Cost-free vigilance during feeding in folivorous primates? Examining the effect of predation risk, scramble competition, and infanticide threat on vigilance in ursine colobus monkeys (Colobus vellerosus)

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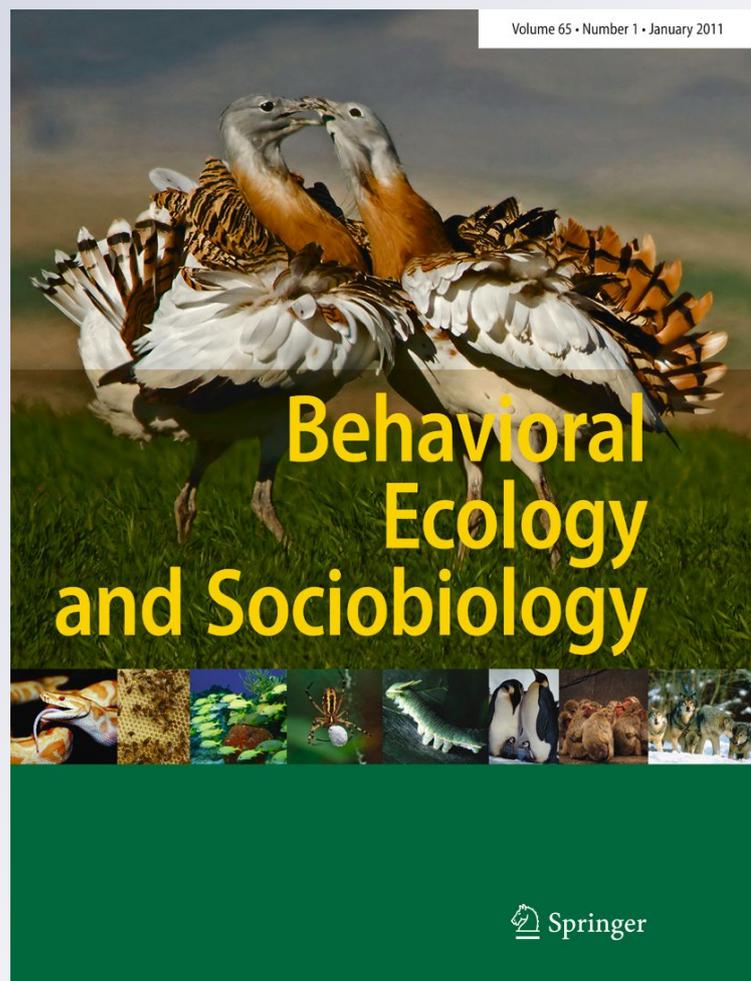
Julie A. Teichroeb · Pascale Sicotte

Abstract Vigilance often decreases with increasing group size, due to lower predation risk or greater scramble competition for food. A group size effect on vigilance is seldom seen in primates, perhaps because scanning and feeding often occur simultaneously or because the distinction between routine and induced vigilance has not been investigated. We analyzed feeding and resting observations separately while distinguishing between routine and induced scans in four groups of wild ursine colobus monkeys (*Colobus vellerosus*) experiencing scramble competition for food and infanticide risk. We used linear mixed-effect models to test the effect of group size, age–sex class, number of neighbors, number of adult male neighbors, and height in the canopy on scanning rates (vigilance) with and without evident conspecific threat. Food type was also examined in the feeding models. Perceived predation risk affected vigilance more than scramble competition for food and infanticide risk. Routine and induced vigilance were greatest at lower canopy heights during feeding and resting and increased when individuals had fewer neighbors while resting. A group size effect was found on induced vigilance while resting, but scanning increased with group size, which probably indicates visual monitoring of conspecifics. Scanning rates decreased while feeding on foods that required extensive manipulation. This supports the idea that vigilance is relatively cost free for upright feeders when eating food that requires little manipulation, a common feature of folivore diets. In the presence of threatening conspecific males, close proximity to resident males decreased individual vigilance, demonstrating the defensive role of these males in the group.

Animals that live in groups face a theoretically decreased risk of predation because the presence of other individuals provides detection and dilution effects (Dehn 1990; Krause and Ruxton 2002), reducing the amount of time each individual has to spend scanning the environment (Pulliam 1973). Indeed, vigilance decreases with increasing group size in several mammal and bird species (Elgar 1989; Quenette 1990). The degree to which this results from a decrease in perceived predation risk is debated however because other behavioral reactions to living in a larger group could also lower vigilance (Beauchamp 2003). For instance, scramble competition for food may lead to decreased vigilance (Beauchamp and Ruxton 2003) because individuals are allocating time to acquiring food resources before they are depleted (by increasing their feeding rate or time spent feeding) rather than to scanning for predators (e.g., Clark and Mangel 1986; Elgar 1989; Cezilly and Brun 1989; Beauchamp and Livoreil 1997; Beauchamp 1998; Grand and Dill 1999; Randler 2005; Rieucau and Giraldeau 2009). Scramble competition does not involve direct aggression and displacements over food (i.e., contest competition) but occurs when others use resources before an individual can encounter them (Janson

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1988). The presence of scramble competition for food is shown when individuals must increase their foraging effort (by moving further, feeding faster, etc.) in the company of other foragers compared to when they are solitary (Wrangham et al. 1993; Chapman and Chapman 2000). Untangling the effects of scramble competition and predation risk on decreased vigilance in larger groups has proven difficult (Lima et al. 1999).

Most studies on primates have shown a lack of effect of group size on vigilance (e.g., blue monkeys, Cords 1990; white-faced capuchins, Rose and Fedigan 1995; baboons, Cowlishaw 1998; red-tail monkeys, red colobus, Treves 1998; Treves 2000; black howler monkeys, Treves et al. 2001; but see de Ruiter 1986). Besides predation risk and scramble competition for food, other factors may affect vigilance and might counteract the expected decrease in scanning in larger groups (Treves 2000). Several of these factors have been found to be at work in primates: (1) within-group social monitoring may increase with group size (e.g., Caine and Marra 1988; Treves 2000; Kutsukake 2007; but see Treves 1999). (2) Monitoring of extra-group males (conspecific threat) (e.g., Steenbeek et al. 1999; MacIntosh and Sicotte 2009) may increase in larger groups because these males are more attracted to groups with more females (e.g., Steenbeek and van Schaik 2001; Teichroeb et al. 2011). (3) Since all group members are unlikely to be seen at the same time, the proximity of immediate neighbors may be more important than overall group size in determining vigilance (e.g., Cowlishaw 1998; Treves 1998; Treves et al. 2001). Familiar neighbors may also decrease vigilance more than the proximity of unfamiliar individuals (e.g., MacIntosh and Sicotte 2009).

