The effects of low food competition on foraging and dominance in folivorous primates

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Abstract

Several different socioecological models have been developed to better understand the social organisation of various primate taxa. This thesis addresses two points of divergence between empirically observed behaviour and that predicted by current models for folivorous (leaf-eating) primates. First, many folivores form small groups despite the assumed low food competition among folivorous primates that would theoretically eliminate a key constraint on group size. This phenomenon is termed the folivore paradox since the small groups that they form have fewer anti-predator and anti-infanticidal advantages than do large groups. Second, defined dominance hierarchies are not expected to occur among females in a group when food competition is low because a founding ecological model proposed that competition between female primates is based on food resources. However, most folivorous primate species have exhibited linear (strong) dominance hierarchies among females where this has been studied.

Chapter 1 examines food patch depletion behaviour in black and white colobus monkeys and compares it to that of red colobus monkeys, which form much larger groups. Implications for food competition within groups of different sizes and for the folivore paradox are discussed. The second chapter is a study on female dominance hierarchies in a group of red colobus. The results are compared to those found for other folivorous primates to determine which traits or conditions may be driving inter-species variation in social structure.

This thesis illustrates that the assumption of low food competition among folivorous primates commonly integrated into leading socioecological models may be applicable to only some primate species. Chapter 1 suggests that the level of food competition within groups varies markedly between folivore species. Chapter 2 demonstrates that, even in species that lack strong female dominance hierarchies (indicating low food competition), reproductive fitness can still be affected by an individual's dominance rank. This suggests a need to refine leading primate socioecological models to allow for more variety in ecological function and social structure among folivorous primate species.

Résumé

Plusieurs modèles socioécologiques ont été développés pour mieux comprendre l'organisation sociale des primates de différentes espèces. Cette thèse traite de deux points de déviation entre le comportement empiriquement observé et celui prédit par les modèles courants pour les primates folivores (ceux qui se nourrissent de feuilles). Tout d'abord, plusieurs espèces folivores forment des petits groupes malgré leurs bas niveau de compétition alimentaire supposé, ce qui les libère théoriquement de former des grands groupes. Ce phénomène est nommé le paradoxe des folivores, car leurs petits groupes n'avaient pas les avantages des grands groupes contre les prédateurs et l'infanticide. Deuxièmement, il est supposé que les hiérarchies parmi les femelles ne se forment pas dans les groupes quand la compétition pour l'alimentation est basse parce qu'un modèle fondateur propose que la compétition entre les primates femelles est basée sur les ressources alimentaires. Toutefois, la plupart des primates folivores dont la dominance entre les femelles a été évaluée présentent des hiérarchies linéaires parmi les femelles.

Dans le premier chapitre j'examine l'épuisement des ressources alimentaires chez les singes colobes noirs et blancs et je le compare à celui découvert chez les colobes rouges, qui forment des groupes beaucoup plus grands. Les implications pour la compétition alimentaire dans les groupes de grandeurs différentes et pour le paradoxe des folivores sont discutées. Le deuxième chapitre est une étude de la hiérarchie parmi les femelles dans un groupe des colobes rouges. Les résultats sont comparés à ceux des autres espèces de primates folivores pour déterminer quels traits ou conditions peuvent pousser la variation dans la structure sociale entre espèces.

Les résultats de cette thèse montrent que la supposition d'un manque de compétition alimentaire dans les groupes des primates folivores, qui est communément intégrée aux modèles socioécologiques courants, est valable seulement pour certaines espèces de primates folivores. Le chapitre 1 démontre que la compétition alimentaire dans les groupes varie entre espèces, et le chapitre 2 démontre que même chez les espèces où il n'y a pas de hiérarchie parmi les femelles, leurs succès reproducteurs peuvent toujours être influencés par le niveau d'agression exprimé par ces individus. Ces résultats suggèrent qu'il y a un besoin de raffiner les modèles socioécologiques courants pour permettre la considération d'une variété

dans la fonction écologique et dans la structure sociale chez les espèces de primates folivores.

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Contributions of Authors

The chapters in this thesis were both co-authored by my supervisor, Dr. Colin Chapman, who was an important actor throughout the process of their preparation. He played a key role in the initial formulation of the ideas for my project proposals, guided me to the most relevant literature, funded much of my work through his grants, particularly in my first year and for both field seasons, provided logistical support in Uganda, edited and provided suggestions for several drafts of each chapter, and guided me during the preparation of the manuscripts for publication.

Andrea Reid, my co-author for the first chapter, provided the inspiration for this study since its earliest version began as her Honours thesis project while she was in her last year of undergraduate studies at McGill University. She worked with Colin to compose the project proposal and plans for fieldwork, and we shared the field work equally in summer 2009, analysed the data and prepared the first version of the manuscript over the following school year together, at which time she was the first author. By summer 2010, we realized we would need a larger sample size to publish the manuscript, and as I was in Uganda that summer completing the data collection and compilation for Chapter 2, I was the one to collect the second half of the data for the first chapter at that time. However, upon my return, we again shared the tasks of data analysis and preparation of the current version of the manuscript equally, and worked so well together that we jointly presented our findings at conferences. For these reasons we submitted the new manuscript with a note indicating that we contributed equally to its production.

The other three co-authors for Chapter 1, Dr. Jessica Rothman, Caley Johnson and Dr. Rafael Reyna-Hurtado stepped in with suggestions for directions we could take with the project, pointed us to relevant literature for ideas for the Discussion section, and helped in editing this section in particular, providing us with useful comments and sometimes writing a paragraph in the manuscript expressing an interesting idea that connected our findings to those of other studies within their specific areas of expertise.

Although each of the authors of these chapters was integral in the development of this thesis, which would have been impossible without them, the work presented here on a whole is primarily the result of my own research. For Chapter 1, I carried out most of the fieldwork and shared the undertaking of data compilation, data analysis and writing all versions of the manuscript equally with Andrea Reid. For Chapter 2, I played a primary role in the conception of the ideas for the original project, the literature review, development of methods, initiating and concluding the fieldwork, compiling and entering all of the hand-written data collected over the year into a computer, data analysis, manuscript writing and its preparation for publication.

Both chapters have been prepared for publication in peer-reviewed journals, although Chapter 2 has not yet been submitted. Chapter 1 has been formatted for *Primates* (submitted) and Chapter 2 for *Behavioral Ecology and Sociobiology*.

