Controversy Over the Application of Current Socioecological Models to Folivorous Primates: *Colobus vellerosus* Fits the Predictions

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ABSTRACT   We explore the applicability of the current socio-ecological model to characterize the social structure of *Colobus vellerosus*, a folivorous primate. The current socio-ecological model predicts that female social relationships should respond in predictable ways to food abundance and distribution and associated competitive regimes. It appears to successfully explain variation in social structure in some primate species; however, recent research indicates that several folivorous or folivore-frugivorous species seem to be exceptions. We present data on social relationships and social structure in two groups of *C. vellerosus* over 15 months at Boabeng-Fiema, Ghana. As predicted by the model, our results indicate the co-occurrence of 1) low levels of grooming between female *C. vellerosus* when compared with other species, 2) an absence of female coalitions over food, and 3) female dispersal. Taken together, these traits suggest a "Dispersal-Egalitarian" species. However, our results also indicate female-female affiliation was higher than male-female affiliation, which was more indicative of a "female resident" species. Our data also suggests intersexual affiliation varied among groups. This variation in inter-sexual affiliation could be due to variation in the intensity of infanticidal threats between groups. The combination of these social characteristics lead us to conclude that *C. vellerosus'* social structure is largely congruent with the ecological indicators of food distribution and female competitive regime that we have previously documented, which indicated high quality foods were not monopolizable or usurpable and behavioral evidence of within-group contest competition (i.e. supplantations over food) was rare. But the combination of higher female-female affiliation (compared to male-female) and female dispersal is difficult to explain in light of predictions, unless future work reveals female residency is more predominant than female dispersal in our population. We also discuss reasons why some folivores do not appear to fit the predictions of the current socioecological model. Am J Phys Anthropol 133:994–1003, 2007.   © 2007 Wiley-Liss, Inc.

Over the past four decades, the diversity in primate social structures (*sensu* Kappeler and van Schaik, 2002) has been attributed primarily to variation in ecological pressures such as food abundance and distribution (Crook and Gartlan, 1966; Eisenberg et al., 1972; Wrangham, 1980; van Schaik, 1989; Sterck et al., 1997; Isbell, 1991, 2004). Current socio-ecological models predict that female social relationships should respond in predictable ways to food abundance and distribution and associated female competitive regime (van Schaik, 1989; Sterck et al., 1997). Female competitive regimes are the outcome of the presence of contest or scramble feeding competition (the "type" of feeding competition) within and between social groups (the "level" of feeding competition; van Schaik, 1989; Koenig, 2002).

Theoretically, differing combinations of the level and type of feeding competition should lead to four different types of social structure (Sterck et al., 1997). Direct competition over monopolizable food resources within or between groups (i.e. contest competition) should make it advantageous for females to remain with kin who they rely on as allies and for cooperative defense of resources. Female dispersal is thus not expected, as a female who attempted to transfer would lose access to allies and would face strong resistance to immigration from resident females in other groups. Contest competition between-groups should lead to a system in which female

dominance relationships are egalitarian and individualistic, and where coalitions are rare. The presence of contest competition within-groups (and its absence between-group) should lead to a nepotistic system in which females form linear and despotic dominance relationships and form coalitions with kin and mutualistic coalitions with other females to acquire and maintain their dominance rank, since high dominance rank should be associated with priority of access to limited food resources. Contest competition at the two levels should lead to a system in which females form linear, nepotistic dominance hierarchies, and form coalitions with kin and

TABLE 1. Examples of folivore and folivore-frugivore species in which aspects of competitive regime and social structure are not predicted by the current socio-ecological model (van Schaik, 1989; Sterck et al., 1997)

Species	Reason for exception	Reference
Trachypithecus phayrei	Female dispersal despite forming linear dominance hierarchy	Koenig et al., 2004
Semnopithecus entellus	Female age-inversed linear dominance hierarchy with infrequent kin coalitions	Hrdy and Hrdy, 1976; Borries et al., 1991; Borries, 1993; Koenig, 2000
Colobus polykomos	Female dispersal despite linear dominance hierarchy and female participation in inter-group encounters	Korstjens et al., 2002, 2005
Piliocolobus temminckii	Female dispersal (sometime co-dispersal) despite female participation in inter-group encounters	Starin, 1994
Alouatta palliata	Female dispersal female participation in inter-group encounters and linear hierarchies	Jones, 1980; Glander, 1992
Alouatta seniculus	Female dispersal (often with kin) despite female participation in inter-group encounters	Pope, 2000
Brachyteles arachnoids	Female dispersal despite female participation in inter-group encounters	Strier et al., 1993

