus* species; in some species, the potential for female group formation is known to be affected by the distribution of food resources, and in others food patch size has been shown to affect group cohesiveness and fission-fusion behaviours (Rubenstein 1986). In a situation analogous to that of the folivorous monkeys, grey kangaroos live in small social groups despite being folivorous and despite any clear ecological or social constraints on group size (Jarman and Southwell 1986). However, they also prefer young, green, low-fiber grasses that may occur patchily (Jarman and Southwell 1986), which creates the potential for food competition in the manner demonstrated in this thesis for red colobus monkeys.

Because we have tested these ideas only for red colobus monkeys, much more research is required among both primate and non-primate taxa to better understand the nature and consequences of food competition in folivorous animals.

References Cited

Chapman CA, Chapman LJ. 2000. Determinants of group size in primates: the importance of travel costs. In: Boinski S, Garber PA, editors. On the move: how and why animals travel in groups. Chicago: University of Chicago Press. p. 24-41.

Clutton-Brock TH, Harvey PH. 1977. Primate ecology and social organization. J Zool Soc Lon. 183:1-39.

Isbell LA. 1991. Contest and scramble competition: patterns of female aggression and ranging behaviour among primates. Behav Ecol. 2:143-155.

Janson CH, Goldsmith ML. 1995. Predicting group size in primates: foraging costs and predation risks. Behav Ecol. 6:326-336.

Jarman PJ, Southwell CJ. 1986. Grouping, associations and reproductive strategies in eastern grey kangaroos. In: Rubenstein DI, Wrangham RW, editors. Ecological aspects of social evolution: birds and mammals. Princeton: Princeton University Press. p. 399-429.

Nunn CL, Altizer S. 2006. Infectious diseases in primates: behavior, ecology and evolution. New York: Oxford University Press.

Rubenstein DI. 1986. Ecology and sociality in horses and zebras. In: Rubenstein DI, Wrangham RW, editors. Ecological aspects of social evolution: birds and mammals. Princeton: Princeton University Press. p. 282-302.

Steenbeek R, van Schaik CP. 2001. Competition and group size in Thomas's langurs (*Presbytis thomasi*): the folivore paradox revisited. Beh Ecol Sociobiol. 49:100-110.

Sterck EHM, Watts DP, van Schaik CP. 1997. The evolution of female social relationships in nonhuman primates. Beh Ecol Sociobiol. 41:291-309.

Struhsaker TT, Leland L. 1987. Colobines: infanticide by adult males. In: Smuts BB, Cheney DL, Seyfarth RM, Wrangham RW, Struhsaker TT, editors. Primate societies. Chicago: University of Chicago Press. p. 83-97.

van Schaik CP. 1989. The ecology of social relationships amongst female primates. In: Standen V, Foley RA, editors. Comparative socioecology: The behavioural ecology of humans and other mammals. Boston: Blackwell Scientific Publications. p. 195-218.