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I would like to first thank Dr. Colin Chapman, my thesis supervisor and mentor, for his consistent support and energy throughout my experience as a master's student. Colin was truly an ideal supervisor for me. When I needed his help, his door was always open and he would immediately stop what he was doing and cheerfully answer my questions and offer suggestions, no matter how stressed or busy he was. One exceptional quality of Colin's is his understanding of the need of many young graduate students for a wide variety of experiences. His flexibility in my working schedule and his trust in allowing me to take some time off to go on exhilarating educational adventures allowed me not only to work well, learn a great a deal, and develop a wide range of skills, but also to enjoy the years of my early twenties to the fullest. Although he made his expectations clear and made sure I kept on top of my work, he understood that I was still searching for what I wanted to develop into a career and was open to my exploring other fields. Furthermore, he fully supported my enthusiasm for teaching even though it meant spending time away from my thesis work at times; as a result I had some of the most valuable experiences of my graduate school years as a teaching assistant for undergraduate courses.

This thesis would not have been possible without the many bright minds of professors and fellow students that were willing to spend time discussing my projects despite their busy schedules. My lab mates Ria Ghai, Aerin Jacob, Dr. Rafael Reyna-Hurtado, Chesley Walsh and Catrina MacKenzie were keen to discuss project proposals, edit manuscript drafts, and listen to practice presentations. Colleagues working on similar projects, such as Dr. Sarah Turner, Dr. Tamaini Snaith, Dr. Tara Harris, Dr. Julie Teichroeb, Dr. Lauren Chapman, Dr. Rhonda Amsel, Dr. Eric Delson, and Dr. Scott McGraw gave very useful comments in discussions on the project material and statistical methods and shared insights from their own findings, sometimes even sharing their data to help in the interpretation of mine. My supervisory committee members, Dr. Louis Lefebvre and Dr. Denis Réale, were a great resource for new perspectives on my results, and when I became caught up in the details of my research, their input drew my attention back to the bigger picture. Andrea Reid and I spent our first visit to Uganda attached at the hip as she helped

me with my red colobus research while I helped her with what was then her Honours project on black and white colobus. Over the past two years we have worked together on the latter project, refining version after version of the manuscript to prepare it for publication and practicing presentations for sharing our work at conferences. Never have I met such a patient and respectful colleague with whom I could work for hours without frustration, and some one who is so compatible with me as an academic teammate. Thank you Andrea for all of the good times we had in Africa, the library, and outside of school - you were great at motivating me to work hard, I learned a lot from you, and you made even the most onerous tasks of our work much more fun. I would like to thank David Paterson, Christine Sykas and Leena Tiismann for helping me edit my thesis, and Kimberley Ann Renaud, Isabelle Arcand and Dr. Jean-François Picher for their assistance in translating the thesis abstract into French.

The bulk of the data collection for these projects was performed by the skilled and dependable field assistants of the Kibale Fish and Monkey Project. Their valuable experience in working with the monkeys in Kibale National Park put their capacities in fieldwork leagues ahead of my own, and their contributions were indispensable as I would never have been able to collect nearly as much accurate data without their help. I would like to extend my deep thanks to Richard Mutegeki, Tusimi Laurence, and particularly to Peter Tuhairwe, Clovis Kaganzi, and Richard Karamagi. I was repeatedly in awe of their ability to recognize any given individual within a group of 94 monkeys, and of their extraordinary tenacity, generosity and spirit. The local project managers, Dennis Twinomugisha and Patrick Omeja, were wonderful for providing a solid base at the research station in Kibale, and their help with logistics and communication overseas is very appreciated.

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General Introduction

Characterising the behaviour of animals is a difficult task, and consequently, models to explain their social behaviour and ecology (socioecological models) are continually evolving as more information becomes available. Building more comprehensive models contributes to a greater understanding of the evolution of social organisation as well as the feeding ecology and predator-prey dynamics within a community, which in turn advance conservation efforts. For example, studies that explore the relationships between group-living and food competition, disease, reproductive fitness, dispersal patterns and/or predator-prey dynamics can greatly inform the management strategies of conservation projects (Young and Isbell 1994, Janson 2000, Chapman et al. 2007, Weghorst 2007, Struhsaker 2008).

Primate socioecology in particular has been a prevalent study subject for decades and several different models have been developed to improve understanding of the social organisation of different primate taxa (Eisenberg et al. 1972, Alexander 1974, Wrangham 1980, Janson 1988, van Schaik 1989, Isbell 1991, Sterck et al. 1997, Snaith and Chapman 2007). Wrangham's (1980) ecological model proposed that the social organisation of male primates is based on mating competition, whereas that of female primates is based on food competition - an idea upon which all subsequent primate socioecological models have been based (van Schaik 1989, Isbell 1991, Sterck et al. 1997, Snaith and Chapman 2007). Van Schaik (1989) defined four types of competition among primates: between-group scramble, between-group contest, within-group scramble, and within-group contest. Contest competition occurs when dominants lower the fitness of subordinates more than vice versa, creating an asymmetry in feeding success and likely in fitness. Scramble is considered a weaker form of competition in which all individuals lower each other's fitness equally (van Schaik 1989, Koenig 2002).

In view of the apparent overabundance and even distribution of leafy food resources in forests, it is commonly assumed that folivorous (leaf-eating) primates are essentially not food-limited (Janson and Goldsmith 1995). This has led to the presumption that they have no within-group contest competition and negligible scramble competition for food (Isbell 1991, Janson and Goldsmith 1995, Sterck et al. 1997, reviewed by Snaith and Chapman 2005). These assumptions have been incorporated into leading primate models, and have had two important implications on how groups of folivorous primates are thought to function ecologically and socially.

First, according to the ecological model, food competition is a key limiting factor on group size, and if it is very low, this constraint on group size is lifted (Wrangham 1980). This has led to the prediction that, relative to primates with other diets, folivorous primates should form large groups due to the anti-predator and anti-infanticidal benefits of aggregating in high numbers (Treves and Chapman 1996; Koenig and Borries 2002; Snaith and Chapman 2005; but see Steenbeek and van Schaik 2001). However, many folivores form much smaller groups than predicted by this model, a phenomenon termed the "folivore paradox" (Steenbeek and van Schaik 2001; Koenig and Borries 2002).

Second, low food competition should affect the social structure within groups, particularly among females whose competition is based primarily on food resources. Defined dominance hierarchies are not expected to occur among females when food competition is low because these are thought to be established in order to minimize potentially dangerous aggressive confrontations in the face of contest competition (Koenig 2002). Where the strength of female dominance hierarchies has been tested, most folivorous primate species have not conformed to this expectation and have exhibited strong female hierarchies (e.g., Hrdy 1977, Ruhiyat 1983, Koenig 2000, Koenig et al. 2004, Robbins et al. 2005), while only a few species have not expressed them (e.g., Korstjens et al. 2002, Pope 2000).