However, one overarching reason for the lack of a group size effect on vigilance in nonhuman primates may be that scramble competition for food affects vigilance differently in primates than in some other animals. Many primates typically feed in an upright position, and when food requires minimal extra-oral processing with the hands, vigilance may not be costly for primates in terms of reduced feeding time (see also "Discussion"; Treves 2000). This means that:

> if the feeding costs of vigilance are small, and in some cases negligible, then animals at low risk of predation will have little to lose by maintaining high levels of vigilance, thus leading to a breakdown in the classic relationships between vigilance and predation risk. Cowlishaw et al. 2003:32

Cowlishaw et al. (2003) proposed that when food processing requires little visual attention, scanning and feeding are not incompatible activities. Many food items require little food processing beyond searching for food, putting it in the mouth, and chewing, making handling time

compatible with scanning the environment. Alternatively, feeding on food that requires visual attention because it needs to be processed with the hands or mouth should not be compatible with scanning.

Here, we analyze scanning rates for both routine and induced vigilance (Blanchard and Fritz 2007) for individuals in four differently sized groups of ursine colobus monkeys (*Colobus vellerosus*) at the Boabeng-Fiema Monkey Sanctuary (BFMS) in Ghana. We examine whether scramble competition for food, perceived predation risk, or infanticide threat had a greater effect on vigilance in this species. We also test Cowlishaw et al.'s (2003) proposition that scanning rates differ depending on whether or not individuals feed on food that requires visual attention. The separation of routine scanning, which is done in animal's spare time and is relatively cost free, from vigilance induced by a stimulus is important. During induced vigilance, individuals often cease to feed, and thus, this type of vigilance is costly (Blanchard and Fritz 2007).

Our study species, *C. vellerosus*, are highly folivorous and relatively few of their food items require extensive processing (Saj and Sicotte 2007a; E. Wikberg, unpublished data). Those food items that do require some handling are seeds that are removed from pods and fruit with a large pit/stone that cannot be swallowed, while the majority of the diet can be fed upon with little manipulation (Table 1). The fact that some food types require visual attention to be processed allows us to compare scanning rates when individuals feed on these foods compared to foods that require little processing. Contest competition, in the form of aggression and displacements over food among *C. vellerosus*, is rare (Saj and Sicotte 2007b), but scramble competition for food occurs in this population and generally increases with group size (Teichroeb and Sicotte 2009). Larger groups have larger home ranges, range further per day, and spend more time feeding than smaller groups in similar quality habitat (Teichroeb and Sicotte 2009). Male infanticide occurs in *C. vellerosus* at BFMS (Teichroeb and Sicotte 2008a), and a previous study in this population on vigilance showed that extra-group conspecific threats caused the greatest increases in scanning behavior (MacIntosh and Sicotte 2009).

Many of predictions for the effects of scramble competition for food, predation risk, and infanticide risk on vigilance overlap (Table 2). To partially separate these effects on vigilance, we separated resting from feeding observations (Bednekoff 2003) and isolated observations with and without detectable threats by extra-group or new immigrant males. While scanning for predators is likely to occur whether individuals are feeding or resting, the effects of food competition on scanning are unlikely to occur when animals are resting. If scramble competition for food is an important determinant of vigilance in this population, we

Table 1 Diet of the study groups and degree of processing for each food item

Food item	Percentage of diet[a]	Amount of processing required
Young leaves/buds	48	Little[b]—grasped, pulled from the plant and eaten or bitten directly off the branch
Mature leaves	36	Little[b]—grasped, pulled from the plant and eaten or bitten directly off the branch
Seeds/seed pods	6	Some, depending on species[c]—very young seed pods may be eaten as leaves (no processing) but mature pods are pulled off the plant, and then bitten open to extract seeds from the pods (some processing)[d]
Fruit	5	Some, depending on species[c]—fruit with small seeds are pulled from the plant and eaten whole (no processing), fruit with pits/stones require the flesh to be bitten off from around the seed (some processing)[d]
Flowers/buds	3	Little[b]—grasped, pulled from the plant and eaten or bitten directly off the branch

[a] The total does not add up to 100% because a few items were eaten rarely and were classified as "others"

[b] Equivalent to "compatible handling time" in Cowlishaw et al. (2003)

[c] Equivalent to "incompatible handling time" in Cowlishaw et al. (2003)

[d] All observations of vigilance during feeding were taken when individuals were feeding on fruit that was eaten whole and required little processing and seeds/seed pods that required processing

predicted that, all else being equal, individuals would scan less: (1) in larger versus smaller groups when feeding only, as feeding time or rate must increase to counteract the effect of scramble competition for food, and (2) when individuals had more near adult/subadult neighbors during feeding only, as these neighbors would cause individuals to scramble to obtain more food resources. These effects should be seen for routine vigilance only, since time is being reallocated from routine scanning to food acquisition.

If food handling is an important determinant of vigilance rates, we predicted that, for routine scanning: (1) individuals would scan less when they were feeding on foods that required more processing, which involved visual attention directed to the food, compared to foods that require little manipulation. (2) Induced vigilance should not generally be affected by feeding, although it could increase when colobus are feeding on high-quality foods (usually foods requiring some processing) to the extent that this food is

Table 2 Predicted effects on routine and induced scanning rates (vigilance) for each hypothesis

Hypothesis	Effect on routine vigilance	Effect on induced vigilance
Scramble competition for food	Decrease with increasing group size while feeding only (no effect while resting)[a,b]	No effect of scramble competition
	Decrease with more near neighbors while feeding only (no effect while resting)	No effect of scramble competition
Food handling	Decrease when feeding on foods that require handling compared to those that do not	Increase when feeding on foods that require handling (if food is usurpable)
Predation risk	Decrease with increasing group size while resting and feeding[a]	Decrease with increasing group size while resting and feeding[a]
	Decrease with more near neighbors while resting and feeding	Decrease with more near neighbors while resting and feeding
	Increase when lower in the canopy while resting and feeding	Increase when lower in the canopy while resting and feeding
	Decrease with more adult male near neighbors	Decrease with more adult male near neighbors
Infanticide risk (e.g., extra-group and new males are in proximity)		Decrease when there are a greater number of resident adult male near neighbors
	Increased for adult females with infants compared to adult females without infants	Increased for adult females with infants compared to adult females without infants
	Decrease when there are a greater number of resident adult male near neighbors	Increased for adult males compared to subadult males
	Increased for adult males compared to subadult males	

[a] Vigilance for predators is likely to take place whether individuals are feeding or resting but vigilance caused by scramble competition for food is unlikely to take place during resting

[b] See "Discussion" for an examination of the validity of this prediction for folivorous primates

usurpable and may attract conspecifics leading to contest competition (Pruetz and Isbell 2000; Saj and Sicotte 2007b) (Table 2). If perceived predation risk is an important determinant of *C. vellerosus* vigilance, we predicted that, all else being equal, individuals would scan more during resting and feeding: (1) in smaller versus larger groups, (2) when they had fewer near adult/subadult neighbors, (3) when they were lower in the canopy, as distances to the safe refuge of the trees increase when individuals are on or near the ground (Elgar 1989), and (4) when there were fewer adult males as near neighbors, since these individuals often defend group mates from outside threats (JAT, personal observation). These effects should be seen during both routine and induced vigilance (Table 2). If infanticide risk is an important influence on vigilance, we predicted that, during resting when threatening males were near or in the group, both routine and induced vigilance: (1) would decrease for individuals when they had a greater number of resident adult male near neighbors because these males may act as defenders, (2) would be greater for adult females with infants compared to adult females without vulnerable offspring, and (3) would be greater for adult males compared with subadult males because adult males may lose their breeding position in the group by being evicted by a new or extra-group male (Table 2).