mutualistic coalitions with other females, but where dominants have to be more lenient towards subordinates (which manifests itself by bidirectional aggression and higher levels of postconflict affiliation), since dominants rely on subordinates for support in between-group encounters. When both within and between-group food competition are of the scramble type because food resources are not monopolizable, females are expected to gain little from forming coalitions with kin. Female dispersal is expected, thus groups are typically composed of unrelated females. Female agonistic relationships are predicted to be rare (so female relationships are egalitarian). Males may or may not disperse in this case. In short, the presence of contest competition should lead to nepotistic female dominance hierarchies and female coalitions, and is predicted to co-occur with female philopatry. When both within and between-group contest competition are absent, females are not expected to engage in agonistic interactions over food, and this should be associated with an absence of linear dominance hierarchies and infrequent coalitions. These characteristics should co-occur with female dispersal, since coalition partners are not needed in feeding competition under these conditions.

Despite the predominance of the current socio-ecological model in primatology, relatively few studies have provided a robust test of the predictions of the model. Such a test requires specifically testing the links between food distribution and abundance, competitive regime, and social relationships. In the few studies that have investigated these relationships, the model appears to successfully link these domains in several primate species (e.g., *Saimiri oerstedii* and *S. boliviensis*: Mitchell et al., 1991; *Papio ursinus* and *P. anubis*: Barton et al., 1996; *Macaca fascicularis*; Sterck and Steenbeek, 1997 (but not with respect to interaction rates inside food patches); *Piliocolobus badius*; Korstjens et al., 2002). However, a number of exceptions can also be found (reviewed in Isbell and Young, 2002; Koenig, 2002). For example, studies of the social relationships and residence patterns of *Saimiri oerstedii* and *S. boliviensis* are consistent with socio-ecological models (Mitchell et al., 1991); however *S. sciureus* demonstrated higher levels of aggression than predicted and some female dispersal (Boinski et al., 2002). While Boinski et al. (2002) attribute this mismatch to the size and quality of the food patches, their study only supports some aspects of the model. Similarly, in a comparison of the food distribution, rate of agonism, and type of

dominance hierarchy between vervets and patas monkey, Isbell and colleagues (Isbell and Pruetz, 1998; Pruetz and Isbell, 2000) found that although the dominance hierarchies of both species were correctly predicted according to habitat type (i.e. weak and non-linear in habitats with randomly distributed foods; linear in habitat with clumped resources), the vervet's rate of agonism was similar in habitats with clumped or randomly distributed food resources.

Some studies provide data in which the link between competitive regime (e.g., type and level of competition, or the resulting behavioral traits of the competitive regime) and social structure can be examined, without concurrent data on food distribution and abundance. Among these studies, a number of mismatches between competitive regime, or the resulting behavioral traits of competitive regime, and social structure can be found (reviewed by Isbell and Young, 2002; Koenig, 2002). Although exceptions occur in species that rely on many types of foods, it is our opinion that the link between female competitive regime and social structure is frequently not clear in folivore or folivore-frugivore species. Although such general categories likely lump together species that have different types of food distribution and abundance, the point remains, that even without access to data on the characteristics of food resources, and relying on behavioral traits alone, many folivore and folivore-frugivore species (listed in Table 1) demonstrate mismatches between the behavioral traits resulting from their competitive regime and their social structure. For example, some folivorous species demonstrate female dispersal in co-occurrence with strong within and/or between-group competition. In other species, linear female dominance hierarchies are not associated with nepotism or frequent female coalitions. Hanuman langur females form coalitions within groups, but rather infrequently (Borries, 1993). Female coalitions are however rather frequent in competition between langur groups (Borries, 1993). Current socio-ecological models do not predict the co-occurrence (or lack of) of these traits (van Schaik, 1989; Sterck et al., 1997). Given these mismatches, the study of folivorous primates is crucial to helping us refine current socio-ecological models and in understanding what ecological and social factors shape the social structure of primates.