This thesis focuses on these two points of divergence between theory and empirical data in terms of the ecological function and social structure of groups of folivorous primates to provide a basis for the refinement of current socioecological models. I studied groups of folivorous monkeys in Kibale National Park, Uganda, where two strongly folivorous monkey species reside: the black and white colobus (*Colobus guereza*) and the red colobus (*Procolobus rufomitratus*). These colobines have a high overlap in diet and habitat and both face very low predation pressure, yet they differ greatly in their group sizes (Delson et al. 2000, Chapman et al. 2002, Struhsaker and Oates 1975, Teelen 1994, Harris and Chapman 2007), providing an extraordinary opportunity for a comparative study exploring the determinants of group size among folivorous primates. Chapter 1 examines food patch depletion behaviour in black and white colobus using the same methods as a previous study on red colobus by Snaith and Chapman (2005). The findings for these two species are compared and implications for food competition within groups of different sizes and for the folivore paradox are discussed. A red colobus group in Kibale, SC, has been studied since 2006 and all individuals in the group are habituated to researchers and are individually identifiable. Chapter 2 comprises my year-long study on the dominance interactions between female red colobus in the SC group. I use these data to test the prediction of current socioecological models of weak or nonexistent female dominance hierarchies within folivorous primate groups. The results are compared to those found for other folivorous primates to determine which traits or conditions may be driving the variation in social structure between the species that exhibit female hierarchies and those that do not.

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Chapter 1: Patch depletion behavior differs between sympatric folivorous primates

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Abstract

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

Keywords Black and white colobus •*Colobus guereza* •Folivore Paradox • Group size •Kibale National Park

Introduction

Identifying the extent to which feeding ecology shapes group size and social structure is a central theme of behavioral ecology (Gartlan and Brian 1968; Eisenberg et al. 1972; Bradbury and Vehrencamp 1976; Terborgh 1983; van Schaik and van Hooff 1983; Jarman and Southwell 1986; Wrangham et al. 1993). Primate feeding ecology is of particular interest when investigating grouping behavior, since primate group sizes are highly variable both within and between species. Intraspecific group size for red colobus (*Procolobus rufomitratus*), for example, varies between 12 and 150 members (Chapman and Chapman 2000). Interspecific variation may range from a single individual, as seen in orangutans (van Schaik and van Hooff 1996), to over 800 members in mandrills (*Mandrillus sphinx*; Abernethy et al. 2002). Diet and feeding competition are ecological factors often invoked to explain variation in primate socioecology (van Schaik 1983; Janson 1988; Snaith and Chapman 2005), but how a primarily leaf-based diet (folivory) influences primate grouping patterns is an area of considerable debate. It is this relationship between diet and group size that our research addresses.

The most common models to evaluate evolutionary causes of group size variation involve comparisons of species that have differing population densities and distributions (Wrangham 1980; Janson 1988; Isbell 1991; Sterck et al. 1997; Snaith and Chapman 2007). If food resources are a critical determinant of group size, a useful approach would be to examine two species that share habitats and food resources, but have different group sizes. The red colobus and guereza (*Colobus guereza*, also known as the black and white colobus) of Kibale National Park, Uganda (hereafter Kibale) are two strongly folivorous species with high overlap in diet and home range, in addition to similarly low local predation pressures and equal body sizes (Delson et al. 2000; Chapman et al. 2002; Chapman et al. unpublished data). Interestingly, red colobus form large social groups (mean=68, range=12-150; Struhsaker 1975; Struhsaker and Oates 1975; Snaith and Chapman 2008), while guerezas form smaller groups (mean=8, range=3-11; Oates 1974; Oates 1977; Teelen 1994; Harris and Chapman 2007). The colobines of Kibale therefore provide an excellent system in which to explore the interactions between group size and the feeding ecology of folivorous primates.

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

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

To better understand how folivory influences smaller primate groups, Harris et al. (2010) studied the response of guerezas to a sharp reduction in food availability. During four months of progressive food scarcity, two guereza groups increased their foraging effort by increasing their daily path length, the number of patches visited per day, the percentage of time spent feeding, and their dietary diversity. These results indicate that small folivorous groups may also be food-limited and compete for food resources, which could point to patch depletion behavior in the long-term in response to low food availability. However, it remains unclear how guerezas use their food resources during a single visit to a feeding tree, i.e., on the same temporal scale as used by Snaith and Chapman (2005) for red colobus.

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

Methods

Study site and species

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

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

Procedure

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

To assess food limitation in guerezas, we examined feeding gain and effort. Because we were interested in changes in a group's feeding behavior over patch occupancy time, the patch served as the sampling unit rather than individual monkeys. This allowed us to select feeding individuals for observation opportunistically, with preference for adults. Since very few individuals fed simultaneously, the feeding group was easily monitored without bias for particular food types or locations in the tree. We used the number of bites and food items consumed in one minute (intake rate) as an index of feeding gain. Over three-minute intervals, we recorded the rate of movements to find food within a patch as a proxy for feeding effort (we measured movement frequency (number/3min) and the distance moved (m/3min) only for movements that were immediately followed by feeding). This closely follows Snaith and Chapman (2005) with the exception that they used a single measure of feeding effort: distance moved (m/3min). If a slowed intake rate were coupled with a constant or increasing feeding effort, this would provide evidence for patch depletion. However, a slowed intake rate paired with a reduced feeding effort may indicate food satiation.

Analysis

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

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

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

Results

In 2009, 28 patch occupancy periods were collected and another 38 were obtained in 2010, totaling more than 100 observation hours. Average patch group size was 2.86 individuals (range=0.5-7.8, SD=1.67) and average feeding patch group size was 1.42 individuals (range=0.1-5.8, SD=0.91), implying that only half of the individuals in a tree were feeding at any given time. Guereza groups fed on 15 tree species, of which *Celtis durandii* was the most common (36% of observation sessions). Young leaves were the most frequently consumed food part (78% of bites in 2009 and 65% in 2010).

Patch occupancy time (mean=64.32 min) was not affected by DBH (mean=50.02 in) or feeding patch group size (R^2=0.005, p=0.850, partial p=0.729 with feeding patch group size constant, partial p=0.636 with DBH constant, n=64 as one DBH and one occupancy time value were missing). We found no correlation between DBH and feeding patch group size (r=0.070, p=0.582, n=65). In addition, we found that guerezas fed in significantly smaller trees than did red colobus (p<0.0001, n=65 and 68 respectively).