Materials and methods

Study site and species

This research was conducted at BFMS in central Ghana (7°43′ N and 1°42′ W), a dry semi-deciduous forest, 192 ha in size, located at an elevation of 350 m in the Nkoranza district of the Brong-Ahafo Region. BFMS is surrounded by farmland but connects to several smaller forest fragments in the area by a narrow, riparian forest. The vegetation is a mosaic of primary forest, regenerating farmland (secondary forest), and woodland (Fargey 1991; Saj et al. 2005).

Ursine colobus monkeys (*C. vellerosus*) at BFMS have been studied under the supervision of PS since 2000. They are medium-sized (mean weights: males, 8.5 kg; females, 6.9 kg, Oates 1994), arboreal primates that are primarily folivorous (Table 1). They are one of five black-and-white colobus species found in Africa (Oates 1994). Groups can be multi-male/multi-female, uni-male/multi-female, or all-male bands (AMBs) (Teichroeb et al. 2003; Saj and Sicotte 2005). All males disperse from the natal group (Teichroeb et al. 2011) while female dispersal is facultative (Teichroeb et al. 2009). There is no mating or birth season (Teichroeb and Sicotte 2008b). Between-group encounters are usually aggressive, with adult males as the main participants.

Group males, solitary males, and males in AMBs attack bisexual groups during male incursions (Sicotte and MacIntosh 2004). Male infanticide has been observed after male takeovers and immigration and accounts for 38.5% of infant mortality (Teichroeb and Sicotte 2008a). If incoming males do not evict them, putative sires may aid females in infant defense (Saj and Sicotte 2005; Teichroeb and Sicotte 2008a, b).

The diurnal primates at BFMS (*C. vellerosus* and Lowe's guenon, *Cercopithecus campelli lowei*) are traditionally sacred, and hunting by humans is taboo and illegal (Saj et al. 2005). Large predators (i.e., leopards) that could take an adult-sized colobus monkey are locally extirpated. People living within BFMS are forbidden from having dogs as pets, though this has only been enforced since the early 1990s and aggressive encounters between monkeys and dogs still occur in some of the forest fragments near Boabeng-Fiema (B.O. Kankam, personal communication). The animals in this study were never seen to encounter a dog. Immature colobus may suffer predation by large eagles. Alarm calling has been recorded towards tawny eagles (*Aquila rapax*) and long-crested eagles (*Lophaetus occipitalis*). Wahlberg's eagles (*Aquila wahlbergi*) have also been observed at BFMS (JAT, personal observation). No predation or predation attempts by these raptors have been seen. The predominant threats close to or on the ground to both young and adult colobus are constricting and venomous snakes (those observed by JAT include: royal python, *Python regius*; black mamba, *Dendroaspis polylepis*; green mamba, *Dendroaspis viridis*; spitting cobra, *Naja nigricollis*, and burrowing vipers, *Atractaspis* spp.; all of which are predominantly terrestrial except the green mamba, Cansdale 1961; Zug and Ernst 2004). Humans also sometimes cause the monkeys to alarm call, though only when the monkeys are suddenly disturbed low, or on the ground, in areas not frequented by people (JAT, personal observation). The subjects of this study were habituated to the presence of the observer, who was also careful never to disturb the monkeys during a focal sampling, so recorded vigilance was not directed at the observer.

Study groups and data collection

Data were collected on four groups of *C. vellerosus* (WW, DA, B2, and RT) for 13 months (July–November 2004, January–August 2005). All individuals in the small study groups (B2, $N=19$; RT, $N=13$) were recognized by features of the face and tail. All adult and subadult males and some adult and subadult females were recognized in the larger study groups (DA, $N=21$; WW, $N=24$). Group size varied for all groups except RT, with the greatest changes seen in DA group (Table 3) due to a takeover by an AMB

Table 3 Study group composition, hours of observation, and distribution of data

Name	Group size	Adults		Subadults		Juveniles/infants	Contact hours[a]	Vigilance focal hours	Known individuals used in analyses[b]	Mean number of focal samples/individual
		M	F	M	F					
RT	13	1	5	1	1	5	567.5	54.5	8	35.5
B2	13–17	1–3	4	2–4	0–1	4–5	574.5	50.2	13	21.3
DA	21–31	3–8	9–10	3–5	1–3	4–5	574	51.5	16	8.6
WW	28–33	6–10	10–11	2–6	2–3	2–5	690	61.3	21	8.5
Totals							2,406	217.5	58	

[a] Including JAT and research assistants

[b] Individuals that could be individually recognized

(Teichroeb and Sicotte 2009). Counts of individuals in RT and B2 could be done easily during follows; counts of the larger DA and WW groups were done opportunistically when they were crossing a narrow gap in the canopy or a road. At least one good group count was obtained per month.

Each study group was followed for two 2-day periods per month from dawn to dusk (6:00 am to 6:00 pm) by JAT and a research assistant. Behavioral observations were done using 10-min focal samples (Altmann 1974) that were alternated among adult and subadult individuals. At least 1 h was left between focal sampling on the same individual. Scan samples were taken every 30 min during follows to record all trees occupied by the group relative to 50×50 m quadrats on a map of the field site. The presence of other groups and their location in the home range of study groups was always noted ad libitum. We were in contact with groups for 2,406 h during 202 follow days. Focal-animal sampling where vigilance was recorded totaled 217.5 h (Table 3).

All behavioral data were recorded by a single observer (JAT) using 10×40 binoculars and a dictaphone and later transcribed to paper. Vigilance focal samples were conducted on adults and subadults of both sexes. Observations were not done on juveniles because young animals often show lowered vigilance when compared with adults and may rely on these older, more experienced individuals for scanning (e.g., Arnez and Leger 2000; Boukhriss et al. 2007). Females were separated into those with suckling infants and those with no dependent offspring, so that in the following analyses "Adult females with infants" is a subcategory of "Adult females" and some individual females are represented in both categories.

