

## 17 Socioecology of African Colobines

Julie A. Teichroeb

### Introduction

Primatologists have used socioecological models for almost four decades to try to explain the wide variability displayed in primate social organization and structure. These models differ in specific predictions but generally agree that differences in the quality and distribution of fitness-limiting resources greatly influence group size, dispersal patterns and social relationships. Though not without controversy and exceptions (Clutton-Brock and Janson 2012; Koenig 2002; Thierry 2008), many of the predictions of socioecological models are upheld for species in the Order Primates (Koenig and Borries 2009).

According to socioecological models (e.g. Table 17.1), for females, who are limited in their reproductive output by food resources (Trivers 1972), the quality and distribution of food is thought to determine the competitive regime both within and between groups and to result in specific female social relationships (Isbell 1991, 2004; Isbell and Pruettz 1998; Isbell and van Vuren 1996; Isbell et al. 1998; van Schaik 1989; Sterck et al. 1997; Wrangham 1980). Food resources that are clumped and worth defending (i.e. high quality) will cause direct and aggressive contest competition (Nicholson 1954), both within and between groups. Within-group contest (WGC) competition will lead to the formation of female dominance hierarchies to decrease the amount of aggression experienced (Maynard Smith and Price 1973) and to female coalition formation. Kin are typically the most reliable allies so WGC leads to female philopatry and despotic, nepotistic dominance hierarchies (van Schaik 1989; Wrangham 1980). Females also benefit by remaining with kin in between-group contest (BGC) competition although the ability to win in inter-group encounters may depend on support from subordinates, which can relax female hierarchies (van Schaik 1989; Sterck et al. 1997). Larger group sizes are also beneficial in winning in BGC (Cheney 1987; Crofoot and Wrangham 2010).

When food resources are lower-quality and distributed more evenly, they are not defensible or worth defending, so little contest competition occurs and kin are not selected to form strong bonds (van Hooff and van Schaik 1994; Sterck et al. 1997; Wrangham 1980). In these situations, within-group scramble (WGS) competition for food may be predominant, leading to a group size effect on feeding efficiency (Chapman et al. 1995; Nicholson 1954) and more food searching for groups of larger

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**Table 17.1.** Summary of the basic predictions of the socioecological model presented by van Schaik (1989) and Sterck et al. (1997)

Food quality/distribution	Population density <sup>a</sup>	Competitive regime	Social outcomes for females	
			Dispersal	Dominance
a. Low quality, highly dispersed or large patches	Low	WGS	Yes	Egalitarian and individualistic
b. High quality, large patches (> group size)	High	WGS, BGC	No	Egalitarian and individualistic
OR				
High quality, scattered patches (> group size)	Low			
c. High quality, small patches (< group size)	Low	WGC	No	Nepotistic and despotic
d. Likely high quality, clumped	High (potentially)	WGC, BGC	No	Nepotistic but tolerant

<sup>a</sup> Relative to carrying capacity.

size in similar home ranges (Chapman and Chapman 2000c), which can ultimately limit group size (Koenig 2002). Since female dispersal is often common in species primarily affected by scramble competition (Table 17.1), females may choose to leave their current group for one with fewer individuals or choose a group based on some other important factor like the risk of predation, the quality of males, or the risk of infanticide (Crockett and Janson 2000; Isbell and van Vuren 1996; Sicotte et al. 2017; Steenbeek and van Schaik 2001; Sterck et al. 2005; Teichroeb et al. 2009a).

Folivore group sizes are often much smaller than one would predict on the basis of the food competition that their diets generate, a phenomenon termed the ‘folivore paradox’ (Janson and Goldsmith 1995; Steenbeek and van Schaik 2001). If folivores are affected by only WGS or no competition at all, they are expected to form large groups. However, many species form very small groups that appear to be far below the threshold where WGS would be experienced. Male reproductive strategies, in particular infanticide by males, may provide an explanation for the folivore paradox (Crockett and Janson 2000), and I will discuss the details of how male and female reproductive strategies interact later in this chapter.

Male reproductive success is predominantly limited by the number of fertilizations they can acquire (Trivers 1972), thus female distribution on the landscape and their patterns of temporal availability are thought to determine male strategies to access and monopolize females (Altmann 1990; Clutton-Brock 1989; Emlen and Oring 1977). The number of males in primate groups is generally determined by the number of females (Altmann 1990; Mitani et al. 1996; Ridley 1986) and when females mate more synchronously, there are usually relatively more males in the group (Nunn 1999). Female driven social evolution in primates is supported by phylogenetic

analyses showing that changes in male group size evolutionarily lag behind changes in female group size (Lindenfors et al. 2004). Since females typically distribute themselves according to the available food resources and males defend groups of females (Koenig et al. 2013), this suggests that the mating system that is most prevalent for primate species is female defence polygyny (Emlen and Oring 1977).

In this chapter, I will review what is currently known about the socioecology of colobus monkeys. There are still biases in the data available on primate behaviour towards species that are easy to observe or more closely related to humans (Ramsay and Teichroeb 2019). This means that largely arboreal colobus monkeys that are hard to observe and difficult to identify individually have been neglected to some extent. Nevertheless, data have accumulated for some species showing interesting trends in the socioecology of colobus monkeys.

For the black-and-white colobus, good behavioural data are still lacking for *Colobus satanas* and most *C. angolensis* subspecies, while other species have been studied more intensively (*C. guereza*, *C. vellerosus*, *C. polykomos*) and data are accumulating for Rwenzori Angolan colobus (*C. a. ruwenzorii*). The black-and-white colobus are an excellent group to test predictions of socioecological models because they show the most varied diets of the colobus monkeys (Fashing 2011; Chapter 10) and thus food distribution and social responses should be different as well. Olive colobus (*Procolobus verus*) have been the subject of two longer-duration studies (Korstjens 2001; Oates 1988a) that examined their feeding and associated behaviour, though food competition has not been specifically addressed. Many red colobus species have not been studied in detail due partly to their distribution in areas that have not been politically stable for long periods (taxonomy following Chapter 2). Other issues with collecting detailed behavioural data are the fact that large, arboreal red colobus groups make individual identification very challenging. Some behavioural data are discussed below for *Ptilinopus badius* (Upper Guinea red colobus, located from Côte d'Ivoire to Sierra Leone), *P. rufomitratu* (Tana River red colobus), *P. temminckii* (Temminck's red colobus) and *P. tephrosceles* (ashy red colobus). Unfortunately, little to no detailed behavioural data are available for *P. bouvieri* (Bouvier's red colobus), *P. epieni* (Niger Delta red colobus), *P. foai* (Foa's red colobus), *P. gordonorum* (Udzungwa red colobus), *P. kirkii* (Zanzibar red colobus), *P. langi* (Lang's red colobus), *P. oustaleti* (Oustalet's red colobus), *P. parmentieri* (Lomami red colobus), *P. pennantii* (Pennant's red colobus), *P. preussi* (Preuss's red colobus), *P. semlikiensis* (Semliki red colobus), *P. tholloni* (Tshuapa red colobus) or *P. waldroneae* (Miss Waldron's red colobus), which is likely extinct (McGraw 2005).