Here we examine the applicability of current socio-ecological models to characterize the social structure of a folivore: *Colobus vellerosus*. In two previous papers, we

TABLE 2. The composition and size of Colobus vellerosus study groups at Boabeng-Fiema Monkey Sanctuary, Ghana

Name	Study period	Focal hours	Group size	Adults/subadults		Juveniles[a]		Infants[a]
WW (P1)	09/00–03/01	140.5	31–33	5	11	3–4	4	7–9
WW (P2)	04/01–08/01	103.6	31–33	5	11	3–4	4	7–9
WW (P3)	06/02–11/02	59.5	32	6	16	6	2	2–6
B (P1)	09/00–03/01	113.7	8	1	3	2	1	1
B (P2)[b]	04/01–08/01	100.9	15–16	8	3–4	2	1	1
B (P3)	06/02–11/02	41.7	10	2	3	3	1	1

A large (WW) and small (B) group were studied over three time periods.
[a] We do not have a fully accurate count of the immatures in WW group.
[b] Subsequent to a take-over by an all male group.

characterized *C. vellerosus'* food resources as non-monopolizable and non-usurpable and reported that agonistic interactions over food resources were rare (Saj and Sicotte, in press a,b). This leads us to conclude that within group contest competition was likely absent in our groups, but that scramble competition was occurring. Earlier work at the site showed that females only rarely participated aggressively in inter-group encounters (Sicotte and MacIntosh, 2004), suggesting that between group contest competition between females for access to food resources was likely absent.

On the basis of current socio-ecological models (e.g. Sterck et al., 1997), we thus predict the social structure of *C. vellerosus* to be characterized by infrequent female coalitions over food and the occurrence of female dispersal. Although the Sterck et al. (1997) model does not make predictions about the intensity or direction of affiliation, the earlier version of this model by van Schaik (1989) incorporates Wrangham's (1980) prediction that in species where females disperse, the frequency of female grooming should be low and female-female bonds should be weak. Thus, we predict low levels of female-female affiliation in relation to other species (as shown in Teichroeb et al., 2003). We also predict higher male-female affiliation than female-female affiliation if female dispersal is more predominant than female residency, because females should be unrelated within groups and should have no need to maintain relationships with female allies, whereas they probably choose their group of destination on the basis of male quality, and hence may need to maintain a good relationship with him (as is the case in gorillas; Sicotte, 2001).

Two elements used to characterize the competitive regime of females *C. vellerosus* (Saj and Sicotte, in press b) need to be examined critically, however. Firstly, we measured the type of competition at the proximate level, which presents some issues. For instance, "frequent" agonistic interactions over food usually lead to the conclusion that contest competition is occurring, although the actual frequency of agonism can vary depending on factors such as group size, group spread, and the stability of the dominance relationships between females (Chapais, 1992; Koenig et al., 2004). This means that a situation of contest competition (where, at the ultimate level, females have predictably different food intake according to dominance status or where females vary in their reproductive output depending on food intake) could possibly be occurring with relatively low rates of agonistic interactions, if group spread is large, or if the female dominance hierarchy is stable. In our case, the combination of extremely low rates of female-female aggression over food and the fact that food resources were non-monopolizable and non-usurpable is suggestive

of the absence of contest competition, but this needs to be confirmed. Secondly, data on female dominance relationships is not available from our study at this point because females are not recognized individually. This poses limitations to the conclusions that we can draw from the data presented here, as an ability to document the presence of dominance relationships between females, as well as the frequency of reversals in agonistic behaviors within dyads, would be important steps in confirming the competitive regime of females *C. vellerosus* (and hence whether there is a match between competitive regime and social behaviors). The absence of ritualized submissive signals in *C. vellerosus* is congruent with the notion that dominance hierarchies are absent (TS and PS unpublished data and Julie Teichroeb pers. comm.; see also Grunau and Kuester (2001) for *C. guereza*).

METHODS
Study site and study species

The Boabeng-Fiema Monkey Sanctuary (BFMS) is a 1.92 km^2 dry semi-deciduous forest (Hall and Swaine, 1981) located in central Ghana (7° 43′ N and 1° 42′ W). BFMS is mostly surrounded by villages and farmland and is more than 50 km away from a large forested area (Beier et al., 2002). More details about the study site are presented in Saj et al. (2005). This species lives in uni-male and multi-male groups that vary in size from 9 to 38 (Wong and Sicotte, 2006). In this study, two groups were observed in three time periods (Table 2). WW group was a large, multi-male group that maintained the same group size and adult composition in all periods. B group was a smaller group whose group size and adult composition varied dramatically as a result of a take-over by an all male group. In the first study period (P1), B group consisted of eight individuals, but 7 months into the study (April, 2001), it was invaded and subsequently taken over by an all-male group of 7–9 males (period 2 [P2]; Saj and Sicotte, 2005). After the take-over, the youngest immature in the group, who was 7 months old at the time, received 11 directed acts of aggression from the new males, but survived (Saj and Sicotte, 2005). The all-male group remained in close proximity to B group for the duration of the study, and by July 2001, seven males (six adults and one juvenile) had integrated into the group. In July 2001, one adult female also transferred into the group and stayed for ≥2 months. No focal data were collected on the new males or adult female. However, they were included in grooming interactions, approaches, and nearest neighbors when the new males or female interacted with original members of B group.