Routine and induced scans were treated as events (no duration was measured). Only looks outside the arms reach of subjects were recorded. Routine scans were defined as a brief (<1 s) movement of the head greater than or equal to 45° in any direction (Steenbeek et al. 1999), where the animal monitored its surroundings and did not interrupt

chewing if it was feeding. Induced scans were higher intensity and were defined as a fast snap of the head greater than or equal to 45° in any direction. Induced scans were of longer duration (>1 s) than routine scans and often occurring in response to an external stimulus (e.g., a falling branch, the call of a bird of prey). If the animal was feeding during an induced scan, it interrupted chewing during the look (JAT, personal observation; Blanchard and Fritz 2007). The return of the head to the normal position after a scan was not counted as a separate event. Scanning was recorded continuously during focal-animal sampling when the head was visible and the numbers of routine or induced scans per minute of observation were analyzed separately. Minutes where the head of the focal animal went out of sight, for any time period, were not included in the analyses. No attempt was made to identify the target of vigilance as this is difficult for animals high in the canopy (Steenbeek et al. 1999). At the beginning of each focal sample, the following contextual variables were noted: (1) behavior of the animal; (2) height in the canopy at 0.5-m intervals, (3) number and age–sex class of neighbors within 5 m, and (4) whether or not a between-group encounter or male incursion was occurring. Any changes in these contextual variables during focal sampling were recorded, and when something changed, that particular minute of observation was not included in the analyses. Only minutes where the focal animal was feeding or resting were analyzed (minutes with moving, grooming, etc. were excluded). The height of focal individuals in the canopy was determined in meters using a clinometer (Suunto, Forestry Suppliers Inc., Jackson, MS). Between-group encounters (BGEs) and male incursions occurred whenever individuals from two groups came within 50 m of one another (Oates 1977). BGEs ($N=163$) involved whole groups and both sexes coming into proximity whereas male incursions ($N=85$) involved only male(s) from one group approaching individuals from another group (Sicotte and MacIntosh 2004). Encounters separated by at least 1 h were considered distinct. The number of groups in the study area has increased since an

earlier study on vigilance (MacIntosh and Sicotte 2009, data collected in 2001), and groups' home ranges usually overlapped extensively with those of other groups. Thus, comparing vigilance in overlap versus non-overlap areas for all groups was not possible anymore.

When individuals were feeding during focal observations, the species and food type (mature leaves, young leaves/buds, fruit, seeds/seed pods, flowers/flower buds, or other) were noted. Though some fruit and some seeds require processing to obtain (Table 1), all focal samples recording vigilance happened to occur when individuals were feeding on fruits eaten whole (i.e., those that require little handling, *Celtis zenkeri*, *Ficus* spp., *Milicia excelsa*, *Pouteria alnifolia*, and *Vitex simplicifolia*) and on seeds that had to be extracted from the pod (i.e., those that required some handling, *Dioscorea dumetorum*, *Distemonanthus benthamianus*, *Pycanthus angolensis*, and mature pods of *Albizia ferruginea*). Therefore, observations where the food type was "seeds" are those where food handling was required, and all other food types showed little food handling.

Data analyses

Linear mixed-effect models were used to describe effects on routine and induced vigilance (scanning rates, number of scans per minute) during focal minutes when individuals were feeding and when they were resting (six models in total). Only feeding observations without new immigrant, extra-group, or infanticidal males within 50 m were used. For the resting models, observations with and without the presence of threatening males (extra-group males, within the first month of a new male(s) immigration, and periods with infanticidal attacks) were examined separately. Only observations on known individuals were analyzed (Table 3). Within a 10-min focal sample, minutes where the situation remained constant (at equal height, number and identity of adult/subadult neighbors, and food type) for the individual were amalgamated, and the mean scanning rates for routine and induced vigilance were determined. Any group size changes that occurred during the study were controlled by the models. Fixed factors included in all the vigilance models were: age–sex class, adult/subadult group size, height in the canopy, number of adult and subadult neighbors within 5 m, and number of resident adult males within 5 m. Observations on subadult females were omitted because of a small sample size. The feeding models also included the food type that the individual was feeding on at the time of the observation (mature leaves (N=64 feeding situations), young leaves/buds (N=144), fruit (N=14), seeds (N=6), flowers/flower buds (N=4), or other (N=30)) as a fixed factor. "Animal ID" was nested within "group ID," and these were included as random factors to control for multiple observations on the same individuals in the same groups (e.g., Meldrum and Ruckstuhl 2009). "Adult/subadult group size" was included as a repeated measure. Backwards model selection was done using a maximum likelihood method. Akaike Information Criteria (AIC) values were compared for all models generated with different covariance parameters, and those with the lowest AIC values were considered best-fit models.

Mann–Whitney U tests were used for post hoc pairwise comparisons of scanning rates for different age–sex classes. Since each age–sex class was used in three comparisons, the significance was lowered to 0.017 using a Bonferroni correction. For post hoc pairwise comparisons of scanning rates for individuals when feeding on different food types, Mann–Whitney U and t tests were used. The use of parametric versus non-parametric tests in these analyses was dependent on sample size. Too few observations were obtained of vigilance while feeding on flowers and flower buds to allow statistical comparisons. Since scanning rates for each food type were used in three comparisons, the significance was lowered to 0.017 using a Bonferroni correction. Comparison of routine and induced scanning rates for individuals when threatening males (new immigrant, extra-group, or infanticidal males) were within 50 m compared to when they were not were performed with paired t tests. To determine if mean scanning rates or number of near neighbors differed for individuals when they were feeding or resting, paired t tests were also employed. Spearman correlations were used to see if there was a relationship between adult/subadult group size and the number of near neighbors within 5 m during resting and feeding. Model selection and tests were done in PASW version 17.0, and statistics were two-tailed with an alpha level of 0.05 set for significance (except where a Bonferroni correction was applied).

Results

Routine vigilance while feeding

During feeding, routine vigilance was significantly affected by height in the canopy, food type, and age–sex class (Table 4). Routine scanning was significantly higher when individuals were lower in the canopy (linear mixed-effects model: F=30.697, df=208.2, P=<0.0001). For the food type eaten (F=5.107, df=179.3, P=<0.0001), post hoc comparisons showed that routine scanning rates were significantly lower when individuals fed on seeds than when they fed on any other food type (t test: $N_{mature\ leaves}$=23, $N_{young\ leaves/buds}$=37, t=0.41, P=0.68; Mann–Whitney U: $N_{mature\ leaves}$=23, N_{fruit}=8, Z=−0.56, P=0.58; $N_{mature\ leaves}$=23, N_{seeds}=6, Z=2.83, P=0.005; $N_{young\ leaves/buds}$=37, N_{fruit}=

Table 4 Linear mixed-effect models describing routine and induced vigilance during feeding without extra-group or new males present