## Diets and Food Distribution

Colobus monkeys are foregut fermenters (Chapter 6) and were originally assumed to eat a large proportion of mature leaves and this, along with inaccurate assessments of scramble competition (see below), led to the supposition that they experience little to no food competition (Isbell 1991; Yeager and Kirkpatrick 1998). However, with greater research effort on different African colobine populations, the dietary

flexibility and selective feeding of this group has become obvious. Most African colobines actually eat a diet low in mature foliage and prefer instead young leaves, fruit and/or seeds (reviewed in: Fashing 2011; Chapter 10). For instance, the annual diet of black colobus monkeys (*C. satanas*) contains relatively large amounts of seeds. The lowest proportion of seeds reported in their annual diets was 41% from the Forêt des Abeilles in Gabon (Fleury and Gautier-Hion 1999) and the highest proportion was 60% in Lopé, Gabon (Harrison 1986; Oates 1994). Fruit can also make up a large portion of colobus monkey diets (Arseneau-Robar et al. 2021; Fashing 2001b). These types of foods tend to be distributed in clumps (van Schaik 1989; Strier et al. 1997) and are easy to digest, being low in fibre, and high in sugar in the case of fruit, and high in protein in the case of seeds (Dasilva 1994; Milton 1999; Waterman 1984). When foliage does make up a large proportion of colobus monkey diets, the focus tends to be on easier to digest young leaves. Red colobus provide a powerful example of this. All but one red colobus populations studied have a diet higher in young leaves than mature leaves (20 populations, reviewed in: Fashing 2011), with the exception of ashy red colobus at Gombe National Park, Tanzania where mature foliage was reported to be 44% of the diet (Clutton-Brock 1975a).

In addition, the flexibility of colobus monkey diets is remarkable. It is not uncommon for the same species to have different food preferences at different field sites. For instance, guerezas at Kakamega in Kenya are mostly frugivorous for half the year (Fashing 2001b), while at Kibale National Park in Uganda, they are consistently folivorous (Harris and Chapman 2007a). Similarly, the Rwenzori subspecies of Angolan colobus (*C. a. ruwenzorii*) have the highest mature leaf consumption (40% of the diet) of all the black-and-white colobus monkeys at the high altitude Nyungwe site in Rwanda (Fimbel et al. 2001) and they also feed on lichen, which can make up more than 50% of the diet some months (Miller et al. 2020a; Vedder and Fashing 2002), while in the mid-altitude forest at Lake Nabugabo, Uganda this subspecies feeds primarily on young leaves (65%) and fruit (31%) (Adams and Teichroeb 2020; Arseneau-Robar et al. 2021). Even within small geographical areas, research has shown that different colobus groups can have quite varied diets depending on their home range and the food species available (e.g. Ashy red colobus in and around Kibale National Park, Chapman and Chapman 1999; *C. a. palliatus* at Diani Beach, Dunham 2017a; guerezas at Kibale, Harris and Chapman 2007a).

Large seasonal variation has also been reported in most African colobine diets. Typically, when the preferred food sources of young leaves, fruit or seeds are not available, mature leaves are eaten more often (e.g., McKey et al. 1981; Oates 1977a; Saj and Sicotte 2007a; Struhsaker 1975). Lianas provide an important staple source of leaves for many colobus, and are often relied on heavily in seasons when other foods are rare (e.g. Dasilva 1992; Preece 2006). In terms of seasonal variation in the diet, the olive colobus stands out as an exception as this species manages to maintain a fairly high-quality diet year-round, which may be due to lower tolerance for mature leaves (Oates 1988a; Chapter 11).

This research demonstrates that, even though colobus monkeys are physiologically equipped to feed on mature leaves, they may only do so when other preferred foods

are not available. The diets of most colobus species contain a large percentage of young leaves, fruit or seeds and because these higher-quality foods tend to be more patchily distributed, this may result in food competition among females. Foregut fermentation also limits the amount of acidic, juicy, ripe fruit that colobines can digest, which may explain why, when fruit is fed upon, it is often unripe or leathery (Davies et al. 1999; Kay and Davies 2004). This point could have a large impact on the degree of competition that female colobus actually experience when feeding on fruit (see Chapter 16 for potential social consequences of this type of fruit-eating). It is also important to note that gross categories, like the amount of leaves or fruit in the diet, may not be very good predictors of the level of female agonism that will be seen. In a review of rates of female agonism in the primates, Wheeler and colleagues (2013) found that the proportion of leaves in the diet did not predict low rates of agonism, and indeed folivores and frugivores showed similar aggression rates among females. However, it is important to note that these comparisons did not control for the quality of the home range. Below, evidence for food competition in African colobines is detailed.

## Food Competition

### Within-Group Scramble Effects on Foraging Effort

A major reason why colobines were thought to be exempt from food competition for so long was inaccurate assessments of the occurrence of WGS. With this type of competition, group size affects food intake because a larger number of individuals deplete patches more quickly and search fields overlap (Chapman and Chapman 2000c; Janson and Goldsmith 1995). Thus, initially researchers compared colobine groups of different size, often in neighbouring home ranges, to see if larger groups ranged further as a test of WGS competition (reviewed in: Snaith and Chapman 2007). However, these comparisons were erroneous without controlling for the quality of the home range. Larger groups may not need to range further than smaller groups if they occupy better quality habitat. This important link was brought to the attention of researchers with the Ecological Constraints Model (Chapman and Chapman 2000c; Wrangham et al. 1993). Another issue with measuring WGS correctly is that animals can use several behavioural modifications (or adjustments) to compensate beyond just ranging further to search for food (Borries et al. 2008; Teichroeb and Sicotte 2009; Wrangham et al. 1993); they may also feed and move for longer durations, eat different foods, eat faster, move faster or undergo fission (reviewed in: Teichroeb and Sicotte 2018).

A better understanding of how to measure WGS has led to research confirming that several African colobine populations are affected by this type of food competition (ESM Table 17.2). The white-thighed colobus (aka ursine colobus or Geoffroy's pied colobus, *C. vellerosus*) are an excellent example. This species forms groups with an average of 15 individuals (Oates 1994; Wong and Sicotte 2006) and consumes a high proportion of foliage (74% of the annual diet, Saj and Sicotte 2007a).

Nonetheless, WGS has been confirmed for this species (Saj and Sicotte 2007b; Teichroeb and Sicotte 2009; Teichroeb et al. 2003). Data collected over an annual cycle on four groups of different size with similar home range quality, showed that larger groups ranged farther (larger home ranges, longer daily paths and larger group spread) and spent more time feeding per day (Teichroeb and Sicotte 2009). Later analyses confirmed that WGS competition was present for these groups in both the lean and abundant seasons, however behavioural compensation strategies occurred more often in the lean season for all groups, demonstrating that WGS intensifies seasonally (Teichroeb and Sicotte 2018). The costs of WGS competition in larger groups may explain why female white-thighed colobus tend to disperse from larger groups towards smaller groups (Teichroeb et al. 2009a), although infanticide pressure appears to be a more over-riding reason for this trend (see below).

Gillespie and Chapman (2001) also compared the behavioural manifestations of WGS in two differently sized ashy red colobus groups at Kibale NP, Uganda while controlling for food availability between the groups' ranges. They found that the larger group had longer day ranges, a larger home range and moved significantly faster than the smaller group, showing evidence of WGS. An extension of this work to nine groups, showed in addition increased group spread, reiterating the costs of being in a larger group (Snaith and Chapman 2008). Furthermore, ashy red colobus deplete their food patches. As patch occupancy increased, food intake rates decreased and movement rates within the patch increased, indicating more searching for food. Patch occupancy was also longer in larger groups (Snaith and Chapman 2005).