Feeding gain did not change significantly over patch occupancy time (p=0.508, n=66). When separated by food type, intake rate of young leaves remained constant (p=0.181, n=66), but the number of mature leaves consumed per minute decreased (p=0.019, n=66). In terms of feeding effort, the distance moved to find food decreased over patch occupancy time for all food items combined (p=0.026, n=66). However, analyzed separately by dominant food type, this trend was significant only for young leaves (young leaves: p=0.014, n=55, mature leaves: p=0.973, n=9) (Fig. 2). Finally, the frequency of movements within a patch did not significantly change over patch occupancy time whether food items were separated (young leaves: p=0.211, n=55 mature leaves: p=0.521, n=9) or combined (p=0.182, n=66). We found no change when observation sessions were separated by time of day, year, or group.

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

Discussion

The folivore paradox is based on the assumption that all folivorous primates have low levels of food competition within their groups, allowing them to have large groups as an anti-predator or anti-infanticide strategy (Treves and Chapman 1996; Koenig and Borries 2002; Snaith and Chapman 2005). Our findings suggest that within-group competition for food among guerezas is lower than in red colobus, implying that they are not as food-limited. Thus, the assumption of low food competition among folivores may hold only for those that form small groups, as in guerezas, but may be invalid for species that form large groups, such as the red colobus.

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

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

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

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

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

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

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Table 1: A comparison of patch depletion results for guereza and red colobus monkeys of Kibale National Park, Uganda, with red colobus data from Snaith and Chapman (2005) ($*p<0.05$, $**p<0.01$, Δ= difference in).

	Guereza	**Red colobus**
Multiple Regressions		
Patch occupancy time		
Sample size	64	44
Mean patch occupancy time (minutes)	64.32	36
Mean DBH (inches)	50.02	81.08
Mean feeding patch group size (number of feeders)	1.42	3.63
Effect of DBH and feeding patch group size (R^2)	0.005	0.145*
Change in intake rate and distance moved		
Sample size	66	45
Effect of number of feeders on Δ intake rate (R^2)	NA	0.001
Effect of number of feeders on Δ distance moved (R^2)	0.009	0.004
Paired *t*-tests		
Feeding gain		
Sample size	66	68
Δ Bites/minute for all food items	-0.24	-2.38**
for young leaves	-1.06	-2.91**
for mature leaves	-0.28*	0.32
Feeding effort		
Sample size	66	45
Δ Movement rate (number/3min) for all food items	-0.11	NA
for young leaves	-0.15	NA
for mature leaves	-0.06	NA
Δ Distance moved (m/3min) for all food items	-0.36*	0.82**
for young leaves	-0.45*	1.14**
for mature leaves	-0.01	-0.10

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

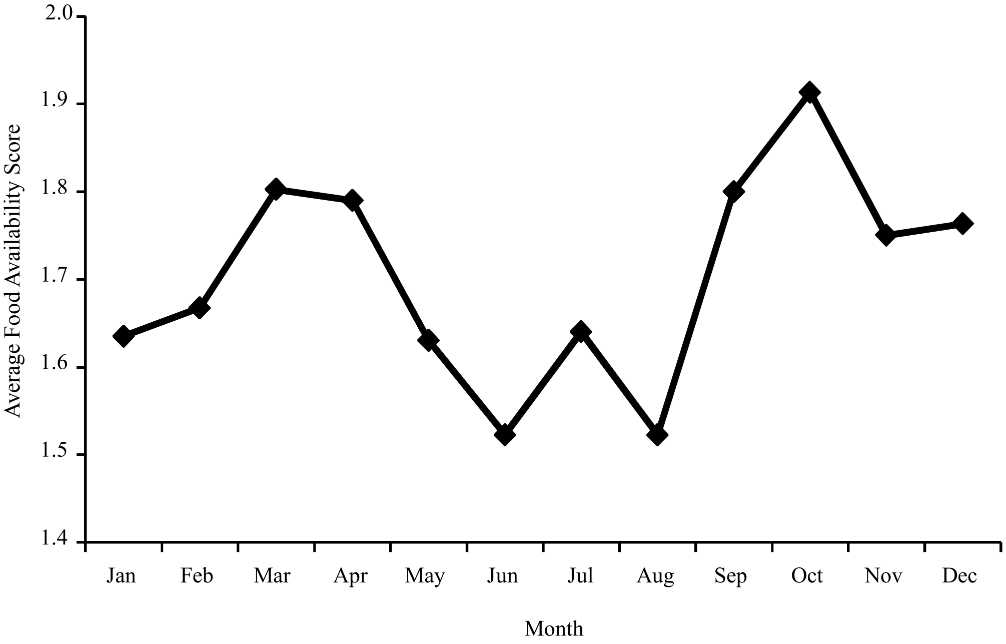
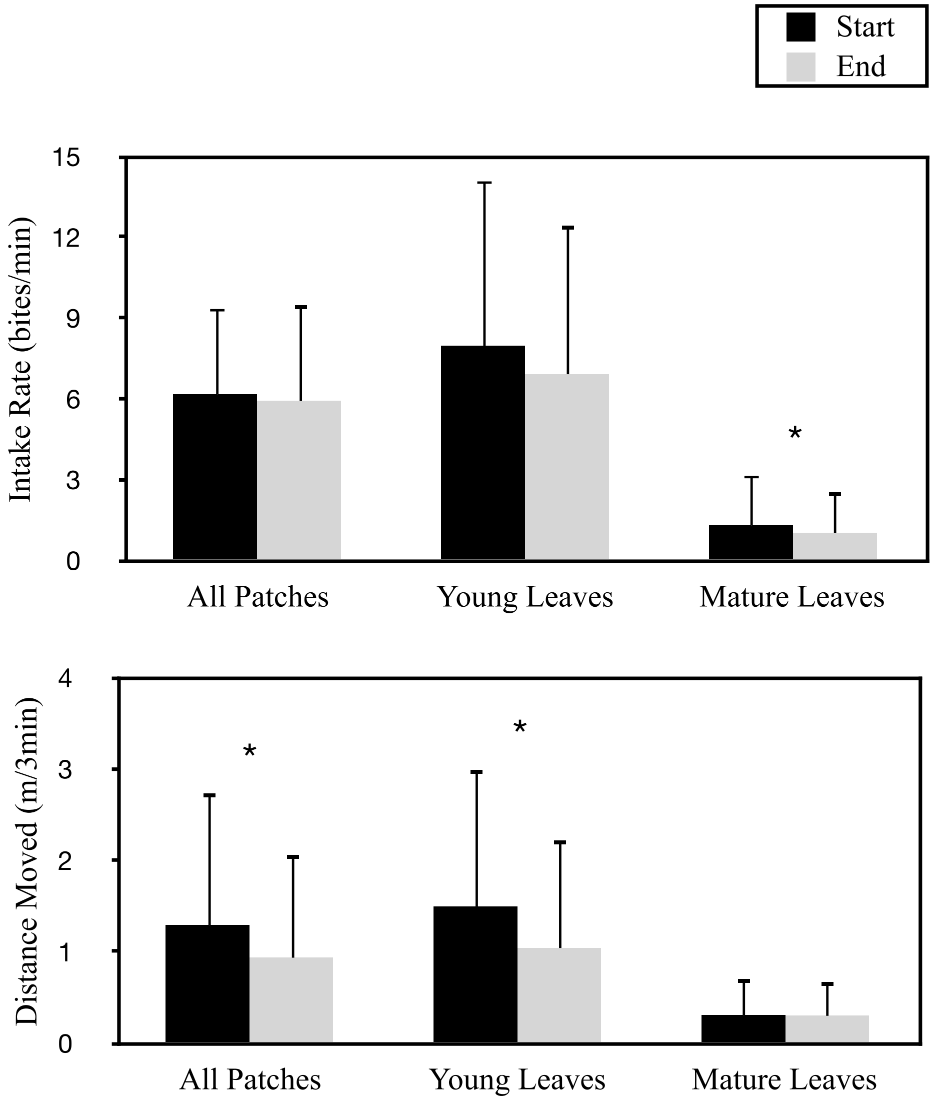