Model term	Estimate (SE)	F	df	P
Routine vigilance				
Adult and subadult group size	−0.039 (0.03)	1.838	96.3	0.178
Age–sex class		3.271	66.5	0.026
Adult male[a]	1.305 (0.44)			0.004
Adult female	1.166 (0.44)			0.012
Adult female with infant	0.805 (0.47)			0.091
Subadult male	0 (0)			–
Height in canopy	−0.114 (0.02)	30.697	208.2	<0.0001
Number of adult and subadult neighbors within 5 m	−0.120 (0.08)	2.013	218.0	0.157
Number of adult male near neighbors within 5 m	−0.415 (0.28)	2.263	211.8	0.134
Food type		5.107	179.3	<0.0001
Mature leaves[a]	1.745 (0.49)			<0.0001
Young leaves and leaf buds	1.135 (0.43)			0.010
Fruit	2.482 (0.63)			<0.0001
Seeds	−0.546 (0.92)			0.554
Flowers and flower buds	1.151 (1.00)			0.253
Other	0 (0)			–
Induced vigilance				
Adult and subadult group size	−0.032 (0.03)	1.904	163.4	0.170
Age–sex class		3.051	131.8	0.031
Adult male[a]	0.285 (0.10)			0.006
Adult female	0.189 (0.10)			0.056
Adult female with infant	0.068 (0.10)			0.500
Subadult male	0 (0)			–
Height in canopy	−0.123 (0.02)	20.436	189.2	<0.0001
Number of adult and subadult neighbors within 5 m	−0.166 (0.08)	3.467	194.8	0.064
Number of adult male near neighbors within 5 m		1.526	188.5	0.218
Food type		0.506	167.8	0.771
Mature leaves[a]	0.020 (0.13)			0.878
Young leaves and leaf buds	0.067 (0.12)			0.566
Fruit	0.041 (0.17)			0.805
Seeds	0.337 (0.24)			0.165
Flowers and flower buds	−0.028 (0.26)			0.915
Other	0 (0)			–

[a] Indented categories are all compared with the final listed categories (subadult males and other food types)

8, $Z=-0.96$, $P=0.34$; $N_{\text{young leaves/buds}}=37$, $N_{\text{seeds}}=6$, $Z=3.73$, $P=0.0002$; $N_{\text{fruit}}=8$, $N_{\text{seeds}}=6$, $Z=-3.10$, $P=0.002$; Fig. 1). Comparisons were not possible for flowers/flower buds; however, mean vigilance rates for flowers were similar to all other food types except seeds (Fig. 1).

The effect of age–sex class on routine vigilance while feeding ($F=3.271$, $df=66.6$, $P=0.026$; Table 4) was also analyzed with post hoc comparisons, which showed no differences in mean scanning rates between age–sex classes (Mann–Whitney U: $N_{\text{adult males}}=14$, $N_{\text{adult females}}=12$, $Z=-0.54$, $P=0.59$; $N_{\text{adult males}}=14$, $N_{\text{adult females with inf/juv}}=11$, $Z=1.37$, $P=0.17$; $N_{\text{adult males}}=14$, $N_{\text{subadult males}}=7$, $Z=1.38$, $P=0.17$; $N_{\text{adult females}}=12$, $N_{\text{subadult males}}=7$, $Z=1.61$, $P=0.11$; $N_{\text{adult females with inf/juv}}=11$, $N_{\text{subadult males}}=7$, $Z=0.18$, $P=0.86$; Fig. 2). Sample sizes were not large enough to allow comparisons with subadult females or those between adult females with and without infants to be done (but see Fig. 2).

Induced vigilance while feeding

Induced vigilance while feeding was significantly higher when individuals were lower in the canopy (linear mixed-effects model: $F=20.436$, $df=189.2$, $P=<0.0001$) and increased with fewer adult/subadult neighbors within 5 m, though not significantly so ($F=3.467$, $df=194.8$, $P=0.064$)
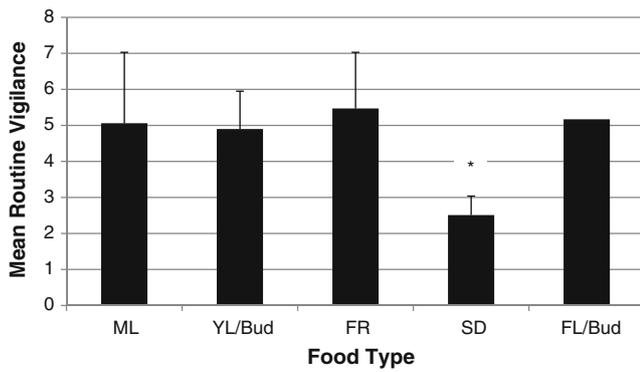
Fig. 1 Mean routine scanning rates (number of scans per minute) for individuals while feeding on each food type. *Numbers in brackets* represent *N* (number of individuals). *ML* mature leaves (23), *YL/Bud* young leaves and buds (47), *FR* fruit (9), *SD* seeds (6), and *FL/Bud* flowers and flower buds (2). *Error bars* represent standard deviation. *Asterisk* Routine scanning rates were significantly lower when feeding on seeds compared to every other food type (a comparison with flowers could not be done)
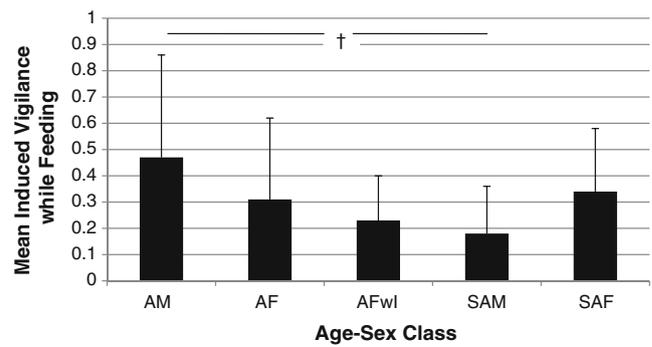

Fig. 3 Mean induced scanning rates (number of scans per minute) for each age–sex class during feeding. *Numbers in brackets* represent *N* (number of individuals). *AM* adult males (14), *AF* adult females without infants (12), *AFwI* adult females with infants (11), *SAM* subadult males (7), and *SAF* subadult females (2). *Error bars* represent standard deviation. *Dagger* Mann–Whitney *U* tests comparing adult males to subadult males were not significant after the application of a Bonferroni correction ($Z=1.98$, $P=0.05$). Comparisons were not possible for subadult females or adult females with versus those without infants

(Table 4). There was also an effect of age–sex class on induced vigilance while feeding ($F=3.051$, $df=131.8$, $P=0.031$) (Table 4); however, post hoc analyses did not show any significant differences (Mann–Whitney U: $N_{adult\ males}=14$, $N_{adult\ females}=12$, $Z=1.41$, $P=0.16$; $N_{adult\ males}=14$, $N_{adult\ females\ with\ inf/juv}=11$, $Z=1.59$, $P=0.11$; $N_{adult\ males}=14$, $N_{subadult\ males}=7$, $Z=1.98$, $P=0.05$; $N_{adult\ females}=12$, $N_{subadult\ males}=7$, $Z=0.85$, $P=0.40$; $N_{adult\ females\ with\ inf/juv}=11$, $N_{subadult\ males}=7$, $Z=0.63$, $P=0.52$; Fig. 3). Sample sizes were not large enough to allow comparisons with subadult females or those between adult females with and without infants to be done (but see Fig. 3). No other factor influenced induced vigilance while feeding (Table 4).
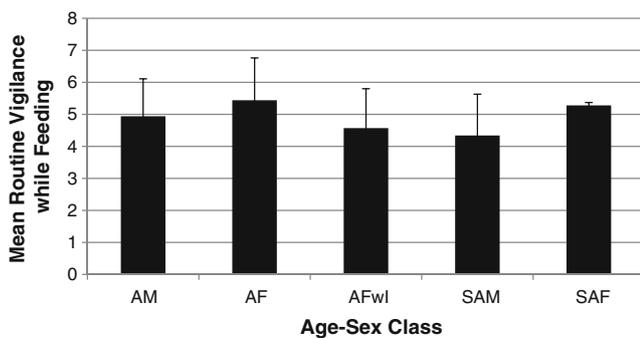
Routine vigilance while resting