Even within the smallest groups of colobus monkeys there is evidence for the effects of WGS. Guerezas form groups with an average of nine individuals (range: 2–23,  $N = 13$  research sites) and their diets are typically quite folivorous (range: 53%–86% of the annual diet, reviewed in: Fashing 2011). Theoretically, within-group food competition in guerezas should be minimal since they usually reside in such small groups and can feed on foliage (Isbell 1991). This appears to be borne out by some data. For instance, at Kibale, where guerezas feed mostly on young leaves, no evidence of food depletion in a patch over time was found (Tombak et al. 2012). However, also at Kibale, other indicators have shown that guerezas can suffer from food depletion. During a four-month period, when the availability of their top two food sources decreased sharply, two guereza groups were found to increase their day range, visit more patches per day, have larger group spread while feeding, spend more time feeding, and have greater dietary diversity (Harris et al. 2010). Similarly, in the Kakamega Forest, Kenya, where guerezas have been reported to eat a high amount of fruit (Fashing 2001b), an indication of WGS competition for food was present in the largest study group, which had the longest daily path length (Fashing 2001a).

The Rwenzori subspecies of Angolan colobus (*C. a. ruwenzorii*) is a clear outlier in terms of group size and social organization in the colobus monkeys. Relatively cohesive groups of >300 individuals have been reported in the montane area of Nyungwe National Park, Rwanda (Fashing et al. 2007b; Fimbel et al. 2001) and more



recently, Miller and colleagues (2020c) counted over 500 animals moving together at the same site. At lower altitude sites, large groups also form but these appear to be more flexible in terms of group size, showing fissions and fusions daily to form subgroups of variable size (Oates 1974; Teichroeb et al. 2019). Research at both Nyungwe and the lower land site of Lake Nabugabo, Uganda has shown that *C. a. ruwenzorii* are forming a multilevel society, the first found in an African colobine (Miller et al. 2020c; Stead and Teichroeb 2019). There does appear to be a cost in terms of WGS to these large aggregations. In the montane forests of Nyungwe, these very large aggregations of colobus appear to be possible because the animals feed on a fairly high proportion of mature leaves (40% of the annual diet) and large amounts of lichens seasonally (Miller et al. 2020a). Mature leaves at Nyungwe have been found to be higher quality (higher in protein and lower in fibre) than is typical of mature leaves at other sites, and this, along with the wide availability of lichens, appears to allow the colobus to aggregate (Fimbel et al. 2001). Even given this, these large colobus societies have very large home ranges, which is indicative of WGS (Fashing et al. 2007b). Miller and colleagues (2020b) also found that *C. a. ruwenzorii* deplete food patches, particularly when feeding on young leaves, leading to intake rates decreasing and movement rates increasing over time in a patch. At the mid-altitude site at Lake Nabugabo, the diet of *C. a. ruwenzorii* has been found to be much different (high in fruit and young leaves, Arseneau-Robar et al. 2021), and the food competition caused by these more patchy resources may explain why there is frequent fission among core units and the maximum number of colobus that have been reported together is just over 200 individuals (Stead and Teichroeb 2019). Feeding on these patchy and higher-quality food resources may be limiting the size of aggregations possible for *C. a. ruwenzorii* in lower altitude areas (Arseneau-Robar et al. 2021). Indeed, analyses of the numbers of core units clustered together through time has shown that the greatest aggregations occur at Nabugabo in seasons with the greatest fruit availability (Adams et al. 2021).

### Fitness Costs of Within-Group Scramble

While indicators of WGS food competition have been found in every colobus species where this question has been assessed, it is still not entirely clear how severely this may influence female reproductive rates. Based on socioecological models, it would be expected that females in larger groups would suffer fitness effects of WGS competition and show decreased energy balance, longer inter-birth intervals or slower infant development (Borries et al. 2008; Koenig 2002; Koenig and Borries 2009). Dunbar (1987) compared reproductive rates in different-sized groups of guerezas in Ethiopia and found that larger, multi-male groups had lower reproductive rates. This result could have been due to WGS competition for food; however, Dunbar (1987) attributed it to the stress females were under due to living with several competing males. Negative physiological effects of limited food availability were found for guerezas in Kibale, in that lactating females had decreased energy balance

and two of three females suffered increased parasitism during the time when less food was available (Harris et al. 2010). In their comparison of nine groups of ashy red colobus at Kibale, Snaith and Chapman (2008) found fewer offspring per adult female in larger groups, which suggests that WGS may have had a cost in terms of slower reproductive rates in these groups. These studies are the only ones available that demonstrate fitness costs to WGS in the colobus monkeys. An additional study in white-thighed colobus that used natal coat colour transitions as a proxy for infant development found contrasting evidence. Bădescu and colleagues (2016) found that, even though WGS competition occurs in the population (Teichroeb and Sicotte 2009, 2018), group size did not affect infant development rates. When controlling for group size, it was rather infants that were at greater risk of infanticide (i.e. males, Teichroeb and Sicotte 2008a, and those in multi-male groups, Teichroeb et al. 2012) that transitioned out of their natal coats faster (Bădescu et al. 2016).

### Within-Group Contest and Female Dominance Hierarchies

The preferred diet of many colobus species often encompass clumped food sources that have the potential to cause WGC competition, yet the actual outcomes of aggressive interactions between females have been investigated relatively rarely (ESM Table 17.3). Among red colobus females, Struhsaker (1975) reports that weakly expressed dominance hierarchies are present in ashy red colobus at Kibale. Accordingly, aggression amongst females was rare and not often observed in feeding contexts, appearing to be primarily used by females to restrict access to their infants (Struhsaker and Leland 1979). At Abuko Nature Reserve in The Gambia, female Temminck's red colobus were also aggressive primarily over infant access but females in this population are reported to form linear dominance hierarchies (Starin 1991). Nonetheless, fitness benefits from high rank have not been documented for Temminck's red colobus females as age at first parturition, birth rate and number of surviving offspring were not found to correlate with rank (Starin 1991). Only Korstjens and colleagues (2002) report that aggression between females in a red colobus species (Upper Guinea red colobus at Taï) was primarily over food but they did not see sufficient interactions to calculate a dominance hierarchy among females.

Black-and-white colobus provide more data on the occurrence and effects of WGC competition in African colobines (ESM Table 17.3). For example, king or western black-and-white colobus (*C. polykomos*) form mid-sized groups (Tiwai, Sierra Leone, range 9–11 individuals, Dasilva 1989; Taï National Park, Côte d'Ivoire, range 14–19 individuals, Korstjens 2001), that eat a fairly high proportion of plant reproductive parts (35%–48% fruit and seed eating, Dasilva 1989; Korstjens et al. 2007a). Given this, one would expect WGC feeding competition in king colobus (Cheney 1987; van Schaik 1989; Wrangham 1980), which is indeed what has been found. Agonistic interactions among females were relatively common at Taï and these typically took place when the animals were foraging. The frequency of agonism was particularly



high when food items had a long handling time (i.e. *Pentaclethra marcophylla* seeds) because females could monopolize these resources and exclude other females (Korstjens et al. 2002). Due to this agonism, Korstjens, Sterck and Noë (2002) were able to construct an individualistic, linear female dominance hierarchy for their study group of king colobus, where four mother-daughter pairs did not occupy adjacent ranks. However, they did not detect an effect of dominance rank on female reproductive success.

In other black-and-white colobus, Harris (2005) reported low rates of agonism between female guerezas but nonetheless, these interactions were directionally consistent, suggesting that a dominance hierarchy among females was present. WGC competition for food also occurs in white-thighed colobus (Wikberg et al. 2013). Agonistic interactions between females primarily occur over food and even occasional foraging on contestable food was sufficient for females to form individualistic dominance relationships that were intermediate in strength (Wikberg et al. 2013). The seasonally available seeds of *Parkia bicolor* and palm nuts of *Borassus aethiopum*, especially caused dominance interactions among females. Wikberg and colleagues (2013) examined female hierarchies in eight groups and these varied in how linear the hierarchy was and the amount of observation required to detect it. Young females began to challenge older females as they matured, so hierarchies were generally predicted by age, while kinship between females was not a factor despite some female philopatry (Wikberg et al. 2013). Although kin did not rank near one another in the female hierarchy in white-thighed colobus, some nepotism was seen in coalition formation. In two groups where females had access to kin as coalition partners, relatedness significantly predicted coalitionary support in one of them and appeared to influence support in the other even though these related females did not necessarily rank closely. This kin support was primarily used to direct aggression at males but also at extra-group females (Wikberg et al. 2014).

