



Cascading competition: the seasonal strength of scramble influences between-group contest in a folivorous primate

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Abstract

Habitat-wide depletion of food leads to scramble feeding competition and animals can mitigate costs with behavioral adjustments in ranging and activity budgets. In seasonal environments, scramble feeding competition may be more intense in lean seasons leading to shifts in the ranges of neighboring groups and cascading changes for other types of competition. Here, we specifically investigated the interplay between within-group scramble (WGS) and between-group contest competition (BGC) using four groups of ursine colobus monkeys (*Colobus vellerosus*) at Boabeng-Fiema, Ghana. These groups were known to be impacted by WGS and our first goal was to assess whether this competition was occurring in both the abundant and lean seasons. Within-season, between-group comparisons showed WGS in both seasons but greater behavioral compensation in the lean season, especially for larger groups. We then focused on differences in ranging behavior within groups, between seasons to examine whether greater WGS in the lean season influenced the intensity of BGC (rates and “wins” of between-group encounters). The largest and the smallest groups entered more trees and ranged slightly further per day in the lean season suggesting stronger WGS. These two groups also faced more between-group encounters with the small uni-male group winning more often in the lean season. Both middle-sized multi-male groups shifted their ranging towards the edge of the fragment in the lean season. They also engaged in fewer between-group encounters, which they usually lost. This study demonstrates the interplay between different types of competition. It also confirms that male membership disproportionately influence group competitiveness in *C. vellerosus*.

Significance statement

Animals face different forms of competition over limited resources every day but the ways that these competition types influence one another is rarely studied. We focused on within-group scramble competition (WGS) for food in four groups of ursine colobus monkeys and examined how seasonal changes in this type of competition influenced between-group contest competition (BGC). We found that the lean season for food availability showed greater WGS, and that animals compensated for this by using more of their home range. Some highly competitive groups were able to move into shared areas with other groups in the lean season, winning encounters with other groups, while groups with poor competitive ability were forced to range into lower quality areas and avoided other groups. Thus, WGS had cascading effects leading to changes in BGC, showing the importance of studying different types of competition collectively.

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Introduction

Nicholson's (1954) distinction between the two different types of competition experienced by animals was a major stride forward for behavioral ecology. While contest (or interference) feeding competition occurs when there are direct aggressive confrontations over food that can be monopolized and defended (Terborgh 1983; Janson 1985, 1988; Janson

and van Schaik 1988; van Schaik 1989), scramble competition (also called exploitation) arises because others use resources before an individual can encounter them (Nicholson 1954). These two types of competition can manifest over any limiting resource and can occur within-groups and/or between-groups (Nicholson 1954; Janson and van Schaik 1988).

Within-group scramble competition (WGS) affects all group members equally because their food intake is reduced and high WGS could lead to reduced reproductive rates (Terborgh 1983; Janson 1988; Janson and van Schaik 1988; Parker 2000). When the diet of a species consists primarily of lower quality, evenly dispersed food sources, food competition tends to be of the scramble type, as conspecifics cannot be excluded from feeding sites (Janson and van Schaik 1988; Isbell 1991; Sterck et al. 1997; Koenig 2002). Group size influences food intake because a large number of individuals deplete patches more quickly and search fields overlap (Janson and Goldsmith 1995; Chapman and Chapman 2000a). Animals use behavioral modifications (or adjustments) to compensate for the impact of WGS (Wrangham et al. 1993; Borries et al. 2008; Teichroeb and Sicotte 2009). One of these behavioral modifications is that animals keep moving forward through their range to encounter enough food to sustain all group members (van Schaik and van Hooff 1983). Since more individuals deplete food resources faster, at equal food availability, a larger group has to travel further per day and visit a greater number of food patches to find sufficient nourishment compared to a smaller group (the ecological constraints model, Chapman and Chapman 2000a). WGS thus increases with group size, so the size of groups is limited by the maximum daily travel distance that individuals can sustain when foraging together (Wrangham et al. 1993). A point will be reached where increased travel becomes impossible because the animals can no longer sustain it. If other behavioral strategies to deal with food competition cannot be found, the group will have to split or individuals will need to disperse to smaller groups so that they can meet their nutritional requirements without incurring too much cost (Table 1; Chapman and Chapman 2000a).

While greater ranging (day range length, home range size, and group spread) for large groups compared to small groups (controlling for habitat quality) is one manifestation of WGS, it is not the only one (Table 1). WGS may also affect activity budgets in several ways. Increased day range length may be reflected in the activity budget with more time spent traveling per day (van Schaik et al. 1983; de Ruiter 1986; Isbell 1991, 2012; Chapman and Chapman 2000b; Steenbeek and van Schaik 2001). Animals in larger groups could also spend a greater amount of time feeding to meet their nutritional requirements; potentially accompanied by a concomitant decrease in resting behavior. Finally, it is also possible that WGS could lead to animals feeding or moving faster in an attempt to get to a feeding site before others (Clark and

Mangel 1986) or to focus on lower-quality resources as food patches in proximity become depleted (Snaith and Chapman 2005). The time available for compensation strategies to WGS is a crucial limiting factor (Dunbar et al. 2009). Animals can only increase movement and feeding up to a certain point, since this time is generally taken away from resting and socializing. Social activities, like grooming, are important for group cohesion (Dunbar 1991) and this time may or may not be flexible, depending on group size or on the species. A minimum of resting time is also necessary for physiological processes to occur (Dunbar et al. 2009). The resting requirements of folivores are even higher than for animals that eat fewer leaves (Korstjens and Dunbar 2007). It is important to note that the expression of one of the behavioral adjustments to WGS may render the expression of other adjustments unnecessary or certain circumstances may not allow some behaviors to be expressed (Snaith and Chapman 2007). For instance, in an environment with high predation, animals may not widen feeding group spread as an expression of WGS if this increases their risk of falling prey.

Changes in group size or resource availability in the current range should lead to changes in the intensity of WGS (Modeling: Shaw et al. 1995; Parker 2000; Lomnicki 2009; Empirical work: Myllymäki 1977; Toquenaga and Fujii 1990; Watts 1991, 1998; Syarifuddin and Kramer 1996; Cameron et al. 2006; Li et al. 2010; Gogarten et al. 2014). Thus, seasonal variation in the food supply should influence the behavioral compensation strategies that animals use. This offers a window into investigating the interplay between WGS and other types of competition. Indeed, changes in WGS might have cascading effects on other types of competition. For instance, if changes in home range size or daily travel are used to compensate for altered food availability, periods with different resources should lead to varied patterns of between-group scramble (BGS) and between-group contest competition (BGC) (e.g., for BGC: red foxes, White and Harris 1994; African elephants, Wittemyer et al. 2007). Predictions from the ideal gas model of animal interactions are useful to understand this concept (Waser 1975, 1976). As each group pushes out and expands group spread as well as the borders of its range into areas of overlap with other group(s), they will be depleting resources in overlap areas and the size and density of groups moving in these overlap areas will be greater, which increases the chance of an encounter between two groups (Hutchinson and Waser 2007). BGS is difficult to quantify (Janson and van Schaik 1988), though presumably depletion by several groups in overlap areas of the home range exacerbates WGS.