During resting, routine scanning rates were significantly higher when individuals were lower in the canopy (linear mixed-effects model: $F=74.755$, $df=856.6$, $P=<0.0001$) and had fewer adult and subadult neighbors within 5 m ($F=10.503$, $df=907.5$, $P=0.001$). No other factor significantly influenced routine vigilance while resting (Table 5).

Induced vigilance while resting

Induced vigilance while resting was significantly higher with larger adult/subadult group size (linear mixed-effects model: $F=7.509$, $df=229.0$, $P=0.007$), when individuals were lower in the canopy ($F=31.909$, $df=660.0$, $P=<0.0001$) and when they had fewer adult and subadult neighbors within 5 m ($F=9.037$, $df=782.7$, $P=0.003$) (Table 5). No other significant effects were seen (Table 5).

Comparison of feeding versus resting

Routine scanning rates were higher for individuals when they were feeding (mean number of focal samplings per individual=3.57, range=1–12) compared to when they were resting (mean number of focal samplings per individual= 13.31, range=1–45) (paired *t* test: $N=42$, $t=-8.24$, $df=41$, $P<0.0001$), while induced vigilance did not differ between feeding and resting ($N=42$, $t=0.47$, $df=41$, $P=0.64$). The mean number adult/subadult neighbors that individuals had was lower when feeding than when resting (paired *t* test: $N=42$, $t=2.29$, $df=41$, $P=0.027$) (Fig. 4). Adult/subadult group size did not correlate with the mean number of near neighbors

Fig. 2 Mean routine scanning rates (number of scans per minute) for each age–sex class during feeding. *Numbers in brackets* represent *N* (number of individuals). *AM* adult males (14), *AF* adult females without infants (12), *AFwI* adult females with infants (11), *SAM* subadult males (7), and *SAF* subadult females (2). *Error bars* represent standard deviation. No significant differences were found. Comparisons were not possible for subadult females or adult females with versus those without infants

Table 5 Linear mixed-effect models describing routine and induced vigilance during resting without extra-group or new males present

Model term	Estimate (SE)	F	df	P
Routine vigilance				
Adult and subadult group size	0.034 (0.02)	2.255	272.7	0.134
Age–sex class		1.716	247.7	0.164
Adult male[a]	0.671 (0.37)			0.073
Adult female	0.716 (0.38)			0.059
Adult female with infant	0.309 (0.36)			0.396
Subadult male	0 (0)			–
Height in canopy	−0.115 (0.01)	74.755	856.6	<0.0001
Number of adult and subadult neighbors within 5 m	−0.171 (0.05)	10.503	907.5	0.001
Number of adult male near neighbors within 5 m	0.125 (0.17)	0.522	912.4	0.470
Induced vigilance				
Adult and subadult group size	0.015 (0.01)	7.509	229.0	0.007
Age–sex class		1.729	182.9	0.163
Adult male[a]	0.146 (0.08)			0.078
Adult female	0.043 (0.09)			0.616
Adult female with infant	0.048 (0.08)			0.565
Subadult male	0 (0)			–
Height in canopy	−0.020 (0.00)	31.909	660.0	<0.0001
Number of adult and subadult neighbors within 5 m	−0.043 (0.01)	9.037	782.7	0.003
Number of adult male near neighbors within 5 m	0.014 (0.05)	0.091	854.0	0.763

[a] Indented categories are all compared with the final listed category (subadult males)

during feeding (Spearman: $N=10$, $r_s=-0.10$, $P=0.78$) or during resting ($N=10$, $r_s=0.47$, $P=0.11$) (Fig. 4).

Near neighbors

Since the number of near neighbors was always an important determinant of induced vigilance and also of routine vigilance while resting when no threatening conspecific males were nearby, the number of neighbors needed to decrease scanning was investigated. As the number of neighbors increased, routine vigilance while feeding and induced vigilance tended to fluctuate in a downward tendency (Fig. 5). Induced scanning rates while resting reached zero by the time there were eight neighbors.
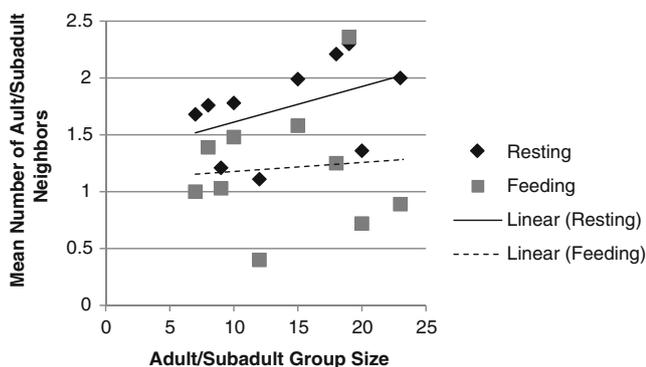

Fig. 4 Mean number of adult/subadult neighbors when resting and feeding for different adult/subadult group sizes

However, routine vigilance while resting showed a slight upward drift between seven and nine neighbors (Fig. 5).

Vigilance in the presence of threatening conspecific males

When extra-group males were within 50 m (e.g., during a BGE or male incursion), when infanticidal attacks were occurring, or within 1 month of new male immigration, mean induced vigilance per minute was higher for individuals while resting and feeding than in the absence of male threat, though not significantly so (resting: mean$_{without\ males}=0.38$, mean$_{with\ males}=0.55$, $N=29$, $t=-1.59$, $P=0.122$; feeding: mean$_{without\ males}=0.24$, mean$_{with\ males}=0.46$, $N=22$, $t=-2.06$, $P=0.52$), and mean routine vigilance was not increased (resting: mean$_{without\ males}=3.57$, mean$_{with\ males}=3.04$, $N=31$, $t=1.77$, $P=0.09$; feeding: mean$_{without\ males}=4.92$, mean$_{with\ males}=4.44$, $N=23$, $t=1.37$, $P=0.184$).