These studies show that when individuals are recognized and female relationships are studied in colobus monkeys, linear dominance hierarchies may exist, even when only a small portion of the diet is contestable. In addition, even if kin do not rank closely in these hierarchies, which may be individualistic and age-inversed, related females may still provide coalitionary support to one another. The level of WGC competition experienced by colobus monkeys may be set by only a few, monopolizable food items that may be seasonally available. This means that female dominance hierarchies only become important at certain times of the year. Thus, a female colobus monkey's need for coalitionary partners to defend food resources is relatively minimal, leading to lower levels of female bonding than is seen in a typical matrilineal cercopithecine, and allowing female dispersal to take place. More detailed research on a greater number of species is needed to determine if this is a ubiquitous pattern in the African colobines. In addition, there are little data available to examine whether the female dominance hierarchies that exist in colobus monkeys lead to rank-effects on female energy intake or reproductive rates (but see Korstjens et al. 2002), which are important for fully testing socioecological models (Koenig and Borries 2009).

### Between-Group Contest

There is good evidence of the effect of BGC feeding competition in a few colobus monkey species (e.g. Fashing 2001; Harris 2005; Korstjens et al. 2005; Miller et al. 2020b; Teichroeb and Sicotte 2018) but participation in encounters varies from high female involvement to almost entirely male involvement. For instance, research at Tai on king colobus found that though males participated in all encounters, the same foods that elicited WGC were important determinants of the level of female involvement in BGC competition. Korstjens (2001) observed total home range overlap (100%) for her study groups at Tai and found that females were involved in 77% ( $N = 52$ ) of between-group conflicts, a high percentage compared to 43.5% ( $N = 62$ ) for female white-thighed colobus (Teichroeb and Sicotte 2018) and 15.2% ( $N = 122$ ) for female guerezas (Fashing 2001c). Korstjens and colleagues (2005) found that females were aggressive in more encounters that occurred in quadrats where a lot of feeding occurred that month (71%) compared to those where food was not at stake (47%) and that their aggressiveness during encounters was seasonal. Females were most intensely aggressive in the two months where fruits of *P. macrophylla*, an important food source with long handling times (Korstjens et al. 2002), were just becoming abundant.

At Kibale, resource quality within guereza home ranges was heterogeneous and groups aggressively defended the core area of their home range, which contained the best resources. Between-group encounters were frequent, leading to a dominance hierarchy between groups, where the highest-ranking groups had higher resource quantity and quality in their core areas (Harris 2006a). Male guerezas in Kibale were more likely to initiate high-level aggression against other groups in areas with valuable food resources (Harris 2010). Smaller groups with a single male of large body size were more likely to win in between-group conflict than larger, multi-male groups (Harris 2010), suggesting that collective action problems were an issue in multi-male groups (Nunn 2000; Willems et al. 2013). Indeed, research at both Kakamega and Kibale has shown that males are the primary participants in between-group conflict in guerezas and that they appear to be defending resources for females (Fashing 2001c; Harris 2005, 2010). Male resource defence may occur indirectly when males drive away reproductive competitors in other groups (i.e. the hired gun strategy, Rubenstein 1986; Wrangham and Rubenstein 1986), however at Kakamega and Kibale, male resource defence appears to be direct (Fashing 2001c; Harris 2005, 2006a, 2010).

The evidence for defence of resources by males in guerezas was the first in the non-human primates and was followed by evidence from chimpanzees (Williams et al. 2004), suggesting that resource defence polygyny (Emlen and Oring 1977) may be more common in the Order Primates than previously thought. Most primate species are still assumed to show female defence polygyny (Altmann 1990); however, more recently evidence has accumulated for resource defence polygyny in all major primate radiations (Koenig et al. 2013). Even when females are typically philopatric, as in guerezas, and are not specifically choosing males based on the home range they

defend, male resource defence may evolve because it is beneficial to males to defend food if the females associated with them can reproduce faster with better resource access. There is a high likelihood that male resource defence led to a positive effect on female fitness in guerezas, since Harris (2006a) found that group dominance rank was directly related to the quantity and quality of the food in the core area. Indeed, she collected two-years of preliminary data that suggested that female reproductive success was better in higher-ranked groups.

Besides guerezas (Fashing 2001c; Harris 2005, 2006a, 2010), male defence of resources during BGC competition in colobus monkeys has also been found in white-thighed colobus (Sicotte and MacIntosh 2004; Teichroeb and Sicotte 2018; see also below 'one well-studied species'). Males in this species participated in all aggressive between-group encounters, while female participation occurred in less than half of encounters (Sicotte and MacIntosh 2004; Teichroeb and Sicotte 2018). Even though very large groups could sometimes win in between-group contests by over-whelming smaller groups, as in guerezas, small, uni-male groups of white-thighed colobus tended to win against larger, multi-male groups (Teichroeb et al. 2012; Teichroeb and Sicotte 2018). Direct food defence by males was most obvious in the lean season when WGS intensified and all groups were trying to expand their ranges into areas occupied by neighbouring groups to get enough food (Teichroeb and Sicotte 2018). In this season, all study groups had to range further, leading to an increase in contact with other groups. But by winning in between-group contests against other groups, small, uni-male groups were found to be able to expand their range into already occupied areas. All the losses suffered by the largest study group that contained a range of 7–10 adult males in the lean season were to small, one-male groups. Mid-sized, multi-male groups had the poorest performance during between-group contests. They could not win encounters through large group size or with large, competitive males and they appeared to suffer the most in the lean season. When forced to range further due to WGS, these groups had to move into suboptimal areas near the edge of the forest and avoid other groups (Teichroeb and Sicotte 2018).

Thus, resource defence mediated by males may be an important way through which male strategies are impacting female strategies and affecting the fit of colobus monkeys to the socioecological model. More investigation is needed to understand if this strategy is used widely by males in African colobines. For instance, for king colobus where females were involved in many between-group encounters, males still participated in all encounters (Korstjens 2001), so male resource defence may be occurring. Males are also the primary participants in between-group encounters in both red colobus (Korstjens 2001; Struhsaker 1975) and olive colobus (Korstjens and Noë 2004) but they may be defending females rather than food. For example, comparison of two populations of Zanzibar red colobus (*P. kirkee*), one living in a protected area and one living at high population density in an agricultural area, showed important effects of BGC competition on social structure and implicate female defence of food rather than male defence. Siex (2003) found that, relative to groups in the more forested area, groups in degraded areas showed more cohesion,

more female philopatry, and more grooming among females and she related this to the high level of BGC seen in the dense colobus population in degraded areas. For Temminck's red colobus, Starin (1994) reports that females frequently participated in and even started between-group encounters. However, it is worth noting that this species was also studied in a forest fragment with a high population density.