Fig. 2: Changes in the mean intake rate and mean distance moved in guerezas for all patches combined and for young leaves and mature leaves separately. The star indicates a statistically significant difference between the first and last quarters of an observation session.



Connecting statement

The findings in Chapter 1 suggest that the assumption of low food competition within groups of folivorous primates is applicable only to some species or populations, and that even species with high overlap in diet and habitat can differ widely in the level of food competition they experience within their groups. Black and white colobus (guerezas) were found not to deplete patches of food over the course of a single visit to a tree, suggesting that competition between group members is much less intense than for red colobus, which Snaith and Chapman (2005) found to deplete food patches. It is possible, however, that even though some folivores exhibit signs of food competition, it does not reach a level that would affect reproductive fitness. If so, food competition in folivorous primates would be less biologically meaningful than in primates that have more monopolisable resources.

In Chapter 2, I take a closer look at food competition in a red colobus group to determine whether it is strong enough to compel them to form dominance hierarchies among females. Dominance rank has been shown to affect reproductive fitness in females of other folivorous species (e.g. Robbins et al. 2007). If food competition is present but not biologically meaningful, the assumption of low food competition among folivorous primates may effectively be correct. On the other hand, if differential aggression between females causes a difference in individual reproductive fitness, this is a sign that socioecological models should be refined to allow for variety in food competition levels across folivorous primate species.

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Chapter 2: Conflicting evidence for dominance among female folivorous primates: Implications for socioecological models

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Abstract

Most studies investigating the social structure of folivorous (leaf-eating) primates, with a few notable exceptions, have found linear dominance hierarchies among females, a sign of food competition that contradicts the predictions of current socio-ecological models. We tested for linear dominance hierarchies in a group of Ugandan red colobus (*Procolobus rufomitratus*) in Kibale National Park, Uganda, to determine whether or not they fit into the predicted social structure. We collected focal and *ad libitum* data on agonistic and affiliative interactions between adult females over one year. All dominance hierarchies among female red colobus based on different measures of aggression, submission, and groom reception rates were extremely nonlinear and no correlations were found between aggressive and grooming behavior between pairs of females. However, female dominance rank surprisingly correlated with reproductive fitness despite the lack of linearity in the dominance hierarchy, suggesting that aggression rate can affect fitness regardless of the strength of the hierarchy. Evidence for linear and nonlinear hierarchies among other folivore species and a comparison of conflict rates among primates suggest a possible physiological basis for the division in social organization among folivorous primates.

Keywords

Procolobus rufomitratus, Red colobus, linear female dominance hierarchy, within-group competition, socio-ecological model

Introduction

Models to explain the social behavior of animals are continually evolving as new information becomes available. The social behavior of primates has received particular attention due to their intricate social systems and consequently a variety of primate socioecological models have been developed (Eisenberg et al. 1972, Alexander 1974, Wrangham 1980, Janson 1988, van Schaik 1989, Isbell 1991, Sterck et al. 1997, Snaith and Chapman 2007).

Diet and food distribution are considered important determinants of social structure. Leaf-eating (folivorous) primates have often been presumed to have weak food competition because of the apparent abundance and relatively even distribution of their food resources (van Schaik 1989, Sterck et al. 1997). Low food competition translates into predictions of weak or non-existent dominance hierarchies among females because female relationships are assumed to be more dependent on food competition than male relationships, which are shaped by mate competition in primates (Wrangham 1980, Isbell 1991, Sterck et al. 1997, Snaith and Chapman 2007). However, most folivorous species that have been assessed for the predicted lack of strong hierarchies among females have not fit into current models. Female linear dominance hierarchies, which are indicative of strong food competition, have been documented for mountain gorillas (*Gorilla beringei*, Robbins et al. 2005), Nilgiri langurs (*Trachypithecus johnii,* by Poirier 1969 as described in Hrdy 1977), Hanuman langurs (*Semnopithecus entellus*, Hrdy 1977, Koenig et al. 1998, Koenig 2000), grizzled leaf monkeys (*Presbytis comata*, Ruhiyat 1983), Phayre's leaf monkeys (*Trachypithecus phayrei*, Koenig et al. 2004), mantled howler monkeys (*Alouatta palliata*, Zucker and Clarke 1998), and black and white colobus monkeys (*Colobus polykomos*, Korstjens et al. 2002), all of which are folivorous species. This deviation from what models predict (specifically, the Isbell 1991 and Sterck et al. 1997 models) has been explained in various ways, including suggestions of contest over preferred leafy foods which may have a more clumped distribution within a forest than leaves in general (Koenig et al. 1998). However, a few folivorous species do exhibit the expected social structure, having no linear dominance hierarchy among females. Agonistic interactions between females were very rare in two howler monkey species (*Alouatta seniculus,* Pope 2000, and *Alouatta pigra*, van Belle et al. 2011), such that female hierarchies were not discernible. Western red colobus (*Procolobus badius*) in Taï National Park, Ivory Coast, also exhibited aggression among females very rarely, and they could not be placed into a hierarchy after a two-year study (Korstjens et al. 2002).