BGC is relatively well studied in primates, although the main context where it has been studied for potential seasonal variation is in relation to the effect of mating seasons (e.g., Saito et al. 1998; Cooper et al. 2004; Cords 2004). Like other group-living animals, large groups tend to win in contests

Table 1 Indications of scramble competition in gregarious animals

Variable	Expected relationship with increased group size ^a
Home range quality:	
Number food trees present	Greater
Size of food trees present	Greater
Monthly dietary plant part availability	Greater
Diet	More high-quality items
Ranging:	
Home range size	Greater (at equal home range quality)
Day range length	Greater (at equal home range quality)
Number of trees entered per day	Greater
Fission of groups while foraging	More often
Activity budget and behavioral adjustments:	
Time spent feeding	Higher
Time spent resting	Lower
Time spent moving	Higher
Ingestion rate	Greater
Rate of travel	Greater
Group spread while feeding	Greater

^a van Schaik and van Hooff 1983; van Schaik et al. 1983; de Ruiter 1986; Isbell 1991; Wrangham et al. 1993; Chapman and Chapman 2000a, b; Steenbeek and van Schaik 2001; Snaith and Chapman 2007

against smaller groups in primates (Cheney 1987), though this effect may be mediated by the location of the encounter (Crofoot et al. 2008), the fighting ability of individuals within the group (Parker 1974; Harris 2006), and their participation decisions (Enquist and Leimar 1983; Zhao and Tan 2011). Between-group hierarchies and avoidance by subordinate groups also appear to influence the expression of BGC in primates (Bernstein 2011). Sex differences in limiting resources (Trivers 1972) are believed to influence to a large degree who participates in between-group encounters (Wrangham 1979, 1980). Female participation is thought to show female defense of food resources, while male participation is often assumed to indicate male defense of mates (reviewed in: Fashing 2001). Direct male mate defense, which usually involves mate-herding and aggression toward outside males, may work to drive away other groups and indirectly defend food resources for individuals in the male's group (i.e., the hired gun strategy, Rubenstein 1986; Wrangham and Rubenstein 1986). However, males can also directly defend food resources to attract and/or retain females (i.e., resource defense polygyny, Emlen and Oring 1977), allowing male(s) mating access to female(s) in exchange for food defense. Recent studies show evidence of male resource defense in primates (Fashing 2001; Williams et al. 2004; Harris 2006; Koenig et al. 2013; Scarry 2013; Richter et al. 2016). In addition, rather than just ensuring future reproductive opportunities, males and females may also participate in between-group conflict to defend infants, which are their current reproductive output (e.g., Kitchen 2004; Arseneau et al. 2015).

Here, we used data from a folivorous primate affected by WGS to investigate: (1) whether the intensity of WGS varied seasonally with temporal food availability; and if so, (2) how this impacted the expression of BGC. We predicted that behavioral adjustments to WGS would be more intense in the lean season versus the abundant season, and potentially more numerous, especially in larger groups. If the expression of WGS involved greater group spread and range use in the lean season, we predicted that groups would experience more BGC by coming into contact with other groups at greater rates in the lean season.

Ursine colobus monkeys (aka white-thighed colobus, *Colobus vellerosus*) at the Boabeng-Fiema Monkey Sanctuary, Ghana, experience WGS (Teichroeb et al. 2003; Saj and Sicotte 2007a, b; Teichroeb and Sicotte 2009). Data from an annual cycle showed that at similar home range qualities (tree densities and monthly food availability), larger groups had larger home ranges, longer day ranges, greater group spread while feeding, and spent more time feeding per day (Teichroeb and Sicotte 2009). Using the same large data set, our first aim here was to determine if this previously documented occurrence of WGS for food was driven by a single season. At Boabeng-Fiema, there are two wet seasons and two dry seasons annually (Fargey 1991). The greatest differences in diet and food availability are seen between the long dry and long wet seasons (Saj and Sicotte 2007a; Teichroeb and Sicotte 2009), so we focused on these two seasons for our analyses. The long wet season shows high mature leaf availability and consumption, and here, we

consider this to be the “lean” season because consumption of other plant parts goes up significantly as soon as they are available (Saj and Sicotte 2007a). The long dry season shows increased availability and consumption of young leaves, fruits, and seed pods (Saj and Sicotte 2007a), and we consider this to be the “abundant” season.

To determine if WGS occurred in both the abundant and lean season for ursine colobus at BFMS, we compared groups within each season and predicted that greater ranging or more time spent feeding would occur in the lean season when compared to the abundant season and to the greatest extent in larger groups. We next examined ranging behavior between the seasons for each group and compared rates of between-group encounters and the number of “wins” a group achieved (our measures of BGC). The home ranges of the four study groups overlap one another and other neighboring groups (Fig. 1), so we predicted that increases in day range length and home range size due to lowered food availability in the lean season would lead to more between-group encounters for those groups. However, a group being able to compensate for fewer resources by expanding their range was only predicted to be viable if they won encounters, so successful group expansion was predicted to occur when groups had high competitive ability (i.e., high resource holding potential—RHP). Previous research in *C. vellerosus* has shown that males are the primary participants in between-group encounters (Sicotte and MacIntosh 2004; Teichroeb et al. 2012). Males also vary widely in strength, with those able to maintain uni-male, multi-female groups being of superior fighting ability (Teichroeb and Sicotte 2010; Teichroeb et al. 2012; Sicotte et al. 2017). Thus, the smallest of our study groups with a single male was predicted to win more between-group encounters relative to the three larger, multi-male study groups and to expand its range in the lean season at the expense of neighboring groups. Thus, small, uni-male groups at BFMS are expected to suffer the least from WGS, and to gain the most in BGC, making these groups optimal for both males and females in terms of access to food resources.

Methods

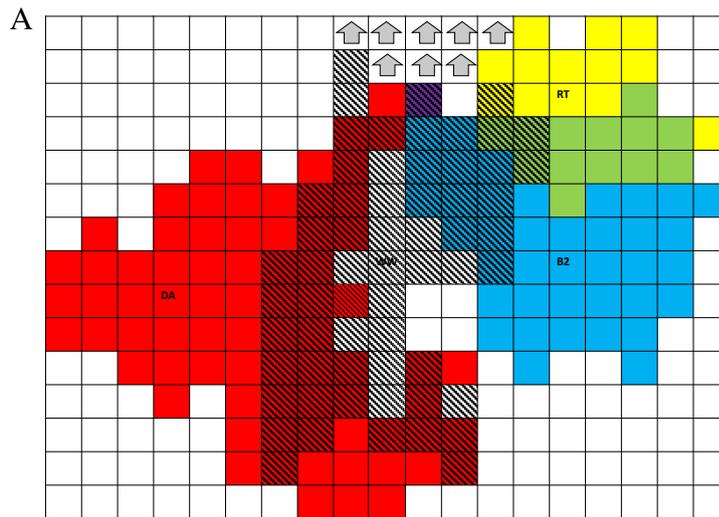
Study site and subjects

We conducted this research at the Boabeng-Fiema Monkey Sanctuary (BFMS) in central Ghana. This area is a dry semi-deciduous series of forest fragments, located at an elevation of 350 m in the Nkoranza district of the Brong-Ahafo Region (7° 43' N and 1° 42' W). The data analyzed here were collected in the Boabeng-Fiema fragment, which is 191.6 ha in size. BFMS is mostly surrounded by farmland and contains primary forest, regenerating farmland (secondary forest), and woodland (Fargey 1991; Saj et al. 2005). The long dry season runs

from November to March, with a short dry period in August; while the long rains fall from April to July, with a short rainy period in September. BFMS sheltered 19 bi-sexual groups of ursine colobus (*Colobus vellerosus*) when the study was conducted (Kankam and Sicotte 2013). PS and her research team have studied *C. vellerosus* at this site since 2000. Group composition is variable and male membership in particular can be rather fluid; groups can be multi-male/multi-female and uni-male/multi-female and there is the occasional presence of all-male bands (AMBs) (Teichroeb et al. 2011).