### Female Dispersal and Affiliation

The ability to rely on mature foliage as a resource in times of food scarcity and perhaps a reliance on males, rather than female kin, to defend food resources, opens up flexibility in the social responses of female colobus leading to more choice of groups and males, compared to a typical cercopithecine. In the black-and-white colobus dispersal is male-biased. The most female philopatric species is the guereza, for whom female dispersal is rare and all males disperse (Harris et al. 2009a). White-thighed colobus show a pattern of all males dispersing and some females dispersing and parallel transfers involving same-sexed individuals occur often (Teichroeb et al. 2009a, 2011). In king colobus, male and female dispersal have been observed, but the overall pattern appears to be male-biased (Korstjens et al. 2002, 2005). Grooming relationships and strong bonds often occur among the philopatric sex (Wrangham 1980), and going along with these more male-biased dispersal patterns in these species of black-and-white colobus, grooming interactions in guerezas, white-thighed colobus, and king colobus are typically seen among females (Oates 1977c; Korstjens et al. 2002; Saj et al. 2007; Wikberg et al. 2012). Indeed, in white-thighed colobus kinship was important in structuring female social relationships in groups where females resided with kin, but long-term residency status was important in groups where few female relatives were available (Wikberg et al. 2014). Though little is known about social behaviour in *C. satanas*, observations of a new male entering a research group in Gabon suggested that dispersal may be male-biased in this species as well (Fleury and Gautier-Hion 1999). Dispersal in most *C. angolensis* subspecies is unstudied as well, but grooming patterns in *C. a. ruwenzorii* differ from the other black-and-white colobus in being predominantly between males and females (Arseneau-Robar et al. 2018), leading to the prediction that dispersal occurs evenly for both sexes, which is indeed what data are showing (Stead and Teichroeb 2019). At Nabugabo, Uganda both sexes disperse from the natal core unit but males appear to stay within larger band of units that cluster together, while most female dispersal has been to other bands (Adams et al. 2021; Stead and Teichroeb 2019; Teichroeb, unpub. data).

Red colobus are generally described as having female-biased dispersal patterns, with male dispersal to a smaller extent (Marsh 1979b; Starin 1994; Struhsaker 1975; Chapter 9). At Kibale, ashy red colobus males are often in proximity to one another, supporting each other in inter-group contests, and grooming one another more often than expected by chance (Struhsaker 1980; Struhsaker and Leland 1979). Similarly, Werre (2000) describes most grooming as occurring among males in Niger Delta red colobus (*P. epieni*) at Gbanraun in Nigeria. At Taï, Upper Guinea red colobus grooming interactions were primarily observed between males and females, with

males receiving most of the grooming (Korstjens 2001). For Temminck's red colobus at the Abuko Nature Reserve, The Gambia, Starin (1994) reports that dispersal occurred for both sexes with females dispersing voluntarily and males often being evicted as subadults and then re-entering their natal group as adults after a period of being solitary. Grooming interactions were primarily seen amongst females despite frequent female dispersal, which was likely due to a high rate of parallel transfer for females (Starin 1994). Coalition formation in Temminck's red colobus occurred primarily between the sexes, however. Only Zanzibar red colobus in degraded areas buck the typical red colobus dispersal pattern by showing male-biased dispersal patterns and despite this, most grooming occurs between the sexes, with females grooming males often. Siex (2003) suggests that females may be more philopatric in this area because of the aforementioned intense between-group conflict they experience.

Olive colobus monkeys also show the dispersal of both sexes and research done at Tai over 5-years indicates that female dispersal is more frequent than male dispersal (Korstjens and Schippers 2003). In agreement with these observations, olive colobus females show very little affiliation and coalitions among females have not been observed (Korstjens et al. 2007a). Grooming among adult males has not been noted in publications but males within the same group appear tolerant of one another and have been seen to form coalitions during inter-group encounters (Korstjens and Noë 2004; McGraw and Zuberbühler 2008).

To summarize this section, female dispersal occurs in all species of African colobine where dispersal patterns have been assessed, although the degree to which females transfer differs (ESM Table 17.3). Males also appear to disperse in all colobus species though again the degree to which this occurs depends on the species. Grooming and proximity among individuals in colobus groups tend to be as expected, given the dispersal patterns that have been observed. Males appear to often be more philopatric in red colobus and to a lesser extent in olive colobus, so female dispersal in these species may be at least partly explained by inbreeding avoidance. In black-and-white colobus, data thus far suggests that all males disperse, so female dispersal in this taxon may require additional explanation. For white-thighed colobus, there are several indications that females disperse to avoid infanticide and not because of food competition and this is discussed below (Sicotte et al. 2017; Teichroeb et al. 2009a) (see 'One Well-Studied Species').

### **Social Factors Constraining Group Size in African Colobines**

The long-held belief that folivores were not affected by food competition (reviewed in Snaith and Chapman 2007), led researchers to wonder why many species of leaf-eaters do not form large groups, a phenomena termed the 'folivore paradox' (Janson and Goldsmith 1995; Steenbeek and van Schaik 2001). Given that large groups provide effective protection from predation (Hamilton 1971) and folivore group sizes were not thought to be constrained by WGS food competition, they were expected to live in large groups. One solution to the folivore paradox is that WGS feeding competition is occurring (as demonstrated above) and that its effect has been

underestimated, so that actually it can lead to groups being capped at relatively small sizes (Snaith and Chapman 2005, 2007). This may well be the best solution to the folivore paradox, since even guerezas, that form the smallest groups in the colobus monkeys have shown negative effects of food depletion (Fashing 2001a; Harris et al. 2010). In addition, as demonstrated above, relatively little research has controlled for all of the ways that animals may compensate for the occurrence of WGS. Given this, does the 'paradox' still remain? Do many folivores form groups far below the threshold at which WGS competition for food appears to occur? Perhaps not. However, the social solution to the folivore paradox, which suggests that the threat of infanticide is constraining group size in folivores, does have some merit (Crockett and Janson 2000; Steenbeek and van Schaik 2001). This hypothesis proposes that since larger female groups are more often a target for immigrating males, which may increase infanticide rates, females may try to maintain smaller group sizes through several methods including, dispersing from large to small groups, evicting other females, resisting the immigration of new females or by group fission (Crockett and Janson 2000).

It is difficult to evaluate the contribution of the risk of infanticide by males to constraining group size with the current data available for colobus monkeys but black-and-white colobus provide some support for this hypothesis. Infanticide by males has only been observed in two species of black-and-white colobus (i.e. guerezas at Kibale, Onderdonk 2000; Harris and Monfort 2003; Chapman and Pavelka 2005; white-thighed colobus at Boabeng-Fiema, Teichroeb and Sicotte 2008a; Teichroeb et al. 2012) and one species of red colobus (ashy red colobus at Kibale, Struhsaker and Leland 1985). Infanticide risk has been implicated in constraining group sizes in guerezas, because they show much smaller group sizes than sympatric red colobus at Kibale but are ecologically very similar (Chapman and Pavelka 2005). Red colobus groups at Kibale, where infanticide by males appears to be rare (Chapman and Pavelka 2005; Struhsaker and Leland 1985), are not small and have been growing over time (Gogarten et al. 2014), which suggests that this social pressure is not negatively impacting group size. Rather, high predation risk for red colobus (Teelen 2008; Watts and Amsler 2013), may be driving large, multi-male groups (van Schaik and Hörstermann 1994) since male primates tend to be more vigilant than females (Cheney and Wrangham 1987) and they also engage in direct counter-attacks towards predators (e.g. Boesch 1994a; Stanford 1995, 1998a). At Boabeng-Fiema in Ghana, where infanticide by males in white-thighed colobus is relatively frequent (Teichroeb and Sicotte 2008a), it does appear to play a role in constraining group size (Teichroeb et al. 2012), though not below the size at which WGS occurs (see below). Thus, with the data available, the folivore paradox does not seem to be explained by infanticide risk in the colobus. Indeed, it is unclear whether or not there truly is a paradox because even small groups are affected by WGS. The occurrence of small groups in the colobines is likely a reflection of several costs to group living, which include both WGS and, in some species, infanticide by males. The next section, on white-thighed colobus, provides a good example as to how these differing constraints can play out.