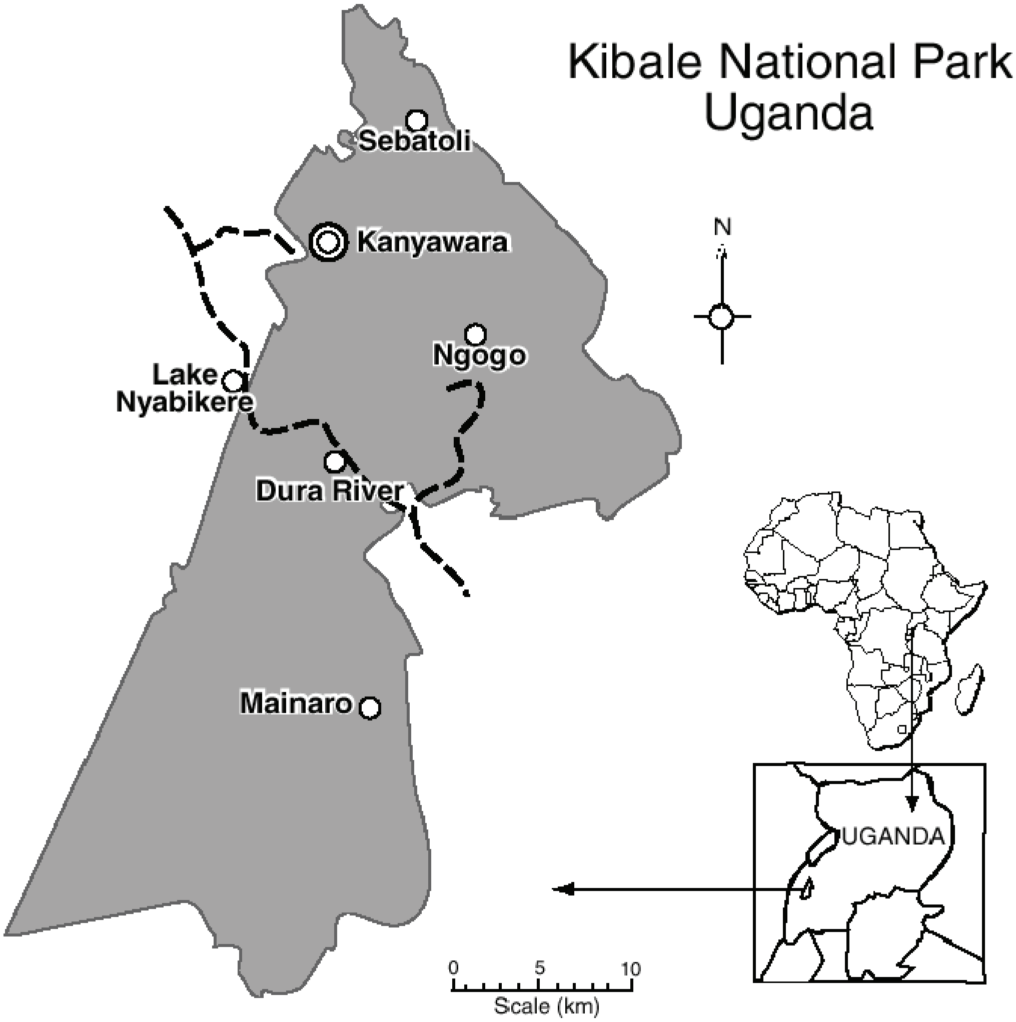
Wrangham RW. 1980. An ecological model of female-bonded primate groups. Behaviour. 75:262-300.

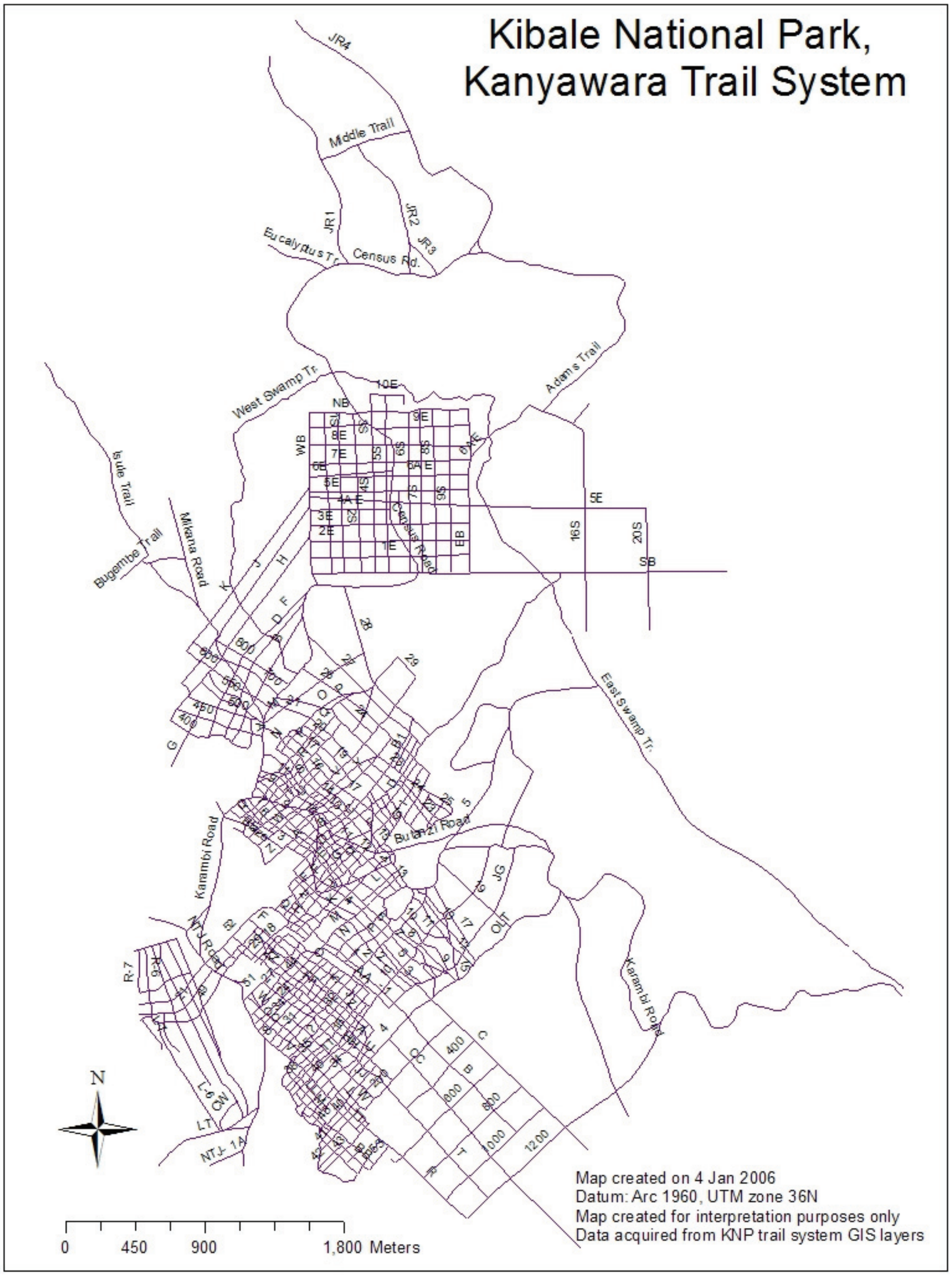
Wrangham RW. 2000. Why are male chimpanzees more gregarious than mothers? A scramble competition hypothesis. In: Kappeler PM, editor. Primate males: causes and consequences of variation in group composition. Cambridge: Cambridge University Press. p. 248-258.