We collected data over 13 months (July–November 2004, January–August 2005) on four differently sized groups of *C. vellerosus* (RT, B2, DA, and WW) with overlapping home ranges. Rainfall and temperature data were collected about 1 km away from the home ranges of the study groups. Annual rainfall was 1329 mm and mean monthly minimum and maximum temperatures were 18.8 °C and 34.6 °C, respectively. These values are comparable to other years at this location (Fargey 1991). The data we compare in this study come from the long dry (“abundant”) season of 2004–05 (November 2004, and January to March 2005, mean monthly rainfall 57.8 mm, range 0.4–167.1 mm, mean monthly min. temp. 18.3 °C, max. temp 35.2 °C) and the long wet (“lean”) season of 2005 (April to July, mean monthly rainfall 133.1 ml, range 88.6–177.4 ml, mean monthly min. temp. 19.4 °C, max. temp 35.5 °C). We obtained at least one good group count per month. In the small groups (RT and B2), all monkeys were individually recognized. In the large groups (DA and WW), some individuals were not yet identifiable so group counts were done opportunistically when they were crossing a narrow gap in the canopy or a road. Table 3 shows group composition and the number of study days in each season. Group size varied widely for one of the study groups (DA, $n = 21–31$) due to an influx of at least seven males from an AMB. This was associated with the subsequent dispersal of three females, and with the eventual eviction of the three resident adult males and many of the AMB males (Teichroeb and Sicotte 2008a, b; Teichroeb et al. 2009, 2011; Sicotte et al. 2017). Even though DA varied in group size more than the other study groups, we still examine data from DA because their group size falls right between the ranges of B2 and WW groups (Table 2). In addition, they were at their largest group size in the abundant season and their smallest in the lean season. Since we predicted the behavioral adjustments to scramble competition would be more intense in the lean season, if we see this effect in DA, it should mean that

Fig. 1 a The home range of all four groups (in 50 × 50 m quadrats) over the entire study (July 2004–Aug. 2005). Yellow = RT, green = overlap between RT and B2, blue = B2, red = DA, purple = overlap of B2, and DA, gray = WW, houses = town of Boabeng. b–e Heat maps comparing each group’s home range use over the lean and abundant seasons with all other group’s ranges noted and the forest edge noted. Dark squares = core area (50% use), mid-tone = used an additional 25%, lightest = used least for an additional 25%



B RT - Abundant Season

↑	AK	AK	AK	AK	AK	AK	AK	AK	AK, FK
↑	↑	AK	AK	AK	AK	AK	AK, FK	AK, FK	AK, FK
↑	AK	AK	AK			FK	FK	FK	FK
	WW	AK			B2	FK	FK	FK	FK
WW, B2	WW, B2	WW, B2	B2	B2	B2	B2	FK	FK	FK
WW, B2	WW, B2		B2	B2	B2	B2	FK	FK	FK
WW, B2	WW, BE	B2	B2	B2	B2	B2	B2, FK	Edge	Edge
WW, B2	WW, B2	B2	B2	B2	B2	B2	Edge	Edge	Edge

RT - Lean Season

↑	AK	AK	AK	AK	AK	AK	AK	AK	AK, FK
↑	↑	AK	AK	AK	AK	AK	AK, FK	AK, FK	AK, FK
↑	AK	AK	AK			FK	FK	FK	FK
	WW	AK			B2	FK	FK	FK	FK
WW, B2	WW, B2	WW, B2	B2	B2	B2	B2	B2	FK	FK
WW, B2	WW, B2		B2	B2	B2	B2	B2	FK	FK
WW, B2	WW, BE	B2	B2	B2	B2	B2	B2	B2, FK	Edge
WW, B2	WW, B2	B2	B2	B2	B2	B2	B2	Edge	Edge

C B2 - Abundant Season

↑	↑	↑	RT	RT, AK	RT, AK	RT	RT	RT	FK	FK
DA, SP	DA, WW		RT, WW	RT, AK	RT	RT	RT	RT	FK	FK
DA, SP, WW	WW	WW	RT, WW	RT, WW	RT	RT	RT	RT	RT, FK	RT, FK
WW	WW	WW	WW	RT, WW	RT	RT	RT	RT	FK	FK
WW	WW	WW	WW		RT				FK	FK
WW	WW	WW	WW						Edge	Edge
WW	WW	WW	WW						Edge	Edge
WW	SK	SK	SK						Edge	Edge
WW	SK	SK	SK	SK	TL	TL	TL	TL	Edge	Edge
WW, SK	WW, SK	DA, SK	SK	SK, TL	TL	TL	TL	TL	Edge	Edge

B2 - Lean Season

↑	↑	↑	RT	RT, AK	RT, AK	RT	RT	RT	FK	FK
DA, SP	DA, WW		RT, WW	RT, AK	RT	RT	RT	RT	FK	FK
DA, SP, WW	WW	WW	RT, WW	RT, WW	RT	RT	RT	RT	RT, FK	RT, FK
WW	WW	WW	WW	RT, WW	RT	RT	RT	RT	FK	FK
WW	WW	WW	WW		RT				FK	FK
WW	WW	WW	WW						Edge	Edge
WW	WW	WW	WW						Edge	Edge
WW	SK	SK	SK						Edge	Edge
WW	SK	SK	SK	SK	TL	TL	TL	TL	Edge	Edge
WW, SK	WW, SK	DA, SK	SK	SK, TL	TL	TL	TL	TL	Edge	Edge

D

DA - Abundant Season

			OD, BO	OD	SP, OD	SP, OD	SP	SP, WW	SP	B2, WW	
		BO	BO	OD, BO	SP, OD	SP, OD	SP	SP, WW	SP, WW	B2, WW	B2, WW
Edge	BO	BO	BO	OD, BO	BO	SP	SP	WW	SP, WW	B2, WW	B2, WW
Edge	BO	BO	BO	BO	BO	SP	WW	WW	WW	B2, WW	B2, WW
Edge	BO	BO	BO	BO			WW	WW	WW	WW	B2, WW
		BO	BO				WW	WW	WW	SK, WW	SK, WW
							WW	WW	SK, WW	SK	SK
							WW	WW	WW	SK, WW	SK
Edge	Edge						WW	WW	WW	SK, WW	SK, WW
Edge	Edge	Edge		Edge			WW	WW	WW	WW	WW
		Edge	Edge	Edge			WW	WW		WW	WW
			Edge	Edge			WW				WW
			Edge	Edge	Edge	Edge	Edge	Edge	Edge	Edge	Edge