Females of another red colobus species, the Ugandan red colobus (*Procolobus rufomitratus*) in Kibale National Park, Uganda, have also been described as having egalitarian relationships (Struhsaker 1980). However, more recent studies have shown converging lines of evidence for food limitation in this species. Snaith and Chapman (2005, 2008) found that red colobus groups deplete trees of food as they move through their home range, and that larger group size corresponds to increased foraging effort and decreased female reproductive success. Furthermore, red colobus biomass is correlated to the protein-to-fiber ratio in their foods, suggesting that they are limited by food quality in addition to food abundance (Chapman and Chapman 2002; Wasserman and Chapman 2003). Kibale harbors a primate biomass that is among the highest ever recorded, including large numbers of folivorous primates (Chapman and Lambert 2000). Socioecological theory, preliminary observations on Ugandan red colobus female social structure, and close genetic relatedness to the western red colobus suggest that no hierarchies should form among red colobus in Kibale. Meanwhile, elevated levels of food competition due to high densities of folivorous monkeys in Kibale and recently documented evidence of food limitation in this species point to the existence of contest competition, in which case a female dominance hierarchy would be beneficial. Thus, this is an interesting context in which to look for female dominance hierarchies.

Methods

Study site and species

We studied a group of red colobus monkeys living in Kibale National Park, Uganda (795 km^2, 0°13’ to 0°41’N and 30°19’ to 30°32’E) for 12 months (June 2009 to June 2010). The area has two rainy seasons per year and receives an annual average of 1,707mm of rainfall (1990-2010) (CAC and L.J. Chapman, unpublished data). The group ranges within the Kanyawara region: a moist, evergreen, mid-altitude forest within Kibale (elevation=1,500m; Chapman and Lambert 2000).

Red colobus monkeys are mid-sized, arboreal and strongly folivorous primates. The study group "SC" consisted of between 78 and 94 individuals during the study (mean group size=85.8, n=10 group counts) with an average adult male-female ratio of 11 to 36 (15 to 42 if subadults are included). Births occur throughout the year, although birth peaks seem to coincide with peaks in rainfall (Struhsaker 1975; KJT and CAC unpublished data). Though both sexes immigrate and emigrate into groups, females are the principal dispersers (Struhsaker 2010; KJT and CAC unpublished data). SC has been studied for the past five years and all members are now well habituated to humans and are individually identifiable. Data on offspring births and deaths for the past five years are also available and were used here to estimate female reproductive fitness (calculated as number of surviving offspring born per year).

Procedure

The SC group was followed from 8:00am to 4:00pm for approximately 20 days each month. Focal observations were conducted on all 39 adult females that were part of the group during the year. Fifteen-minute focal observations were taken opportunistically with preference for females with fewer observations to balance the distribution of samples among females (mean number of focal minutes per female= 904.8, range= 155-1286). For each social interaction involving a focal individual, the time of day, identity and role of participants, social context, outcome, duration, and details of the interaction were recorded. In the event that the focal individual was lost from sight, the observation was suspended and completed once the individual was found again.

When agonistic interactions not involving a focal individual occurred within the group, focal observations were paused for the duration of the event and *ad libitum* notes on these interactions were recorded, including the identity and role of all participants. Detailed descriptions of these events were entered into a journal and were used to supplement the focal data (see below).

Statistical analyses

We created interaction matrices based on the frequency of aggressive behaviors given, submissive behaviors received and grooming episodes received, as well as the sum duration of grooming events received between all pairwise combinations of adult females. These data were not normally distributed and not normalizable through transformation due to the large number of zeros in each matrix. The matrices were thus tested for associations with each other using the nonparametric Spearman's rank correlation test. To increase our confidence in the results, for each correlated matrix pair, the matrices were reduced in two ways: first by excluding individuals that were not involved in the kind of interaction in question with another adult female in both matrices and then by doing so for females without interactions in either matrix. The correlation tests were rerun on the reduced matrices to determine whether the large number of zeros in the matrices changed the results. In addition, the distribution of focal observation hours among females was not even due to changes in female demography (emigration, immigration, death or disappearance, and maturation into adulthood), which caused some females to be observed during only part of the study. We ran regression analyses to determine whether there was an effect of the number of focal hours for individual females on each of the factors used to make the matrices. For each factor that was affected, the female with the fewest focal hours was excluded from the matrix and the regression was rerun to test for an effect. This was performed repeatedly for each factor until no effect was found. The matrices were then reduced prior to being correlated by excluding females according to the matrix with fewest females within each matrix pair; in this way the analyses were corrected for the effect of number of focal hours.

Females were ranked into a dominance hierarchy by the Zumpe and Michael (1986) method, which uses the mean percent of aggressive behaviors given and submissive behaviors received of all agonistic interactions per pair to calculate rank for each individual:

$$D_x = \frac{\sum_{i \neq x} \left(A_{xi} + S_{xi} \right)}{N}$$

where D_x is the dominance status of individual *x,* A_{xi} is the percent of aggressive behaviors given by *x* to another hierarchy member *i* of the total aggressive interactions between the *x-i* pair, S_{xi} is the percent of submissive behaviors received by *x* from that same hierarchy member *i* of the total submissive interactions between the *x-i* pair, and N is the number of members in the hierarchy. We chose this method over other, more commonly employed calculations because it is more robust in situations where there are many group members and agonistic and submissive interactions are infrequent, such as is the case among large groups of female red colobus (Bayly et al. 2006, this study). Alternative hierarchies were then computed by simply ordering females by total frequency of aggression given, the sum of percent aggression given within pairs, total frequency of submissive behaviors received, total frequency of grooming bouts received, or total time spent being groomed.

Each hierarchy was assessed for its linearity and strength. Linearity pertains to the transitivity of dominance relationships in a group (i.e., the frequency of rank reversals; van Schaik 1989). The significance of linearity is calculated based on the observed number of circular triads (where A dominates B and B dominates C, but C dominates A) compared to that expected under a hierarchy of random dominance relationships (de Vries et al. 1993). Landau's modified linearity index *h'* is a descriptive measure of the degree of linearity in a hierarchy that corrects for unknown and tied relationships, and varies from 0 (no hierarchy) to 1 (a completely linear hierarchy) (de Vries 1995, Bergstrom and Fedigan 2010). It is defined as:

$$h' = \left[\left(\frac{12}{N^3 - N} \right) \sum_{x=1}^{N} \left(\frac{V_x - (N-1)}{2} \right) \right]^2 + \frac{6u}{N^3 - N}$$

where N is the number of individuals in the hierarchy, V_x is the number of individuals dominated by individual *x* plus half of the number of individuals with a tied relationship to *x*, and *u* is the number of unknown relationships in the hierarchy (de Vries 1995). The Directional Consistency Index (DCI), a commonly used indicator of hierarchical strength, is calculated as the total number of times the outcome of an interaction was the same as the most prevalent outcome within each pair, minus the total number of times the outcome was the opposite within each pair, divided by the total number of interactions among all individuals (de Vries et al. 1993, Pelletier and Festa-Bianchet 2006).