When threatening males were within 50 m, routine resting vigilance was significantly affected by height in the canopy, the number resident adult males within 5 m, and the age–sex class of the individual (Table 6). Routine scanning was significantly higher when individuals were lower in the canopy (linear mixed-effects model: $F=27.858$, $df=196.1$, $P=<0.0001$) and when fewer resident males were within 5 m ($F=5.319$, $df=214.2$, $P=0.022$). Though age–sex class showed an effect in the linear mixed model ($F=2.855$, $df=76.5$, $P=0.043$), post hoc comparisons of mean routine resting vigilance in the presence of threatening males was not different between each

Fig. 5 Mean routine (**a**) and induced (**b**) scanning rates while resting and feeding with an increasing number of near neighbors within 5 m. Means are for the total number of minutes with that number of neighbors without controlling for individuals
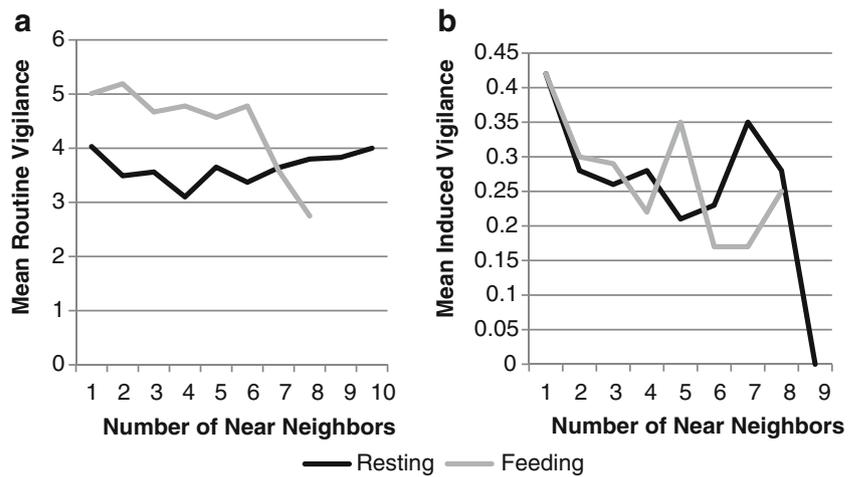
age–sex class (Mann–Whitney U: $N_{\text{adult males}}$=17, $N_{\text{adult females}}$=18, Z=0.61, P=0.54; $N_{\text{adult males}}$=17, $N_{\text{adult females with inf/juv}}$=9, Z=0.62, P=0.54; $N_{\text{adult males}}$=18, $N_{\text{subadult males}}$=7, Z=0.70, P=0.48; $N_{\text{adult females}}$=18, $N_{\text{subadult males}}$=7, Z=1.12, P=0.26; $N_{\text{adult females with inf/juv}}$=9, $N_{\text{subadult males}}$=7, Z=0.74, P=0.45; Wilcoxon for adult females without infants and with infants: N=6, W=7, P=0.46).

Induced vigilance during resting when threatening males were within 50 m was higher when individuals were lower in the canopy (linear mixed-effects model: F=6.169, df=197.9, P=0.014) and when fewer resident males were within 5 m, though not significantly so

(F=3.707, df=211.5, P=0.056; Table 6). No other factor affected induced vigilance when threatening males were nearby.

Discussion

We found evidence that perceived predation risk is more important in determining scanning behavior than scramble competition for food or infanticide risk in our population of folivorous primate. None of our predictions for the effect of scramble competition on vigilance were upheld (Table 2),

Table 6 Linear mixed-effect models describing routine and induced vigilance during resting with extra-group or new males present

Model term	Estimate (SE)	F	df	P
Routine vigilance				
Adult and subadult group size	0.025 (0.04)	0.418	84.8	0.520
Age–sex class		2.855	76.5	0.043
Adult male[a]	0.886 (0.53)			0.101
Adult female	0.337 (0.71)			0.635
Adult female with infant	−0.580 (0.55)			0.297
Subadult male	0 (0)			–
Height in canopy	−0.168 (0.03)	27.858	196.1	<0.0001
Number of adult and subadult neighbors within 5 m	0.045 (0.09)	0.252	214.6	0.616
Number of adult male near neighbors within 5 m	−0.674 (0.29)	5.319	214.2	0.022
Induced vigilance				
Adult and subadult group size	0.008 (0.01)	0.490	69.4	0.486
Age–sex class		1.607	63.7	0.196
Adult male[a]	0.318 (0.17)			0.063
Adult female	0.121 (0.22)			0.589
Adult female with infant	0.025 (0.17)			0.883
Subadult male	0 (0)			–
Height in canopy	−0.024 (0.01)	6.196	197.9	0.014
Number of adult and subadult neighbors within 5 m	−0.013 (0.03)	0.262	212.5	0.609
Number of adult male near neighbors within 5 m	0.168 (0.09)	3.707	211.5	0.056

[a] Indented categories are all compared with the final listed category (subadult males)

though food type had an important influence on routine vigilance. When *C. vellerosus* individuals were feeding on food that required processing, they decreased their routine scanning, a result that needs to be replicated in further studies, as our sample size was small. However, this effect has also been reported in samango monkeys (Cowlishaw et al. 2003) and vervet monkeys (Isbell and Young 1993). Conversely, when *C. vellerosus* ate food that required little manipulation, their routine vigilance was unaffected. These results show that when food can just be placed in the mouth and chewed, scanning is relatively cost free and can be done while feeding. This needs to be tested in other folivorous primates, but if the majority of the diet of a species requires little processing, the predictions for the effect of group size on vigilance during feeding may not be upheld (Table 2). It is assumed that scramble competition for food increases with group size and leads to decreased vigilance because individuals reallocate time from scanning to acquiring food before it is depleted (e.g., Clark and Mangel 1986; Elgar 1989; Cezilly and Brun 1989; Beauchamp and Livoreil 1997; Beauchamp 1998; Grand and Dill 1999; Beauchamp and Ruxton 2003; Randler 2005; Rieucau and Giraldeau 2009). However, when acquiring food and scanning are compatible (Cowlishaw et al. 2003; this study), there may be no effect of group size on routine scanning while feeding or, alternatively, there may be a positive effect of group size on vigilance because individuals may scan group mates more when feeding to avoid visiting depleted food patches. This effect may be more evident in primates, which often use upright feeding postures, when compared to several ungulates and birds, who feed with their heads down (e.g., Lima 1987; Illius and Fitzgibbon 1994; Lima and Bednekoff 1999; Fortin et al. 2004; Devereux et al. 2006). The upright feeding postures of many primates strengthen the notion that vigilance while feeding may not be costly when food does not require much processing. Treves (2000) investigated this idea and rejected it as a reason for the lack of a group size effect on vigilance in primates because the four primate species he compared had different diets and feeding postures, and interrupted their feeding at similar rates while feeding. However, his analyses lumped the two variables of feeding posture and degree of food handling. For primates that feed upright but need to process their food (peeling a stem, removing a pit/stone from a fruit, extracting a seed, etc.), we expect vigilance to be costly. What is now needed are comparisons of vigilance between species that feed with their heads up versus those that feed with their heads down, but which show the same degree of food processing, and alternatively, comparisons of species that feed upright, but have different degrees of food processing, to evaluate the effect of upright feeding postures versus food processing on routine vigilance.