In the third period (P3), which was conducted a year after the all-male takeover, only one of the new males remained in the group. In this period the group consisted of the original male, a new male, three adult females (all parous), four juveniles, and one infant. The ecological data in Saj and Sicotte (in press a,b) were collected in P1 and P2.

Data collection

Data were collected on the two groups during two 4-day blocks per month over 15 months by T.L.S. and S.M. (September 2000–November 2000; January 2001–August 2001; July 2002–November 2002). Ten minute continuous focal sampling (Altmann, 1974) was conducted on adult females and males, where the behavior and the social partners of the focal animal were recorded. The behaviors analyzed in this article are defined below. In P1 and P2, we also recorded the proximity of a focal adult female to other adult females and males at two intervals during the focal sessions: 2 and 10 min. All adults within 1.5 m of the focal female were recorded. We excluded scans in which the focal was engaged in grooming to ensure that time spent in close proximity was independent of direct social activity.

Individuals were not recognizable in WW group, therefore, focals of the same age-sex class were combined and analysis for both groups was done on age-sex classes. If a focal animal was out-of-sight for more than 10% of the 10-min sample, the sample was discarded. Focal sessions were conducted using a hand-held tape recorder and binoculars (10×40); information obtained in the field was transcribed to focal sheets at the end of the day. Animals that were visible were selected starting at the left side of the group and moving to the right. For the relatively inactive *C. vellerosus*, this reduced the likelihood that individuals were sampled more than once per hour.

Proportion of time spent grooming

The age-sex class of participants and the direction of grooming (i.e., given or received) were recorded. The proportion of time spent grooming was obtained by dividing time spent grooming per age-sex class by the overall grooming time. Only adult grooming was analyzed and age-sex class data were pooled for comparison of dyad types (AF-AF, AF-AM).

Grooming bout rate

A grooming bout was defined as an event of continuous grooming between the same two individuals with breaks of less than 30 s (Schino et al., 1988). When partners switched between giving and receiving grooming with a break of less than 30 s, the bout was counted twice for the focal individual, once as receiving grooming and once as giving grooming (Schino et al., 1988). The number of bouts were converted into a mean rate/hour/adult individual to control for differences in group composition. For each day, a bout rate was calculated for AF-AF and AF-AM dyads. For inter-sexual dyads, only days with at least one male and one female focal were included. In B group, the mean rate did not include the new males or transfer female because they did not groom original B members. In WW group, we combined data across periods because group composition was similar and no differences were found among periods in AF-AF grooming bout rate (Wilcoxon Signed Rank test,

$z = -1.069$, $n_{P1+P2} = 87$, $n_{P3} = 30$, $P = 0.285$) or AF-AM grooming (Wilcoxon Signed Rank test, $z = -1.342$, $n_{P1+P2} = 87$, $n_{P3} = 32$, $P = 0.180$).

Approach rate

Non-agonistic approaches to and made by the focal were recorded between adults. Non-agonistic approaches were defined as approaches within 1.5 m (~3 arm's lengths) in which the approached individual did not move immediately after the approach (to differentiate it from a supplant, where the approached individual moved immediately after being approached). Non-agonistic approaches are behaviors that might aim at establishing proximity to an individual, and have been used as indicators of social relationships (c.f. Hinde and Atkinson, 1970). Inter-individual proximity itself is often used as an affiliative measure, in species such as *Colobus badius* (Firos, 2001) and *Gorilla g. beringei* (Robbins, 2001) (also see below, number of nearest neighbors). The age-sex class of both the approacher and approachee were recorded. The number of approaches were converted into a mean rate/hour/adult individual. In B group, the mean rate included the new males and transfer female because they approached original B members. For each day, an approach rate was calculated for AF-AF and AF-AM dyads (even if the rate was zero). For inter-sexual dyads (AF-AM), only days with at least one male and one female focal were included. In WW group, we combined data across periods because group composition was similar and no differences were found (P1 and P2 vs. P3) in AF-AM approach rates (Wilcoxon Signed Rank test, $z = -1.069$, $n_{P1+P2} = 56$, $n_{P3} = 31$, $P = 0.285$), although the AF-AF approach rate was significantly different (Mann–Whitney U test, $z = -2.268$, $n_{P1+P2} = 56$, $n_{P3} = 31$, $P = 0.023$).