Yeager CP, Kirkpatrick CR. 1998. Asian colobine social structure: ecological and evolutionary constraints. Primates. 39:147-155.

Yeager CP, Kool K. 2000. The behavioral ecology of Asian colobines. In: Whitehead PF, Jolly CJ, editors. Old world monkeys. Cambridge: Cambridge University Press. p. 496-521.

APPENDIX 1: MAPS OF KIBALE

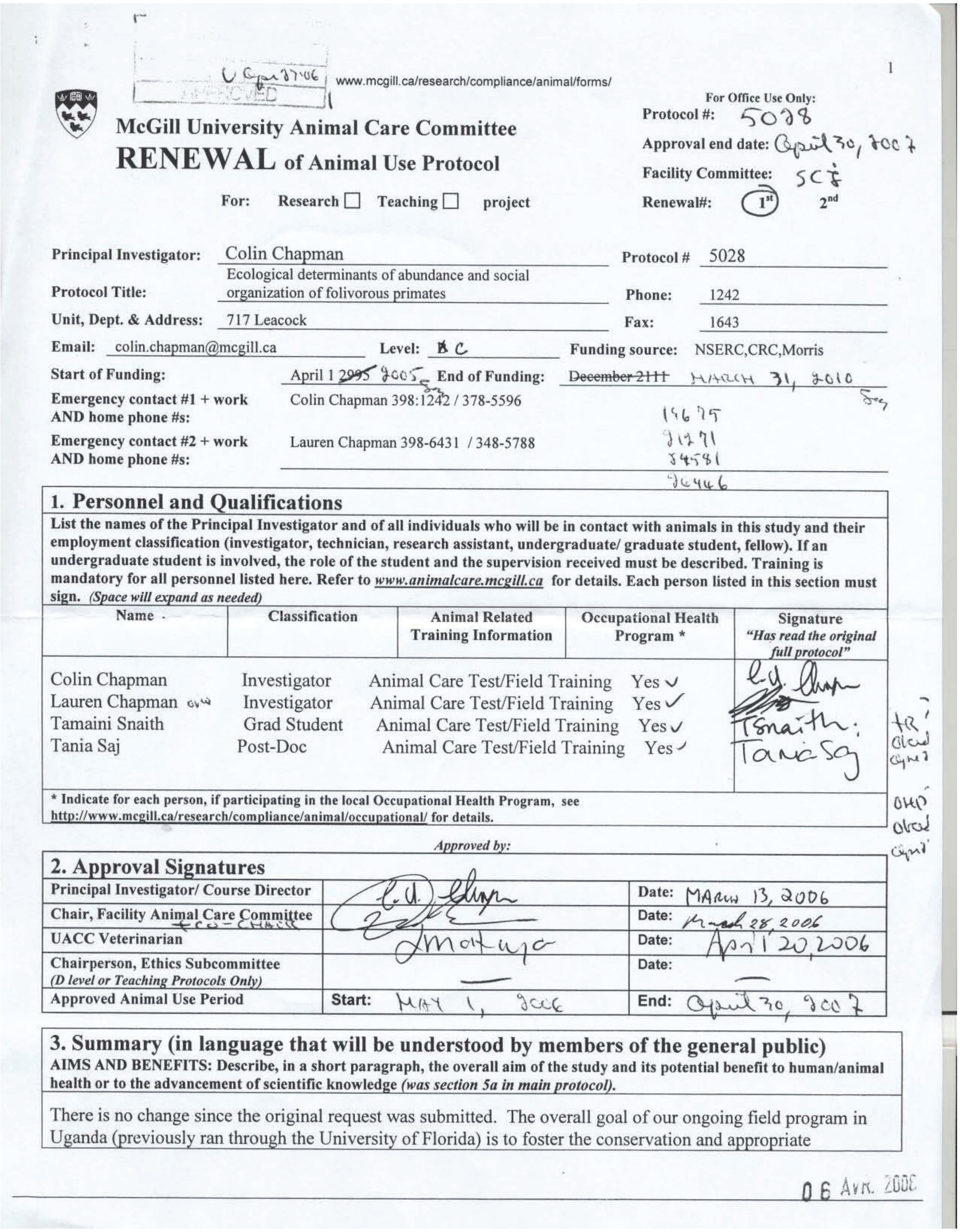




Kibale National Park, Kanyawara Trail System

Map created on 4 Jan 2006
Datum: Arc 1960, UTM zone 36N
Map created for interpretation purposes only
Data acquired from KNP trail system GIS layers

APPENDIX 2: ANIMAL CARE APPROVAL



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For: **Research** ☐ **Teaching** ☐ **project**

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Approval end date: April 30, 2007

Facility Committee: SCI

Renewal#: [✓ 1st] 2nd

Principal Investigator:	Colin Chapman	**Protocol #**	5028
Protocol Title:	Ecological determinants of abundance and social organization of folivorous primates	**Phone:**	1242
Unit, Dept. & Address:	717 Leacock	**Fax:**	1643

Email: colin.chapman@mcgill.ca **Level:** ~~B~~ C **Funding source:** NSERC,CRC,Morris

Start of Funding: April 1 ~~2995~~ 2005 **End of Funding:** ~~December 2111~~ MARCH 31, 2010

Emergency contact #1 + work AND home phone #s: Colin Chapman 398:1242 / 378-5596

Emergency contact #2 + work AND home phone #s: Lauren Chapman 398-6431 / 348-5788

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1. Personnel and Qualifications

List the names of the Principal Investigator and of all individuals who will be in contact with animals in this study and their employment classification (investigator, technician, research assistant, undergraduate/ graduate student, fellow). If an undergraduate student is involved, the role of the student and the supervision received must be described. Training is mandatory for all personnel listed here. Refer to *www.animalcare.mcgill.ca* for details. Each person listed in this section must sign. *(Space will expand as needed)*

Name	Classification	Animal Related Training Information	Occupational Health Program *	Signature *"Has read the original full protocol"*
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Lauren Chapman	Investigator	Animal Care Test/Field Training	Yes ✓	
Tamaini Snaith	Grad Student	Animal Care Test/Field Training	Yes ✓	T Snaith
Tania Saj	Post-Doc	Animal Care Test/Field Training	Yes ✓	Tania Saj

TR okay apr'd

*** Indicate for each person, if participating in the local Occupational Health Program, see http://www.mcgill.ca/research/compliance/animal/occupational/ for details.**

OHP okay apr'd

Approved by:

2. Approval Signatures

Principal Investigator/ Course Director		**Date:**	MARCH 13, 2006
Chair, Facility Animal Care Committee + CO-CHAIR		**Date:**	March 28, 2006
UACC Veterinarian		**Date:**	April 20, 2006
Chairperson, Ethics Subcommittee *(D level or Teaching Protocols Only)*	—	**Date:**	—
Approved Animal Use Period	**Start:** MAY 1, 2006	**End:**	April 30, 2007

3. Summary (in language that will be understood by members of the general public)

AIMS AND BENEFITS: Describe, in a short paragraph, the overall aim of the study and its potential benefit to human/animal health or to the advancement of scientific knowledge *(was section 5a in main protocol).*

There is no change since the original request was submitted. The overall goal of our ongoing field program in Uganda (previously ran through the University of Florida) is to foster the conservation and appropriate

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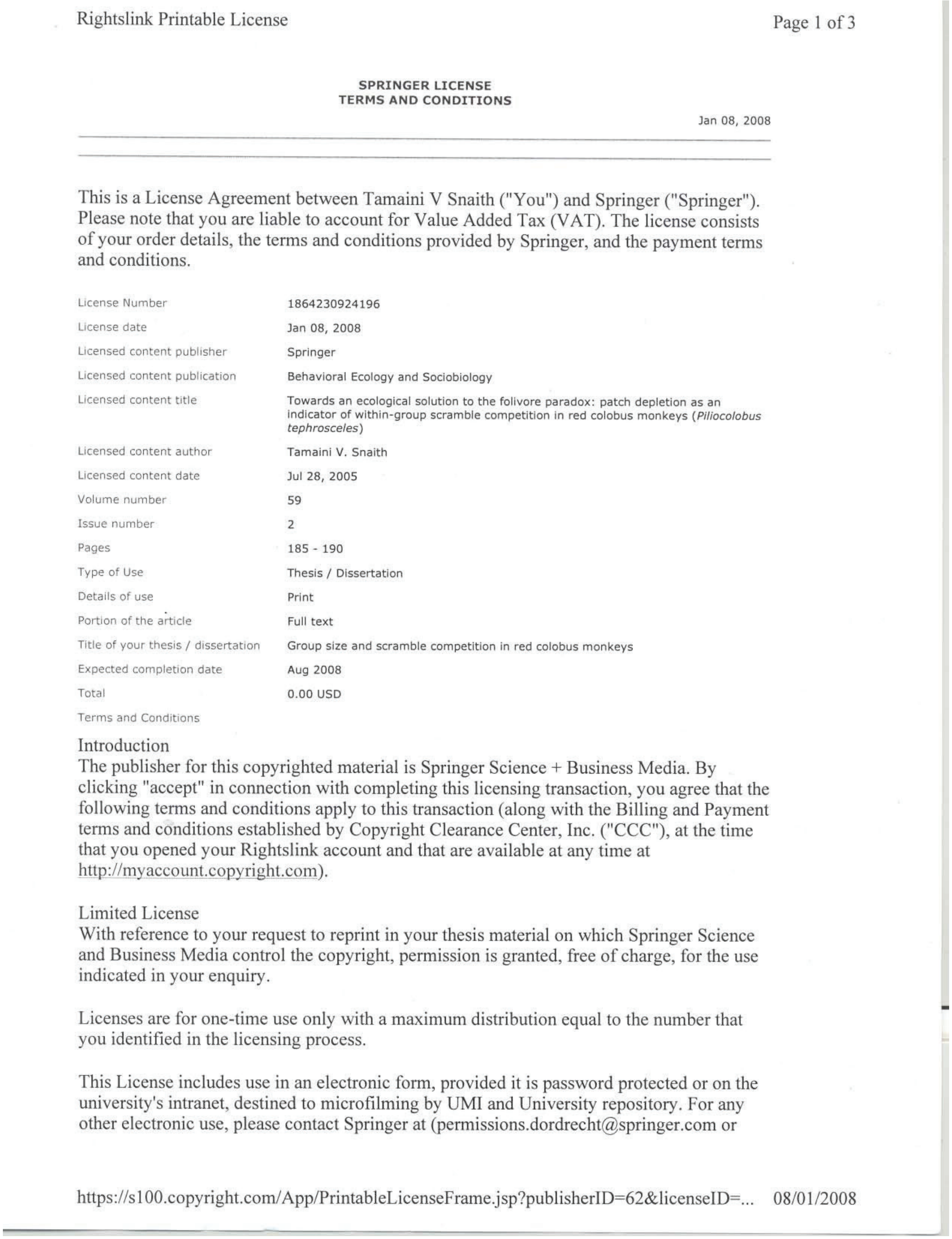