Two lines of evidence show that perceived predation risk was a more important effect on vigilance than food competition and infanticide risk. First, height had the greatest effect on routine and induced vigilance during feeding and resting, with and without the presence of threatening males. Individuals scanned significantly more when they were lower in the canopy. This same effect has been found in several other primate studies (e.g., de Ruiter 1986; van Schaik and van Noordwijk 1989; Steenbeek et al. 1999; Hirsch 2002; Kutsukake 2006) including for *C. vellerosus* in the same population (MacIntosh and Sicotte 2009). Greater scanning when lower in the canopy is congruent with the fact that, at BFMS, snakes, humans, and potentially dogs are more of a danger close to the ground, while predatory birds are rare and not large enough to take an adult colobus monkey. Sites close to the ground are further from the cover and safe refuges provided by the tree tops. Indeed, when predator alarms are sounded by colobus on the ground, the group reacts by moving up into the trees (JAT, personal observation). Areas further from cover or safe refuges commonly lead to increased vigilance in animal studies (e.g., Elgar 1989; van Schaik and van Noordwijk 1989; Pöysä 1994; Cowlishaw 1998).

The second piece of evidence for the importance of perceived predation risk for *C. vellerosus* was that when individuals had fewer neighbors within 5 m, they increased their induced vigilance in all situations, except when threatening males were within 50 m, and increased their routine scanning during resting, without the presence of threatening males. The mean number of neighbors was not related to adult/subadult group size, so inter-individual distances remained similar in groups of different size. In several animal species, a greater number of near neighbors has been shown to be more important in decreasing vigilance than absolute group size (e.g., teals, Pöysä 1994; baboons, Cowlishaw 1998; red-tailed monkeys, red colobus, Treves 1998; rock wallabies, Blumstein et al. 2001; red-billed choughs, Rolando et al. 2001; black howler monkeys, Treves et al. 2001; brown-headed cowbirds, Fernández-Juricic et al. 2007; guanacos, Marino and Baldi 2008). However, the effect of near neighbors could potentially be explained by decreased predation risk or by the usually cited effects of increased food competition and subsequent greater feeding rates caused by the presence of near neighbors (Beauchamp and Ruxton 2003) both of which may lead to less scanning. For *C. vellerosus*, the fact that, during resting, the effect of more near neighbors on scanning was stronger than during feeding suggests that near neighbors do indeed decrease perceived predation risk.

When animals forage or rest far apart, the benefits of collective predator detection and risk dilution are less likely to apply and the advantages of larger group size might level off relatively quickly (Lima and Zollner 1996; Treves et al.

2001; Fernández-Juricic et al. 2007). There is some evidence that animals can adjust the timing of their scans based on the behavior of others (Pays et al. 2007) and that they may modify their scanning when they can see or are aware of nearby individuals (e.g., Metcalfe 1984; Pöysä 1994), effects which seem to be regulated by the limits of collective detection (i.e., an individual's ability to see and benefit from the detection of a predator by their near neighbor, Lima and Zollner 1996). Visibility fluctuates for *C. vellerosus* in their forested habitat, but in most cases, individuals would not be able to see the entire group because of foliage and varying height levels. Individuals are much more likely to be aware of their neighbors in relatively close proximity. Supporting this notion, Isbell and Young's (1993) study of vervet monkey vigilance is also one of the few to find a group size effect on vigilance in primates, and these animals live in an open, savannah-type habitat, where they are more likely to benefit from the scanning of most or all group members. The ways that animals perceive group size may be different from the way that human observers define the social group, making immediate neighbors more important in defining perceived predation risk for individuals (Treves 1998; Rolando et al. 2001). A more biologically relevant definition of group size may be those individuals within the radius around a focal animal who can be seen at least peripherally and whose vigilance still allows the benefits of collective detection and dilution of risk (Fernández-Juricic et al. 2007).

An effect of group size on vigilance was found in this study but only for induced vigilance while resting, and the effect was in the opposite direction predicted for both the predation risk and the scramble competition hypotheses (Table 2). Individuals in the larger groups were found to routinely scan more when resting. This increase in scanning can be explained by the greater within-group social monitoring that may occur more in larger groups, a factor that has been shown to be important in primate vigilance (e.g., squirrel monkeys, Caine and Marra 1988; yellow baboons, Alberts 1994; mountain gorillas, Watts 1998; chimpanzees, Kutsukake 2007). It could also be due to the fact that these larger groups are more attractive to extra-group males and thus are a target for male incursions (Teichroeb et al. 2011), potentially leading to increased scanning for possible conspecific threat (e.g., Thomas langurs, Steenbeek et al. 1999).

For *C. vellerosus*, males were not more vigilant than females, as has been reported in some other primate species (e.g., vervet monkeys, Baldellou and Henzi 1992; Isbell and Young 1993; brown capuchins, white-fronted capuchins, van Schaik and van Noordwijk 1989; white-faced capuchins, Rose and Fedigan 1995). While primate males in some species may scan more and thus detect predators more often than females (van Schaik and van Noordwijk

1989), their vigilance frequently appears to be directed at other males due to sexual competition (Baldellou and Henzi 1992; Rose and Fedigan 1995). For *C. vellerosus*, we did find that, even though having resident males as near neighbors did not influence vigilance when no threatening conspecific males were present, when these threatening males were present, having resident males within 5 m decreased individual vigilance. Indeed, when there was a conspecific threat, the importance of resident male near neighbors in decreasing scanning rates seems to supersede the effect of having an overall greater number of near neighbors. This demonstrates the important defensive role that resident adult males play in *C. vellerosus* groups, aggressively dissuading extra-group males from entering the group and defending infants from attacks by new and outside males (Saj and Sicotte 2005; Teichroeb and Sicotte 2008a; Teichroeb et al. 2011). Our other two hypotheses for the effect of infanticide risk on vigilance were not upheld (Table 2). In the presence of threatening males, adult males did not scan more than subadult males nor did adult females with infants scan more than those without infants. The lack of an effect of threatening males on vigilance for adult females with infants is surprising, given the high rates of male infanticide in this population (Teichroeb and Sicotte 2008a). Perhaps, these females rely heavily on the presence and protective abilities of resident males and thus do not increase their individual scanning as a result.

In a previous study on these same groups (Teichroeb and Sicotte 2009), we found that individuals spent more time feeding in the larger compared to the smaller groups but did not feed at faster rates. However, we could not determine if increased feeding time was an indicator of scramble competition or if individuals in larger groups were afforded more time to feed because they could spend less time scanning for predators. This study shows that increased group size at the levels seen in *C. vellerosus* does not lead to decreased scanning, rather the height and number of near neighbors are more indicative of the danger perceived by individuals, and this does not differ for groups of different size. Thus, we can now conclude more confidently that increased feeding time in larger versus smaller groups is indeed a sign of greater scramble competition for food in these groups (Teichroeb and Sicotte 2009).

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

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Ethical standards