DA - Lean Season

			OD, BO	OD	SP, OD	SP, OD	SP	SP, WW	WW	B2, WW	
		BO	BO	OD, BO	BO	SP	SP	WW	WW	B2, WW	B2, WW
Edge	BO	BO	BO	OD, BO	BO	SP	SP	WW	WW	B2, WW	B2, WW
Edge	BO	BO	BO	BO	BO	SP	WW	WW	WW	B2, WW	B2, WW
Edge	BO	BO	BO	BO			WW	WW	WW	WW	B2, WW
		BO	BO				WW	WW	WW	SK, WW	SK, WW
							WW	WW	WW	SK, WW	SK
							WW	WW	WW	SK, WW	SK
Edge	Edge						WW	WW	WW	SK, WW	SK, WW
Edge	Edge	Edge		Edge			WW	WW	WW	WW	WW
		Edge	Edge	Edge	Edge		WW	WW		WW	WW
			Edge	Edge			WW				WW
			Edge	Edge	Edge	Edge	Edge	Edge	Edge	Edge	Edge

E

WW - Abundant Season

SP, OD	SP, OD	SP	SP	↑	↑	↑	RT	RT, AK	RT, AK
SP, OD	SP, OD	SP	SP	DA, SP	DA, B2		RT	RT, AK	RT
SP, OD	SP, OD	SP	DA	DA	B2	B2	RT, B2	RT, B2	RT, B2
DA, BO	SP	DA, SP	DA		B2	B2	B2	RT, B2	RT, B2
DA, BO	DA, SP	DA	DA		B2	B2	B2	B2	RT, B2
DA	DA	DA	DA		B2	B2	B2	B2	B2
DA	DA	DA			SK	SK	B2	B2	B2
DA	DA	DA	DA, SK	SK	SK	SK	B2, SK	B2	B2
DA	DA	DA		SK	SK	SK	B2, SK	B2, SK	B2
DA	DA	DA	DA	SK	DA, SK	DA, SK	SK	B2, SK, TL	TL
DA	DA	DA	DA		DA	SK	SK	SK, TL	SK, TL
DA	SK	SK, TL							
DA	SK								
Edge		DA	DA	DA					

WW - Lean Season

SP, OD	SP, OD	SP	SP	↑	↑	↑	RT	RT, AK	RT, AK
SP, OD	SP, OD	SP	SP	DA, SP	DA, B2		RT	RT, AK	RT
SP, OD	SP, OD	SP	DA	DA	B2	B2	RT, B2	RT, B2	RT, B2
DA, BO	SP	DA, SP	DA		B2	B2	B2	RT, B2	RT, B2
DA, BO	DA, SP	DA	DA		B2	B2	B2	B2	RT, B2
DA	DA	DA	DA		B2	B2	B2	B2	B2
DA	DA	DA			SK	SK	B2	B2	B2
DA	DA	DA	DA, SK	SK	SK	SK	B2, SK	B2	B2
DA	DA	DA		SK	SK	SK	B2, SK	B2, SK	B2
DA	DA	DA	DA	SK	DA, SK	DA, SK	SK	B2, SK, TL	TL
DA	DA	DA	DA		DA	SK	SK	SK, TL	SK, TL
DA	SK	SK, TL							
DA	SK								
Edge		DA	DA	DA					

Fig. 1 (continued)

this effect is indeed driven primarily by changes in the food supply, as opposed to changes in group size.

Behavioral data collection

We followed each study group for at least two, two-day periods per month from dawn to dusk (6:00 am to 6:00 pm). It was not

possible to record data blind because our study involved focal animals in the field. We collected continuous behavioral observations using 10-min focal samples (Altmann 1974) on adult and subadult individuals, and ad libitum sampling during between-group encounters. We left at least 1 h between focal samples on the same individual. Overall, we were in contact with the study groups for 2406 h during 202 full-day follows and we collected

Table 2 Size of study groups of *Colobus vellerosus* at Boabeng-Fiema and number of follow days

Group	Mean group size	Group size range	No. of AM range	Long dry (abundant) season:		Long wet (lean) season:	
				No. of follow days	No. of focal hours	No. of follow days	No. of focal hours
RT	13	13	1	14	30.7	18	41.2
B2	15	13–17	1–3	14	31.5	16	34.8
DA	24.5	21–31	3–4	16	30.8	16	37.2
WW	30.5	28–33	7–10	27	54.8	16	37.7

433.3 h of focal-animal data. Table 2 shows the number of hours analyzed for this study during the abundant and lean seasons for each group. We used focal-animal data to determine the activity budget and diet. For all individuals in each group, the duration of time spent in four main behavioral categories was calculated for the activity budget: (1) feed—the manipulation and ingestion of food items; (2) move—all travel with no manipulation of food; (3) social behavior—grooming, play, copulations, and aggression; and (4) rest—all times when the individual was stationary and not feeding, moving, or in a social interaction. The diet of each group was determined for each season as the total proportion of feeding time spent on different plant parts during focal samples on all individuals. To collect group spread estimates, scans were taken at the end of focal samples when the location of > 75% of the group was known. We recorded the trees that represented the widest distance between individuals, and later, we measured the distance between the boles on a map of the field site, then half the distance of the crown diameter of these trees was added to get an estimate of group spread (Saj and Sicotte 2007b). During group-spread scans, the “group activity” was recorded and defined as the activity of at least 75% of the group. Group spread estimates when the group was feeding are compared here between the lean and abundant seasons.

We defined a between-group encounter as any time individuals of both sexes from two groups came within 50 m of one another. In contrast, male incursions occurred when only males from one group approached (and often attacked) members of another group to within 50 m. Male incursions in this population allow non-alpha males to assess neighboring groups for dispersal opportunities and alpha males to demonstrate their fighting abilities (Teichroeb et al. 2011). We therefore, only retained between-group encounters as a measure of BGC caused by changes in food availability. All occurrences of between-group encounters were noted during full-day follows. Encounters separated by at least 2 h were considered to be distinct. The same two groups met on the same day on 11 occasions and these encounters averaged 5 h and 45 min apart. Our data set includes 126 encounters. We have detailed data on the group approaching, the individuals initiating aggression, the type of aggression, and the group retreating in a subset of this sample (63/126, 50%). An individual was defined as “participating” in an encounter if they directed any aggressive behaviors towards the other group (e.g., jump-

display, open-mouth, stiff-leg, chase, contact aggression, etc.) or if they approached individuals in the encountered group to interact with them in some way (e.g., affiliatively, sexually, etc.). Encounters were not always aggressive and, on occasion, groups did come to within 50 m of one another and ignore, or just stare at, one another (16/126, 12.7%). In aggressive encounters (110/126, 87.3%), the “winners” were considered to be those groups that displaced the other group, forced it to retreat, or change direction (Fashing 2001; Harris 2006; Teichroeb et al. 2012). If the aggression between groups was mild (49/110 aggressive encounters, 44.5%) and just involved displays directed towards one another, a winner was usually difficult to determine. Encounters could also be highly aggressive but without any group able to force the other to retreat. A clear winner could be determined in 52 of the 126 (41.3%) between-group encounters analyzed here ($n = RT-30, B2-14, DA-29, WW-53$).