We used the program MatMan (version 1.1, de Vries et al. 1993; de Vries 1995) to calculate the statistical significance of the linearity, the Landau's modified linearity index *h'*, and the DCI of each hierarchy. Significant linearity, a high linearity index and a high directional consistency index are considered characteristics of a strong, well-established hierarchy (Bergstrom and Fedigan 2010).

After running Kolmogorov-Smirnov tests to demonstrate normality, a Pearson's correlation was run between dominance rank and reproductive rate to determine whether rank could explain variance in the reproductive fitness of individual females. Reproductive rate was calculated using the number of surviving offspring recorded over the past five years for a female (CAC unpublished data), divided by the number of years since the first recorded birth from that female.

Results

Thirty-nine adult females were incorporated into the analysis and between 32 and 34 were included for the matrix correlations using reduced matrices to correct for the number of focal hours on individual females as needed for each correlation. A total of 588 focal observation hours were performed on these females over the year. Fifteen aggressive events between adult females (chases, fights, and displacements) were observed in these focal samples. This translates into approximately 0.026 agonistic events observed in total between any adult females in the group per hour or one event every 4.8 observation days. The average number of adult females in the group over the year was 35.7, meaning that approximately 0.0007 agonistic events per female, per hour were observed. An additional 92 aggressive events were observed during *ad libitum* data collection, bringing the total number of agonistic interactions included in the analyses to 107. Submissive behaviors were less common; they were observed only once during focal observation and only three more were added to the matrices from the *ad libitum* data. Grooming was much more common and was observed between adult females 566 times (focal and *ad libitum* data combined); a total of 17.3 hours of grooming were recorded (including focal data only since groom duration was not recorded during *ad libitum* data collection).

None of the matrix correlation tests performed produced significant correlations (range of Spearman's rho= 0.010-0.046, *N*= 32-34, *p (two-tailed)* = 0.108-0.718). These results did not change in significance for any of the reduced matrices where females without interactions were excluded (range of Spearman's rho= 0.010-0.095, *N*= 5-34, *p (two-tailed)* = 0.108-0.731).

Each hierarchy created (based on dominance, aggression frequency, percent aggression, submission reception frequency, grooming reception frequency and time groomed) was nonlinear (range of *p*= 0.46-0.57 for linearity). Based on Bergstrom and Fedigan's (2010) categorization of Landau's modified *h'* values, where an *h'* of 0-0.5 represents a weak hierarchy, 0.5-0.8 a moderate hierarchy, and 0.8-1.0 a strong hierarchy, all of our *h'* values indicated extremely weak hierarchies (range of *h'*=0.071-0.078). However, directional consistency was high for all hierarchies (range of DCI= 0.81-1.0), except those based on grooming, where directional consistency was moderate (grooming frequency DCI= 0.55, grooming duration DCI= 0.62). The results for directional consistency seem to indicate an established hierarchy, but are more likely due to the rarity of agonistic interactions: avenging an aggressive act was unlikely simply because agonism was infrequent in general. Grooming bouts were often reciprocated between pairs, but not evenly in terms of groom duration, explaining the levels of directional consistency for hierarchies based on these events.

Surprisingly, although the dominance hierarchy created by the Zumpe and Michael method was very nonlinear, dominance rank calculated by the same method significantly explained 11% of the variance in a female's reproductive success (Pearson's *r*=0.333, *p*=0.041).

Discussion

Our findings regarding hierarchical linearity, in combination with those of Korstjens et al. (2002), Pope (2000), and van Belle et al. (2011), suggest that the predictions of leading socioecological models regarding the lack of contest competition in folivorous primates do hold for some species. This leads to an interesting question: what makes the social structure of these species different from that of other folivorous primates?

One characteristic of red colobus that may be of significance is an extra chamber in their foreguts called the presaccus. The presaccus is thought to play a role in preliminary digestion and storage of food, which may enhance digestive efficiency (Chivers 1994; Stevens and Hume 1995; Caton 1998; NRC 2003; Wright et al. 2008). Folivores possessing a presaccus (the *Procolobus, Rhinopithecus, Nasalis,* and *Pygathrix* genera; NRC 2003) may be able to ingest and store more food at once than folivores without a presaccus, an idea that has already been suggested for *Nasalis* and *Trachypithecus* species (Yeager 1993, Wright et al. 2008). The presaccus may mitigate within-group food competition in a similar way that storing food in cheek pouches does among *Cercopithecus* monkeys (Lambert 2005). This leads us to predict that primates possessing a presaccus will, in general, have lower food competition pressure and will be less likely to exhibit dominance hierarchies between females than primates without a presaccus. The presaccus is absent in the *Colobus, Presbytis, Trachypithecus,* and *Semnopithecus* genera (NRC 2003), all of which are folivores that have been found to have linear female dominance hierarchies (see Introduction). The few species possessing a presaccus that have been tested for such hierarchies have exhibited none (*Procolobus badius,* Korstjens et al. 2002; *Rhinopithecus roxellana,* Li et al. 2006; *Procolobus rufomitratus*, this study), and furthermore, the golden snub-nosed monkey (*R. roxellana*) population that was tested fed on high-quality and clumped foods where hierarchies would be expected (Li et al. 2006). In addition, primates that possess a presaccus appear to have lower female-female aggression rates compared to primates without a presaccus (Fig. 1). This trend may hold to a somewhat lesser extent for folivorous primates as compared to non-folivorous primates (Fig. 1). Verifying our prediction will require a broader comparative data set and it would be particularly useful to see whether more species with a presaccus lack female dominance hierarchies.

Previous studies on Kibale red colobus have provided several lines of evidence for food limitation within their groups. For example, larger groups were found to have larger home ranges, longer daily travel distances, higher group spread, and lower reproductive success per female (Snaith and Chapman 2008). Red colobus groups were also found to deplete the food patches they use, increasing their feeding effort despite a decreasing rate of food gain over their visit to a feeding tree (Snaith and Chapman 2005). In addition, our study found that despite the lack of linearity in a female hierarchy created based on the Zumpe and Michael (1986) dominance index, a female's reproductive fitness was a function of her dominance rank. Assuming that between-female aggression arises from conflicts over food resources, as is predicted by Wrangham's (1980) original ecological model, this indicates that food competition among red colobus is high enough to cause an effect on female fitness, but paradoxically is not high enough to induce the establishment of a female dominance hierarchy that is detectable over a year-long study. It is possible that a hierarchy does exist among females, but is so subtle that it was not detected over the year. A full year of data on the ursine colobus (*Colobus vellerosus*) in the Boabeng-Fiema Monkey Sanctuary, Ghana, did not produce linear female dominance hierarchies, but a linear hierarchy was detectable in one group after four years and in another group after six years (Julie A. Teichroeb and Pascale Sicotte, unpublished data). Since the latency to detect a dominance hierarchy is also considered a measure of its strength, it is evident that even if Kibale red colobus have a subtle female hierarchy that we were unable to detect, it would be considered very weak (Bergstrom and Fedigan 2010). The relation we found between dominance rank and reproductive fitness suggests that dominance rank is still biologically meaningful.