## One Well-Studied Species

So, how does infanticide risk affect social organization in folivores where scramble competition for food is known to limit group size? White-thighed colobus, which have now been studied at the Boabeng-Fiema Monkey Sanctuary (BFMS) in Ghana under the supervision of Pascale Sicotte (University of Calgary) for 20 years are an excellent case study for understanding the interaction of the constraints imposed by WGS food competition and infanticide risk. WGC and BGC competition for food also occur for this species and their contributions to the social organization and structure are informative.

At BFMS, about one quarter of groups are uni-male/multi-female and three quarters are multi-male/multi-female. Dispersal is male-biased with all males leaving their natal group, most before sexual maturity and dispersing secondarily throughout their lives (Teichroeb et al. 2011). Female dispersal is facultative, with some females dispersing and some remaining in their natal group and female dispersal occurs secondarily though less often than for males (Teichroeb et al. 2009a). All-male bands (AMBs) occur in the population but are not permanent. Dispersing males form groups (range: 2–7) that sometimes associate for a few months before they choose a bisexual group to attack and attempt immigration into (Saj and Sicotte 2005; Saj et al. 2005; Teichroeb and Sicotte 2008a; Teichroeb et al. 2011). These takeovers are typically successful but slow (mean duration: 7 months) with males from the AMB attempting to evict resident males and then one another. In contrast, group takeovers also occur by single adult males and these are usually quick and decisive (mean duration: 1 month) (Sicotte et al. 2017).

Infanticide by males appears to have a major influence on white-thighed colobus grouping patterns, which also affects how females experience food competition. At BFMS, 38.5% of infant mortality has been attributed to infanticide by males (Teichroeb and Sicotte 2008a). In all observed cases, the perpetrator has been a new immigrant male who became the alpha male, although attacks between groups also occur (Teichroeb et al. 2012). Infanticide is equally likely after fast takeovers by single males and after slow takeovers by AMB males (Sicotte et al. 2017). The sexual selection hypothesis for infanticide (Hrdy 1977b, 1979) has been supported in all observed cases at BFMS. Infanticidal males improve their chances of siring a female's next infant when they kill her current infant because female interbirth intervals are shortened and males have the opportunity to mate with the mother after her infant dies (Teichroeb and Sicotte 2008a; Teichroeb et al. 2012).

Immigrant males in white-thighed colobus are more attracted to larger female groups, which increases infanticide risk in larger groups (Teichroeb et al. 2011, 2012), a common finding in gregarious mammals (e.g. *Alouatta seniculus*, Crockett and Janson 2000; *Theropithecus gelada*, Dunbar 1984; *Panthera leo*, Packer et al. 1988). However, an investigation into group composition and infanticide risk in white-thighed colobus showed that, even when controlling for female group size, groups with relatively more males had significantly more male immigration and higher infanticide rates (Teichroeb et al. 2012). In this respect, white-thighed colobus differ

from several other species where multi-male groups have lower rates of infanticide by males (e.g. *G. b. beringei*, Robbins 1995; *Semnopithecus sp.*, Newton 1986; but see Borries 1997). In white-thighed colobus, males in uni-male groups that are able to keep out immigrant males and successfully defend infants show several additional indicators of having better competitive ability compared to males in multi-male groups (i.e. performing longer displays and often winning in between-group encounters against larger, multi-male groups, Teichroeb and Sicotte 2010, 2018; Teichroeb et al. 2012).

The severe effect that infanticide by males has on female and sire reproductive success has led to the evolution of several counter-strategies in white-thighed colobus (Bădescu et al. 2016; Sicotte et al. 2017; Teichroeb and Sicotte 2008a; Teichroeb et al. 2009a; 2012). The most relevant of which, to socioecological theory, are evidence of a female preference for smaller, uni-male groups that tend to have high-quality resident males(s) (Teichroeb et al. 2012). Females demonstrate this preference in several ways. First, they tend to emigrate from larger groups and immigrate into smaller groups. Attempted transfers are also usually to smaller, uni-male groups if the resident male often wins in inter-group encounters against the male(s) in the female's own group. Second, mature, breeding females will force the emigration of young females that have just reached reproductive age in larger groups (13/23 cases of dispersal documented, 56.5%) (Teichroeb et al. 2009a). These young females may attempt to join a nearby group or may form their own group. Third, resident females will aggressively prevent new female immigration into their group, especially in large groups. Additionally, female white-thighed colobus voluntarily emigrate from groups where the male hierarchy is unstable (Sicotte et al. 2017; Teichroeb et al. 2009a). Furthermore, male takeovers in this species are often followed closely by female dispersal if the group is taken over by an AMB that has undecided dominance relationships. However, fast takeovers by single males have never been seen to be followed by female dispersal (Sicotte et al. 2017). Thus, in support of the social solution to the folivore paradox (Crockett and Janson 2000), larger multi-male groups in white-thighed colobus do have greater infanticide risk and are avoided by females. So, infanticide risk is constraining group size but importantly, so is WGS food competition (Teichroeb and Sicotte 2009; Teichroeb et al. 2012). Large groups may persist in the population because of predation risk or because food is patchy to some degree and better home ranges attract more females, but this remains to be substantiated.

Infanticide risk seems to play a prominent role in female preference for smaller groups with higher-quality males in white-thighed colobus, however these strategies have benefits for reducing WGS and WGC food competition, as well as improving competitive ability in BGC competition. First, individuals in smaller groups suffer less from WGS (Chapman and Chapman 2000c; Janson and Goldsmith 1995; Teichroeb and Sicotte 2009). Second, WGC competition for food would also be decreased in white-thighed colobus when breeding females force the emigration of young adult females (Teichroeb et al. 2009a). Wikberg and colleagues (2013) found that maturing females begin to challenge older females in the dominance hierarchy when they become full body size, leading to older females dropping in rank over time. Forcing

these young females out of the group before this occurs, allows older females to avoid a drop in rank. Third, recall that in white-thighed colobus smaller, uni-male groups are better at defeating other groups in between-group encounters allowing a range expansion in lean seasons (Teichroeb and Sicotte 2018). Therefore, group size in white-thighed colobus appears to be constrained by several interacting pressures. While there is some support for the social solution to the folivore paradox (Crockett and Janson 2000), the situation is much more complicated than a single blanket solution allows.