Scan samples to measure ranging behavior were taken every 30 min during full-day follows (“location scans”). We recorded all trees occupied by the group relative to 50 × 50 m quadrats on a map of the field site, as well as the approximate center of mass of the group in relation to the location of trees (Waser 1974). Home ranges and day ranges were determined from a total of 3336 location scans taken during follows in the abundant and lean seasons (for each group, respectively for each season—RT, 325 abundant, 447 lean; B2, 349, 425; DA, 372, 375; WW, 643, 400). We defined the home range of each group as all 50 × 50 m quadrats entered during follows in each season. To be sure that sampling effort was equal for the abundant and lean seasons for our comparisons of home ranges, we used the maximum number of days available in one season and randomly selected an equal number of days for representation in the other (RT, 14 follow days in each season; B2, 14; DA, 15; and WW, 16). Day ranges were determined using center of mass points recorded during full-day follows. We then used straight-line measurements between these points to estimate the distance moved by the group from dawn until dusk.

Data analyses

We examined the seasonal diets of the four study groups to ensure that they followed previous research on *C. vellerosus* at BFMS (Saj and Sicotte 2007a) in feeding on more mature

leaves in the lean season and more varied food items in the abundant season. The proportion of feeding records made up by mature leaves, young leaves/buds, fruit, seeds/seed pods, and flowers was compared between seasons for each group using z tests. We then ran a test to ensure that seasonal patterns in colobus range use were due to changes in food availability and not simply to differences in temperature and rainfall between the seasons. We used a generalized linear mixed model with day range length as the response variable and rainfall in mm, minimum temperature, maximum temperature, and group size as predictor variables with group ID included as a random effect.

Between-group, within-season comparisons

To determine if scramble feeding competition was occurring in both the abundant and lean seasons, we compared data from each season between our four groups. We only compared behavioral adjustments to scramble competition that were previously shown to be significant between the groups (mean day range length, group spread while feeding, home range size, and proportion of the day spent feeding, Teichroeb and Sicotte 2009). Kruskal-Wallis tests with Dunn's post hoc comparisons were used for all comparisons except home range size. Home range area size was just a single value for each group (a count of the number of quadrats entered) in each season, so both seasons were compared together in a single linear regression after ensuring that the data were normal using a Shapiro-Wilk test ($p = 0.38$). Home range size was the response variable, and group and season were included as predictor variables. For comparative purposes, we also present effect sizes for each behavioral measure of WGS between the smallest (RT) and largest (WW) of our study groups. Effect sizes were calculated as Cohen's d , the difference between the means for each study group divided by the pooled standard deviation.

Between-season, within-group comparisons

To examine patterns of ranging between seasons within each group, we first compared home range size in the abundant and lean seasons with Fisher's exact tests. Again, since home range size was a single number (a count of quadrats entered), we compared seasons using 2×2 contingency tables of the number of quadrats within that group's total home range used versus unused in each season. Seasonal changes in range use and the number of between-group encounters were examined with generalized linear mixed models for each group. The variables analyzed this way included day range length, the number of trees entered daily, mean daily group spread while feeding, and the number of between-group encounters experienced daily. Group was included as a random factor in all models to account for multiple observations over time. Day range lengths and group spreads were normally distributed, so

linear distributions were used for these models, while the number of trees entered and number of between-group encounters experienced were counted per day, so we used log-linear (Poisson) distributions for these models.

Finally, Fisher's exact tests and point biserial correlations were also used to examine seasonal differences in winning between-group encounters and avoidance of other groups, respectively. We quantified avoidance of other groups by examining whether there was a correlation in the number of scans a group spent in a quadrat and whether or not other groups shared that quadrat. Though this is an indirect measure of avoidance, simultaneous follows of groups were not conducted to assess avoidance more directly. All statistics were two-tailed and were done using R version 3.2.0 (R Core Team 2015), SPSS version 24.0, and Excel for Windows. An alpha level of 0.05 was set for significance.

Data availability The data used for this manuscript are available from the corresponding author upon reasonable request.

Results

Seasonal diets

Compared to the abundant season, diets in the lean season showed significant increases in mature leaf consumption and decreases in young leaf, fruit, and flower consumption for all groups (Table 3). Three groups out of four also showed a decrease in seed/seed pod consumption in the lean season, though the largest group (WW) increased their seed feeding in the lean season relative to the abundant season (Table 3).

Rainfall and temperature effects on day range

The GLMM showed that neither rainfall ($t = 0.994$, $p = 0.34$), minimum temperature ($t = 1.647$, $p = 0.102$), nor maximum temperature ($t = 1.85$, $p = 0.067$) were significantly associated with changes in day range length over the study. Only group size showed a significant effect ($t = 2.241$, $p = 0.027$).

Is WGS occurring in both the abundant and lean seasons? Between-group, within-season comparisons

Abundant season

Mean day range lengths were significantly different between groups ($H = 13.97$, $df = 3$, $p = 0.0029$, Kruskal-Wallis; Table 4). Post hoc tests showed that this was due to RT and DA having significantly smaller day ranges compared to the largest group, WW (RT vs. WW— $p = 0.028$, DA vs. WW—

Table 3 Diet of each study group of *Colobus vellerosus* at Boabeng-Fiema in the abundant and lean seasons

Group/ season	Mature leaves (%)	Mature leaves seasonal difference (<i>z, p</i>) ^a	Young leaves/ buds (%)	Young leaves/ seasonal difference (<i>z, p</i>) ^a	Leaves (unknown age) (%)	Fruit (%)	Fruit seasonal difference (<i>z, p</i>) ^a	Seed/ seed pods (%)	Seeds seasonal difference (<i>z, p</i>) ^a	Flower (%)	Flower seasonal difference (<i>z, p</i>) ^a	Other ^b (%)
RT												
Abundant	3.6	-107, <0.01	47.6	9.3, <0.01	5.2	31.2	71.2, <0.01	7.4	c	4.9	33.6, <0.01	0.2
Lean	47.5		43.3		1.5	5.8		0		0.1		1.8
B2												
Abundant	5.6	-86.9, <0.01	67.1	38.7, <0.01	1.7	10.1	26, <0.01	6	c	2.6	c	7
Lean	38.3		49.3		1.5	3.8		0		0		7.1
DA												
Abundant	18.5	-77.8, <0.01	54.2	31.1, <0.01	3.6	9.2	c	5.7	c	8.7	36, <0.01	0.1
Lean	52.1		40		1.5	0		0		1.4		5
WW												
Abundant	12.1	-42.8, <0.01	67	39.6, <0.01	2.6	3	31.5, <0.01	5.1	-4.9, <0.01	9.5	55.5, <0.01	0.7
Lean	36.6		53.8		3	0.03		5.9		0.4		0.4

^a Z test for the significant difference between the proportions of records for that plant part between the seasons

^b Includes bark, pith, sap, stems, soil, *Ceiba pentandra* cotton fiber, and drinking water.