To date, most studies investigating the applicability of primate socio-ecological models to folivorous primates have found that, counter to their predictions, linear female dominance hierarchies are exhibited. This study reveals that the Ugandan red colobus is among a small group of folivores that are exceptions to this in the strict sense that they do not form a linear female dominance hierarchy. We present the possibility that primates possessing a presaccus may have lower food competition pressure, allowing them to avoid the need for linear female hierarchies, which may explain some of the discrepancy between theory and empirical data. However, if Wrangham's (1980) fundamental theory that female dominance in primate groups is based on food competition is correct, the relationship between dominance rank and fitness we found in red colobus agrees with a number of previous studies that indicate that folivores do experience feeding competition. This suggests that hierarchical nonlinearity does not mean that dominance is not important or that biologically meaningful contest competition is not present. Primates seem not to fit into exact categories imposed by currently leading socioecological models, such as those based on diet, and placing them onto continua where food competition and other ecological pressures affect their behavioral tendencies to different extents may more accurately model their behavior.

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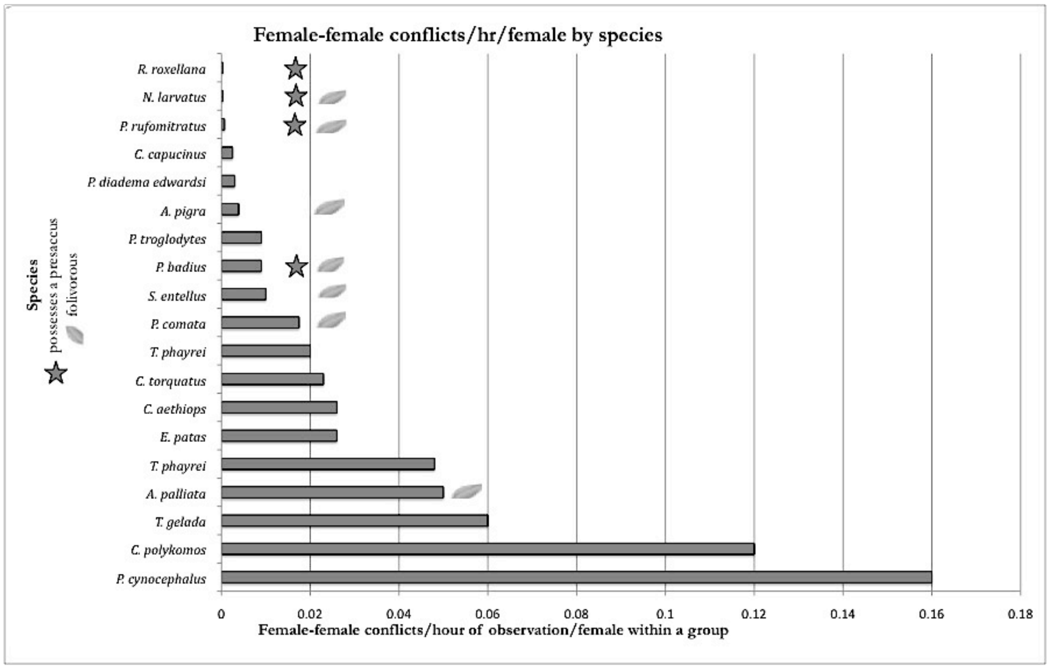
Figures

Figure 1. Number of conflicts between adult females per hour of observation, where this has been measured in wild primate populations, corrected for the number of females within groups. Species with various diets were included to give a more general idea of relative conflict rates among primates- primates with diets consisting of at least 50% leaves were considered folivorous (indicated by a leaf symbol). Data for *R. roxellana* are included despite the provision of food to this population because their very low conflict rate indicates that it is not considerably inflated by this provision of food. Folivorous primates and especially primates with a presaccus generally appear to have low rates of conflict between females compared to other primates.



References for conflict rates: *Rhinopithecus roxellana*: Zhang et al. 2010; *Nasalis larvatus*: Yeager 1990; *Procolobus rufomitratus*: this study; *Cebus capucinus*: Manson et al. 1999; *Propithecus diadema edwardsi*: Pochron et al. 2003; *Alouatta pigra*: van Belle et al. 2011; *Pan troglodytes*: Wittig and Boesch 2003; *Procolobus badius*: Korstjens et al. 2002; *Semnopithecus entellus*: Koenig 2000; *Presbytis comata*: Ruhiyat 1983; *Trachypithecus phayrei*: Koenig et al. 2004 (two groups with different aggression rates); *Cercocebus torquatus*: Range and Noë 2002; *Cercopithecus aethiops*: Pruetz and Isbell 2000; *Erythrocebus patas*: Pruetz and Isbell 2000; *Alouatta palliata*: Zucker and Clarke 1998; *Theropithecus gelada*: Dunbar 1980; *Colobus polykomos*: Korstjens et al. 2002; *Papio cynocephalus*: Seyfarth 1976. The source used for percentage of leaves in the diet was Campbell et al. 2011, except for *R. roxellana, S. entellus* and *T. phayrei* (Guo et al. 2007, NRC 2003 and Koenig et al. 2004 were used, respectively).

General conclusions

The results of this thesis have shown that the validity of the assumption of low food competition among folivorous primates commonly integrated into leading socioecological models may be more species-specific than conventionally assumed. As is indicated in Chapter 1, the level of food competition within groups of folivores varies considerably between species. This may be due to physiological differences that can affect digestive efficiency and feeding rate and/or differences in social behaviour that change the feeding needs of groups of folivores. Chapter 2 demonstrates that even in species that fit the models in terms of lacking strong female dominance hierarchies, reproductive fitness may still be affected by an individual's dominance rank (as measured by aggression level in females). This creates a disparity in reproductive rate within the group. Thus, even under conditions of low food competition, submissive individuals may still suffer fitness consequences, rendering the implications of low food competition for folivorous primates questionable. This suggests a need to refine leading primate socioecological models to allow for more variety in ecological function and social structure among folivorous primate species, and cautions against generalizing the behaviour of animals based solely on their membership to broad categories, such as those based on diet.