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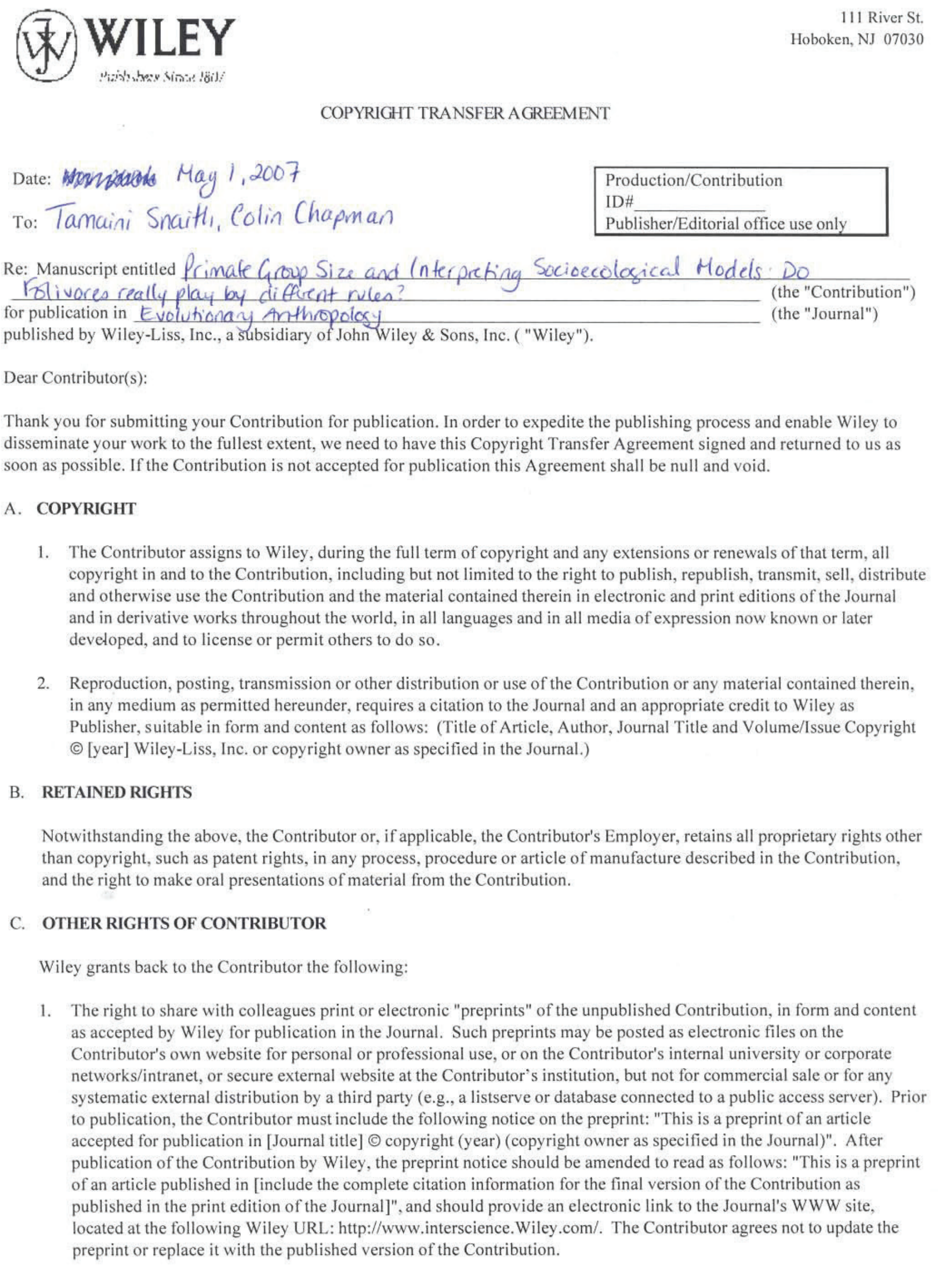

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