^c A sample size of zero in one season does not allow statistics to be performed

Table 4 Seasonal means and standard deviations of each behavioral manifestation of within-group scramble competition compared for each study group

Group	Mean day range length (m)		Home range size (ha)		Mean feeding group spread (m)		Mean time spent feeding per day	
	Abundant	Lean	Abundant	Lean	Abundant	Lean	Abundant	Lean
RT	331 (± 105)	342 (± 91)	5.5	5.75	34.7 (± 18)	37.4 (± 20)	21.8% (± 8)	16.8% (± 7)
B2	358 (± 102)	314 (± 102)	6.75	9	51 (± 26)	39 (± 10)	24.6% (± 9)	15.7% (± 8)
DA	337 (± 120)	335 (± 142)	8.5	12.75	50.6 (± 15)	43.9 (± 10)	23.8% (± 10)	16.8% (± 11)
WW	446 (± 112)	475 (± 101)	8.25	12	65.7 (± 31)	61.5 (± 19)	26.4% (± 8)	23.4% (± 13)

$p = 0.01$, Dunn's Test). The effect size (Cohen's d) between the smallest (RT) and largest (WW) group for mean day range length was 0.88. Mean group spreads while feeding were significantly different between groups ($H = 9.11$, $df = 3$, $p = 0.028$, Kruskal-Wallis; Table 4) and post hoc pairwise tests showed that this difference was driven by the smallest group, RT, having significantly smaller group spreads compared to the largest group, WW (RT vs. WW— $p = 0.022$, Dunn's test; effect size 0.95). The proportion of the day spent feeding was not significantly different between the study groups ($H = 1.71$, $df = 3$, $p = 0.635$, Kruskal-Wallis; Table 4) and the effect size between the smallest and largest group was 0.31.

Lean season

Mean day range lengths were significantly different between groups ($H = 18.76$, $df = 3$, $p = 0.0003$, Kruskal-Wallis; Table 4). A post hoc Dunn's test showed that this was due to all other groups having significantly smaller daily ranges than the largest group (RT vs. WW— $p = 0.013$, B2 vs. WW— $p < 0.0001$, DA vs. WW— $p = 0.013$). The effect size between the smallest and largest group for day range length in this season was 0.98. Mean group spreads while feeding were significantly different between groups, as well ($H = 11.61$, $df = 3$, $p = 0.009$, Kruskal-Wallis; Table 4). Post hoc pairwise tests showed that this difference was again driven by the smallest group, RT, having significantly smaller group spreads than the largest group, WW (RT vs. WW— $p = 0.014$, Dunn's test; effect size 0.97). The proportion of the day spent feeding was not significantly different between the study groups although the p value approached significance ($H = 7.55$, $df = 3$, $p = 0.056$, Kruskal-Wallis). The mean values suggest that the individuals in the largest group spent a larger proportion of their day feeding (Table 4) and the effect size between the smallest and largest group was 0.58.

Home range size comparisons showed a significant effect of both group ($p = 0.015$) and season ($p = 0.047$) (overall model adjusted $R^2 = 0.72$, $F = 10.02$, $p = 0.018$, linear regression; Online resource, Fig. S1). These results combined show that behavioral manifestations of scramble competition were expressed in both seasons but were more intense in the lean

season. Effect sizes were greater in the lean season compared to the abundant season for every measure of competition between the smallest and the largest groups.

Is WGS influencing the occurrence and intensity of BGC?: Between-season, within-group comparisons

Ranging

At equal sampling effort, the proportion of the home range used was larger for all of the groups in the lean season compared to the abundant season (Fig. 1, Online resource Fig. S1) and significantly so for the smallest and the two largest groups (RT, $p = 0$; B2, $p = 0.103$; DA, $p = 0.002$; WW, $p = 0.002$; Fisher's exact test; Online resource Fig. S1, Table 4). Every group also showed seasonal changes in their usage of certain home range areas over others (Fig. 1b–e). Day range lengths were longer in the lean season for the smallest (RT) and the largest groups (WW), though not significantly so (RT, $p = 0.74$; WW, $p = 0.4$; generalized linear mixed model; Fig. 2, Tables 4 and 5). These two groups also entered more trees in

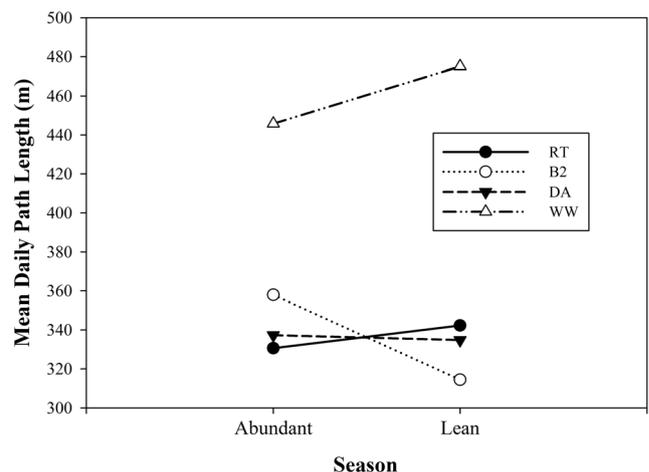


Fig. 2 Interactions between group and season in mean day range lengths. Mean day range lengths (m) for each group in the abundant and lean seasons (groups displayed in legend in order of increasing group size)

Table 5 Results of generalized linear mixed models for each group showing the effect of season on ranging and number of between-group encounters

Group/dependent variable	Coefficient	SE	<i>t</i>	<i>p</i>	Seasonal relationship
RT					
Day range length	-11.714	35.399	-0.331	0.743	-
No. of trees entered	-0.172	0.087	-1.991	0.056	Lean > abundant*
Group spread while feeding	-2.690	8.905	-0.302	0.766	-
No. of between-group encounters	-0.110	0.327	-0.336	0.739	-
B2					
Day range length	43.473	37.329	1.165	0.254	-
No. of trees entered	-0.056	0.094	-0.593	0.558	-
Group spread while feeding	11.749	11.326	1.037	0.315	-
No. of between-group encounters	1.050	0.485	2.166	0.039	Lean < abundant
DA					
Day range length	2.466	47.419	0.052	0.959	-
No. of trees entered	-0.080	0.117	-0.681	0.502	-
Group spread while feeding	6.782	5.816	1.166	0.257	-
No. of between-group encounters	0.352	0.320	1.100	0.280	-
WW					
Day range length	-29.268	34.328	-0.853	0.399	-
No. of trees entered	-0.171	0.081	-2.117	0.041	Lean > abundant
Group spread while feeding	4.164	9.549	0.436	0.665	-
No. of between-group encounters	-0.114	0.260	-0.439	0.663	-

*Strong trend

the lean season compared to the abundant season, though this was only significant for WW (RT, $p = 0.056$; WW, $p = 0.041$; Table 5). The two middle-sized groups (B2 and DA) showed on average shorter daily path lengths in the lean season, though again this was not significant (B2, $p = 0.25$; DA, $p = 0.96$; Table 5, Fig. 2) and they did not enter significantly more trees in the lean season (B2, $p = 0.56$; DA, $p = 0.5$). No group showed significant changes in group spread while feeding between the seasons (Table 5).