## Discussion

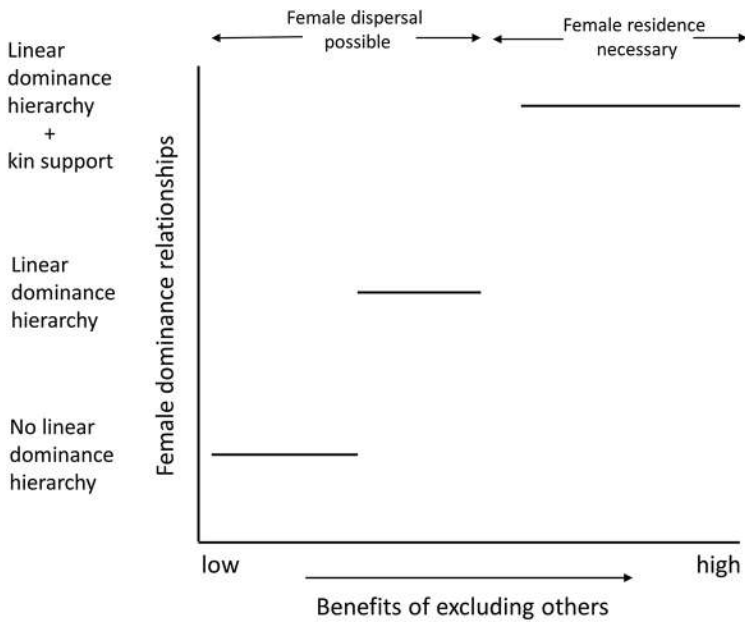
This overview of our understanding of the socioecology of African colobines demonstrates that the, often surprising, ecological flexibility of this group of animals makes it difficult to predict their social responses to food competition. Five key findings are evident. First, despite early assumptions, the diets of colobus monkeys are variable and mature leaves are often avoided (reviewed in Fashing 2011). This means that colobus do feed on food items that tend to be high quality (low in fibre and high in protein) and have clumped distributions, and which therefore cause competition. Second, when researchers actually look for WGS competition while controlling for differences in range quality for different-sized groups (Chapman and Chapman 2000c), evidence that colobus monkey foraging efficiency is negatively affected by large group size emerges (Gillespie and Chapman 2001; Harris et al. 2010; Snaith and Chapman 2007, 2008; Teichroeb and Sicotte 2009, 2018). What is not clear yet in most populations, however, is whether the intensity of WGS is enough to lead to a negative effect on female reproductive rates (ESM Table 17.2) and most species remain to be studied in regard to the occurrence and effects of WGS. Third, WGC competition is evident for a few species where it has been looked for and even if food is only contestable for brief periods at certain times of year, this appears to be enough to lead to female dominance hierarchies (Korstjens 2001; Wikberg et al. 2013). These dominance hierarchies tend to be individualistic and co-occur with female dispersal, which is also the case in several Asian colobines (Chapter 16). Fourth, BGC competition is also evident in several populations of colobus monkeys that have been studied, however again the social response appears to differ from what is typically seen in cercopithecines. Rather than matrilineal groups becoming ubiquitous to defend the range against other groups (Wrangham 1980), males may be more commonly involved in resource defence in colobus monkeys (Fashing 2001c; Harris 2005, 2006a, 2010; Sicotte and MacIntosh 2004; Teichroeb and Sicotte 2018). Finally, the fifth thing that became clear during this review is that there is not much support for the social solution to the folivore paradox thus far in the colobus monkeys. Many species actually form quite large groups with multiple males, which may be due to predation risk in Africa (van Schaik and Hörstermann 1994), and the effects of food depletion are seen in even the smallest groups (i.e. guerezas, Harris et al. 2010). Thus, it seems more likely that the costs of WGS and its occurrence have been underestimated (Snaith and Chapman 2005, 2007). Infanticide risk does play a

part in limiting group size in white-thighed colobus but groups do get large enough to be affected by WGS (Teichroeb et al. 2012; Teichroeb and Sicotte 2018). In other colobus monkeys, there is almost no evidence for the occurrence of infanticide on a regular basis and red colobus form such large groups that the folivore paradox does not seem to really apply to them. Our overall picture of all that constrains colobus monkeys is still skewed however, due to the lack of data on so many species.

### How Do African Colobines Fit Current Socioecological Models?

Given the evidence for different types of food competition in African colobines, as well as patterns of dispersal and female dominance relationships, it seems that this group of animals does not fit well into any of the four social categories presented by Sterck et al. (1997): Dispersal Egalitarian, Resident Egalitarian, Resident Nepotistic or Resident Nepotistic Tolerant (Table 17.1). Rather, the picture that emerges from the species of colobus monkeys for which we have data is WGS food competition, at least seasonal WGC and fairly high BGC (likely depending on population density), co-occurring with female dispersal, linear, individualistic female dominance hierarchies and fairly weak affiliative relationships between females. This suggests that the African colobine pattern may be best described by the intermediate situation between WGS and WGC that Sterck and colleagues describe (1997, page 295); where ‘food distribution is such that contest occurs, but the benefits are too small to lead to predictable kin support and consistent philopatry (which have costs). Females are thus still likely to disperse despite their forming decided dominance relations’ (Figure 17.1). In the two colobus species where we understand the form that female dominance hierarchies take, king colobus and white-thighed colobus, this intermediate situation seems to be occurring. In both species, we see linear female dominance hierarchies that co-occur with female dispersal (Korstjens et al. 2002; Wikberg et al. 2013). The individualistic nature of these hierarchies means that it is possible for transferring females to enter groups without related allies and fight their way up the hierarchy in the new group. There is also evidence in white-thighed colobus that these hierarchies are age-inversed, such that younger, stronger females can attain higher ranks (Wikberg et al. 2013).

It appears that the seasonal nature of WGC competition that these folivores experience does not strongly select for kin-based coalitions to defend food, which would lead to nepotistic female hierarchies. Since this competition is transitory in nature compared to the WGC experienced by species with nepotistic female hierarchies, female dominance hierarchies become important for controlling aggression only at certain times of the year. In addition, the evolutionary benefits of female dispersal can be great and outweigh the benefits of kin-based coalitions to defend food sporadically. In species that usually show female philopatry, it can be extremely costly for females to transfer between groups, leading to them experiencing intense aggression from coalitions of females that can even be fatal (Hammond et al. 2006; Jack and Fedigan 2009; Miller 1998; Payne et al. 2003). Indeed, female philopatry tends to be strongly conserved in evolution (Di Fiore and Rendall 1994), suggesting



**Figure 17.1** Replication of Sterck et al. (1997, figure 5) showing predicted relationships between the reproductive benefits of excluding other females from resources and the impacts on female dominance relationships and dispersal patterns. Reproduced with permission from Springer

that once female dispersal is lost in a lineage it is difficult to get back. Females can benefit in many ways by being able to disperse. They can disperse to smaller groups or those with a better home range to decrease WGS feeding competition (Sterck 1997). It is also the best way for females to practice mate choice since most primates live in bisexual groups and only have within-group males as options for mates unless they disperse (Fedigan 1992; Sterck 1997). Perhaps most important though, female dispersal can lead to several powerful counter-strategies to infanticide by males (van Schaik 1996; Sterck and Korstjens 2000), including choosing the best sire/protector, dispersing with deposed males, and avoiding risky factors like unstable male dominance hierarchies (reviewed in Palombit 2015; Sicotte et al. 2017). Some degree of female dispersal is seen in all the colobus monkey species where it has been investigated, suggesting that all of these benefits outweigh kin-based coalitions to defend food sources which are only defensible sometimes.