Between-group encounters

Each study group used more of its home range in the lean season (Fig. 1). We investigated the effect of this increased range use on BGC by examining seasonal changes in between-group encounters. Groups that ranged further per day in the lean season showed a slight increase in the number of between-group encounters experienced per day in this season (means—RT, abundant 0.93, lean 0.94; WW, abundant 1.15, lean 1.25) and groups that ranged less showed a decrease (means—B2, abundant 0.71, lean 0.25; DA, abundant 1, lean 0.75; Online resource Fig. S2). However, generalized linear mixed models showed that this was only significantly different in the case of group B2, which was involved in significantly fewer between-group encounters in the lean season compared to the abundant season (RT, $p = 0.74$; B2, $p = 0.039$; DA, $p = 0.28$; WW, $p = 0.66$; Table 5).

Male participation occurred in 95.2% of between-group encounters (60/63) and was only absent during three encounters where groups came within 50 m of one another but did not react. Females participated in 43.5% of between-group encounters (27/62 encounters where observers were certain of participants). Using only cases where a winner could be determined at the end of between-group encounters, the two groups that had slightly longer day range lengths and got into more between-group encounters in the lean season also won encounters at high rates (wins RT—76.9% (10/13), WW—77.3% (17/22)). The groups that did not have longer day ranges in the lean season and got into fewer between-group encounters compared to the abundant season were less successful at winning the encounters in which they were involved (wins B2—25% (2/8), DA—22.2% (2/9); RT and WW winning rate vs. B2 and DA winning rate, $p = 0.0003$; Fisher's exact test). The groups that won more encounters (RT and WW) were different in composition. RT was the smallest group and had a single male, while WW was the largest group that had the most adult males. The groups that lost most between-group encounters (B2 and DA) were middle-sized and had several adult males (Table 2; Fig. 3).

Seasonal differences in the rate of winning also occurred (Online resource Fig. S3). RT had high rates of winning in both seasons with a slight non-significant increase in the lean season (abundant—66.7% (4/6), lean—85.7% (6/7), $p = 0.56$; Fisher's exact test). The rates of winning for B2 and DA were low in both seasons (B2, abundant—33.3% (2/6), lean—0%

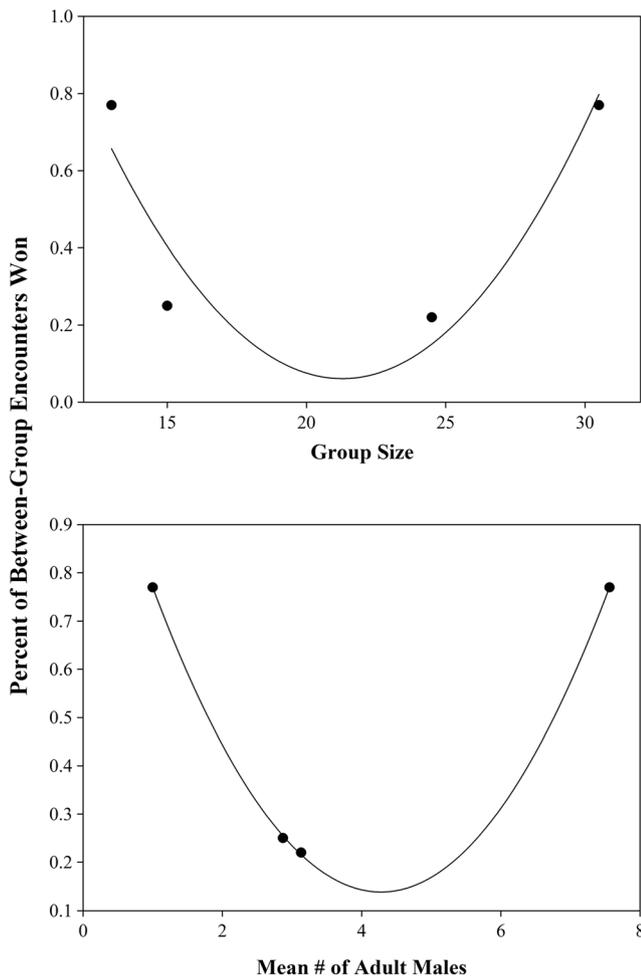


Fig. 3 Plots showing the percent of between-group encounters that were won overall against group size and the mean number of adult males in the group with fitted quadratic curves

(0/2), $p = 1$; DA, abundant—25% (1/4), lean—20% (1/5), $p = 1$; Fisher's exact test). The largest group, WW, had a significant drop in their ability to win in the lean season (abundant—100% (14/14), lean—37.5% (3/8), $p = 0.002$; Fisher's exact test). All the losses that WW suffered in the lean season were to small groups with a single male ($n = 4$ groups).

Are some groups avoiding others in the lean season?

The results above suggest that the B2 and DA, the two groups that were involved in fewer between-group encounters and lost many of them (B2 and DA) were in fact actively avoiding other groups in the lean season. The heat maps comparing range use in the wet and dry seasons (Fig. 1) show that these two groups were on the edge of the forest fragment and could move into lower-quality forest near the edge to avoid other groups. B2 showed a clear shift in their core area (area used 50% of the time) in the lean season away from shared boundaries with other groups (Fig. 1c). In the abundant season, there was no correlation between the number of scans B2 spent in a

quadrat and whether or not other groups shared that quadrat ($r_{pb} = -0.14$, $df = 25$, $p = 0.49$; Point biserial correlation), while in the lean season, we found a negative correlation ($r_{pb} = -0.36$, $df = 38$, $p = 0.022$). For DA, while the heat map does show that they spent more time towards the edge of the fragment in the lean season compared to the abundant season (Fig. 1d), there was no correlation between the number of scans they spent in a particular quadrat and whether or not other groups shared that quadrat in either season (abundant $r_{pb} = -0.23$, $df = 32$, $p = 0.2$; lean $r_{pb} = 0.08$, $df = 48$, $p = 0.57$).

Discussion

Previously, we showed that our four study groups of *C. vellerosus* at Boabeng-Fiema were experiencing within-group scramble feeding competition (WGS) over an annual cycle. Larger groups, with similar home range quality to smaller groups, had larger home ranges, longer day ranges, greater group spread while feeding, and spent more time feeding per day (Teichroeb and Sicotte 2009). Here, we show that these effects did not just occur in a single season. There was variation in the intensity of WGS experienced over the year, as food availability varied. We predicted that the behavioral adjustments to WGS would be more intense in the lean season when compared to the abundant season, and, more crucially, that these effects would be stronger in larger groups, as this would mean that the intensity of WGS is stronger in larger groups. Indeed, while some behavioral manifestations of WGS were seen in the abundant season (day range lengths were longer in the largest group (WW) compared to two smaller groups (RT and DA), and WW had a larger feeding group spread than RT), the lean season was associated with more manifestations of WGS. The largest group's day range lengths were longer than all other groups. Home range sizes were significantly different between the groups with larger groups using more area. Feeding group spread was again larger in the largest group (WW) compared to the smallest group (RT) and the percent of time spent feeding tended to be greatest in the largest group as well. Importantly, comparisons between the smallest and the largest groups showed that the effect sizes on all measures of WGS were greater in the lean season compared to the abundant season. We did not expect that groups or individuals would need to use all of the behavioral adjustments to scramble competition, as using one modification may render the expression of the others unnecessary (Snaith and Chapman 2007). Our results suggest that, by searching a larger area daily, using more of the home range, and feeding longer over the course of the lean season, our larger groups were able to compensate for food depletion and presumably (although this remains to be tested) meet their nutritional requirements.

The need for greater range use in the lean season did appear to impact between-group contest competition (BGC), although in different ways for different groups. RT and WW were able to range slightly further per day and enter more trees daily in the lean season compared to the abundant season, leading to them being involved in more between-group encounters. The small, uni-male, multi-female RT won encounters at high rates in both the abundant and the lean seasons (when a winner could be determined). The large, multi-male, multi-female WW group won all of their between-group encounters in the abundant season but did less well in the lean season, when they lost all their encounters with small, uni-male groups. These two groups, the small RT and the large WW, appeared to have better competitive ability than the two medium-sized groups. The importance of large group size in the ability to win between-group encounters is well documented in the primate literature and large groups can often just overwhelm and drive away smaller groups (reviewed in: Cheney 1987; Crofoot et al. 2008). The primate literature is also rife with examples of groups doing better in between-group contests when they have a greater number of males, which often correlates with group size (e.g., *Papio cynocephalus ursinus*, Kitchen et al. 2004; *P. cynocephalus*, Markham et al. 2012; *Propithecus verreauxi*, Benadi et al. 2008; *Sapajus nigritus*, Scarry 2013; *Macaca assamensis*, Richter et al. 2016). Males were the main participants in BGC in *C. vellerosus*; however, as we have previously documented, males in multi-male groups seem to have reduced fighting ability relative to males in uni-male groups. Males in uni-male groups are able to monopolize a group of females because they have succeeded at evicting other males and are able to keep them out of the group, while males in multi-male groups seem unable to do this and are often involved in lengthy dominance struggles (i.e., they have lower resource holding potential (RHP)) (Teichroeb and Sicotte 2010; Teichroeb et al. 2012). In *C. vellerosus*, this appears to translate into uni-male groups having a competitive advantage in BGC because the males have superior fighting ability but perhaps also because males in multi-male groups suffer from collective action problems (Olson 1965; Teichroeb et al. 2012). Several males, working together, should be able to defeat a single male, even if that single male has higher competitive ability. However, males in multi-male *C. vellerosus* groups do not appear to form lasting coalitions (Teichroeb et al. 2013). This is likely partly due to natural selection favoring free riders over cooperators when it comes to defending shared resources (i.e., a range and females) (Hawkes 1992). In a comparative analysis with 138 species, Willems and van Schaik (2015) have shown that animal groups are particularly affected by collective action problems if they are not cooperative breeders, the dominant sex disperses, and group size is large with several members of the dominant sex; characteristics that perfectly describe multi-male groups of *C. vellerosus*.

The two medium-sized groups in this study (B2 and DA) were multi-male, and thus, had neither the advantage of male(s) with high RHP nor large group size to help them in BGC. These groups lost most of their between-group encounters in both the abundant and lean seasons. Though B2 and DA also used more of their home range in the lean season, they got into fewer between-group encounters in this season and ranged into areas closer to the fragment edge. In the case of B2, this indicated active avoidance of other groups in the lean season, as they spent significantly more time in unshared quadrats at this time. When any kind of contest competition occurs, dominance hierarchies are likely formed between groups (Sterck et al. 1997). Knowledge of the competitive abilities of neighboring groups and knowing that you are likely to lose to them drives avoidance behavior and allows animals to avert costly aggression (Enquist and Leimar 1983; Bernstein 2011). Thus, the medium-sized, multi-male groups in this study seemed doubly disadvantaged in the lean season, given that they needed to range further to acquire sufficient resources but could not do this where their range bordered other groups. This appears to have forced them to spend more time closer to edge of the forest fragment, habitat areas that were less species diverse, with fewer large trees, and a lower basal area of food trees (JAT, unpubl. data, within 100 m of edge sampled area 1.75 ha, no. of species = 56, no. of food species = 26, mean diameter at breast height (DBH) = 25.7 cm, food tree basal area = 11.7 m²/ha; Interior part of the forest, sampled area 3.75 ha, no. of species = 79, no. of food species = 41, mean DBH = 30.3 cm, food tree basal area = 16.7 m²/ha).

What are males defending?

Male *C. vellerosus* were involved in all between-group encounters where aggression occurred. Sicotte and MacIntosh (2004) showed that this aggression is most often by adult males and targeted towards other adult males. This suggests that between-group encounters function, at least partly, in mate defense (Wrangham 1980; Sicotte 1993). In fact, males are always expected to directly defend mates when faced with other males (Fashing 2001). However, this does not preclude the use of other strategies by males to ensure their reproductive success. For example, male *C. vellerosus* have been observed to directly defend infants during between-group encounters (Teichroeb et al. 2012). The results of the present study provide further evidence that *C. vellerosus* males are also engaging in resource defense during between-group encounters, which was also suggested earlier (Sicotte and MacIntosh 2004; Teichroeb et al. 2012). Here, we show that male success in between-group encounters was important in allowing groups to be able to range further and enter more trees during lean seasons, especially in areas that were densely populated by other groups. Groups that did not have competitive males did not win between-group encounters, and ranged

towards the forest fragment edge, avoiding other groups. The question still remains though as to whether resource defense by male *C. vellerosus* was direct or indirect (i.e., hired guns, Rubenstein 1986). Indirect resource defense arises as a result of mate defense and males are not expected to participate in between-group encounters when females are not receptive to mating (Fashing 2011). Male *C. vellerosus* are always active in between-group encounters, regardless of season, but because mating occurs across seasons (Teichroeb and Sicotte 2008b), this does not provide evidence for either direct or indirect resource defense without greater investigation into the exact composition of groups and the reproductive state of females. If males are defending infants, this may also occur across the seasons. The greater success of small, uni-male *C. vellerosus* groups in between-group encounters across seasons and especially in the lean season is interesting. Fashing (2001) predicted that resource defense would be particularly beneficial for males in small, uni-male groups where the male can benefit from attracting females to defended areas because he can monopolize all the mating in the group. Male *C. vellerosus* in uni-male groups stand to gain a lot if they defend resources, mates, and infants, and given their high RHP, they may be defending all these things, while additionally exposing females in their group to less WGS.

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Compliance with ethical standards This research was purely observational and non-invasive. Research was carried out with permission from the Ghana Wildlife Division and the management committee of the Boabeng-Fiema Monkey Sanctuary. Data collection methods were compliant with the University of Calgary's Animal Care Committee and with the laws of Ghana.

Conflict of interest The authors declare that they have no conflict of interest.

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