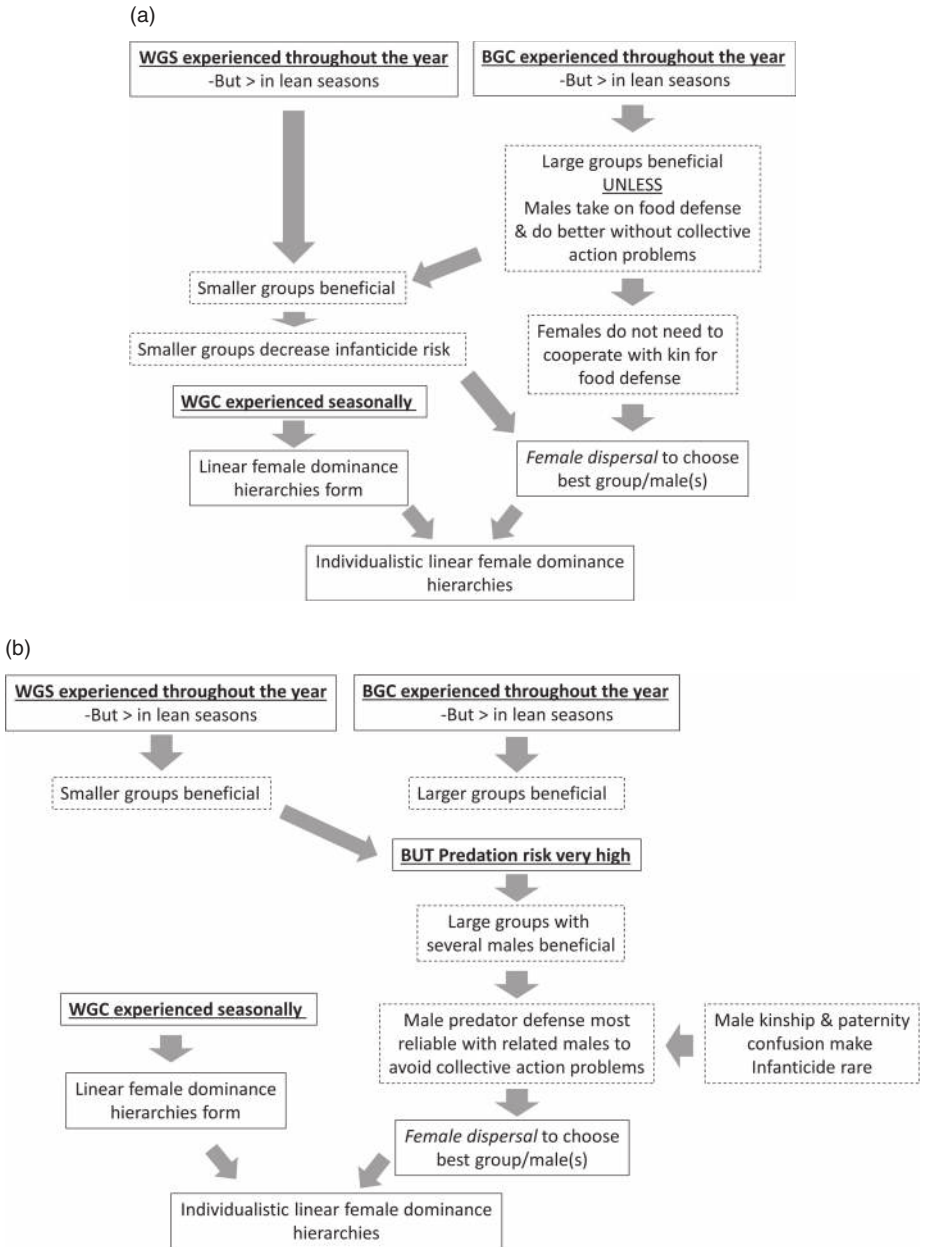
The social response to BGC competition in colobus monkeys may more commonly involve male resource defence than in other primate taxa (Fashing 2001c; Harris 2005, 2006, 2010; Sicotte and MacIntosh 2004; Teichroeb and Sicotte 2018). This has been shown in black-and-white colobus monkeys, and the potential for male resource defence in red and olive colobus deserves further investigation. This strategy by males may have also evolved due to the importance of female dispersal for colobus monkeys because it gives males an opportunity to demonstrate their mate quality to females.

So, given the predictions of socioecological models, what effects could the male strategy of defending resources for females in BGC have on female social behaviour and dispersal patterns? And how could this be expressed given that female colobus monkeys appear to also be experiencing a mixture of WGS with seasonal impacts of BGC competition? In Figure 17.2, I present two flow charts to summarize how these pressures may work to shape African colobine societies. I predict that the differences in group size, dispersal patterns and male strategies that we observe between black-and-white (Figure 17.2a) and red colobus (Figure 17.2b) are due to differences in predation risk, ultimately, which has cascading effects on other social strategies. I do not present a scenario for olive colobus since they are so unique and the most important resource for them may be their partner guenon group (Chapter 11).

For both red and black-and-white colobus monkeys, WGS competition for food may occur throughout the year and likely becomes greater in lean seasons (e.g. Teichroeb and Sicotte 2018), which makes small groups beneficial because there are fewer mouths to feed (Chapman and Chapman 2000c). However, if BGC competition is also occurring throughout the year and intensifies when resources are rare, this would select for larger group size, since larger groups tend to win in between-group contests by overwhelming their competitors (Crofoot and Wrangham 2010). If males take on the defence of the range for females though, contests between groups become more about the quality of males and how well they work together, than about group size per se. In black-and-white colobus, the differences in male quality may be large (Teichroeb et al. 2012) or collective action problems are serious enough in multi-male groups, that one-male groups tend to do better in resource defence (at least in guerezas and white-thighed colobus) (Harris 2006, 2010; Teichroeb et al. 2012; Teichroeb and Sicotte 2018). This also makes small groups more advantageous because one male is able to monopolize them. Smaller female groups also have the advantage of being less of a target to infanticidal immigrant males, which is an additional important advantage for females (Figure 17.2a). These factors may explain the smaller group sizes that we see in the black-and-white colobus relative to red colobus.

For red colobus, predation risk is much higher than for black-and-white colobus, at least in forests where they co-occur with chimpanzees. The reasons for this are debated but researchers have hypothesized that red colobus suffer more predation due to their conspicuousness (i.e. noisy groups) and relative ease of capture compared to black-and-white colobus (Mitani and Watts 1999), leading to chimpanzees in particular having evolved a preference for red colobus as prey (Stanford 1998a). The fact that predation pressure is so high (van Schaik and H ostermann 1994; Teelen 2008; Watts and Amsler 2013) means that large groups remain advantageous for dilution and detection (Hamilton 1971), and multiple males become an asset to defend the group from predators (Boesch 1994a; Stanford 1995, 1998a; Struhsaker 2000b) but perhaps also to defend resources. To decrease collective action problems, it then becomes beneficial for males to be closely related when working together to defend the group (Stanford 1998a). Male kinship and the ability for females to confuse paternity in multi-male groups may be what keeps infanticide rates low in red colobus (Figure 17.2b).





**Figure 17.2** Summary of the ways that (a) black-and-white colobus and (b) red colobus may be reacting to a competitive regime with WGS, seasonal WGC and BGC. Solid boxes represent ecological effects and their ultimate outcomes, while ticked boxes represent resulting social strategies. The main difference between the groups is the greater predation risk for red colobus, which leads to different group size requirements and different strategies by males, which in turn influence infanticide risk.

In both scenarios, for black-and-white and red colobus, since females do not have to stay in their natal groups and bond with other females to defend resources, they can disperse allowing them to choose the best situation for them in terms of group size, male quality and male number. In addition, since males take on resource defence, females do not have to appease other females to acquire their help in defence of the home range, so they can form linear dominance hierarchies to deal with the seasonal impact of WGC competition.

### **Summary and Conclusions**

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Research over the last 20 years has greatly increased our understanding of the socioecology of the colobus monkeys. However, there are still large gaps in our knowledge because many species have not been studied at all and those that have been studied have often not been examined intensively or with individual recognition. For many of the species where research has been done, we now know their diets and activity budgets and have some understanding of their natural history, however we do not yet fully understand how these ecological factors are shaping competitive regimes and female social relationships. It appears that African colobines do not fit the four social categories normally linked to the socioecological model but rather are falling somewhere in between WGS and WGC. This appears to give rise to very specific male strategies, like male defence of food resources for females, which alters female social strategies in interesting ways and changes how the sexes affect one another. More research on a greater number of colobus species is urgently needed given the state of primate conservation (Estrada et al. 2017). There is a very real possibility that we will lose more colobus monkey species to extinction without there ever being any research on them, as we likely already have with Miss Waldron's red colobus (McGraw 2005).

### **Acknowledgements**

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