Number of nearest neighbors

The number of neighbors was converted into a mean number/individual (for both male and female neighbors). In B group, mean proximity rates included the new males and transfer female. In WW group, we combined data across periods because group composition was similar and no differences were found (P1 vs. P2) in the number of female neighbors the focal female had (Wilcoxon Signed Rank test, $z = -0.821$, $n_{P1} = 44$, $n_{P2} = 38$, $P = 0.411$) or male neighbors (Wilcoxon Signed Rank test, $z = -0.801$, $n_{P1} = 44$, $n_{P2} = 38$, $P = 0.423$).

Female-female coalitions

The presence of coalitions between adult females was documented in focal and *ad libitum* sampling. A coalition was defined as joint aggression by two or more individuals towards a third party (Perry, 1996).

Dispersal events

Individuals in B group were individually recognizable, which allowed us to determine when a new individual entered the group. Immigrations in the large WW group were not discernible because of lack of individual recognition and large group size.

*TABLE 3. The distribution of affiliative interactions of Colobus vellerosus study groups
at Boabeng-Fiema Monkey Sanctuary, Ghana*

Comparison	WW (across periods)	B (P1)	B (P2)	B (P3)
Time spent grooming (%)				
Day AF-AF	98.5	78.6	80.3	49.2
Day AF-AM	1.5	21.4	19.7	50.2
Direction of AF-AM grooming (%)				
Day AF > AM		70.2	74.9	49.6
Day AM > AF		29.8	25.1	50.4
Grooming bout rate				
Day AF-AF	$0.002/0.06 \pm 0.08$	$0/0.05 \pm 0.15$	$0/0.07 \pm 0.17$	$0/0.02 \pm 0.08$
Day AF-AM	$0/0.002 \pm 0.02$	$0/0.01 \pm 0.02$	$0/0.01 \pm 0.05$	$0/0.03 \pm 0.11$
Day P value	<0.001	0.019	0.026	0.893
Block AF-AF	$0.007/0.025 \pm 0.035$	$0/0.015 \pm 0.027$	$0.009/0.017 \pm 0.022$	$0.03/0.098 \pm 0.162$
Block AF-AM	$0/0.001 \pm 0.003$	$0/0.001 \pm 0.002$	$0/0.001 \pm 0.001$	$0.025/0.051 \pm 0.043$
Approach rate				
Day AF-AF	$0.050/0.07 \pm 0.08$	$0/0.11 \pm 0.16$	$0/0.11 \pm 0.20$	$0/0.05 \pm 0.13$
Day AF-AM	$0/0.01 \pm 0.03$	$0.07/0.08 \pm 0.08$	$0/0.02 \pm 0.06$	$0/0.07 \pm 0.10$
Day P value	<0.001	0.660	0.002	0.701
Block AF-AF	$0.008/0.028 \pm 0.044$	$0.053/0.040 \pm 0.030$	$0.020/0.026 \pm 0.024$	$0/0.050 \pm 0.099$
Block AF-AM	$0.002/0.007 \pm 0.014$	$0.016/0.021 \pm 0.008$	$0/0.002 \pm 0.004$	$0.05/0.094 \pm 0.099$
No. of nearest neighbors				
Day AF-AF	$0.001/0.01 \pm 0.01$	$0.042/0.06 \pm 0.07$	$0.006/0.01 \pm 0.01$	
Day AF-AM	$0/0.001 \pm 0.003$	$0/0.01 \pm 0.02$	$0.006/0.00 \pm 0.008$	
Day P value	<0.001	<0.001	0.617	
Block AF-AF	$0.021/0.021 \pm 0.009$	$0.067/0.081 \pm 0.056$	$0.033/0.031 \pm 0.017$	
Block AF-AM	$0.006/0.006 \pm 0.005$	$0.044/0.060 \pm 0.037$	$0.013/0.015 \pm 0.009$	

A large (WW) and small (B) group were studied over three time periods. AF, all adult females; AM, adult male. For grooming, approach, and nearest neighbors, the first value in the column is the median and the second value is the mean ± SD.

Data analyses

The lack of individual recognition in our large study group required that we combine individuals (males and females) in each group for analysis. It is unlikely that we systematically re-sampled the same individual over and over, as the data collection involved moving through the group of relatively inactive colobus between focals, and selecting individuals based on their location in relation to the observer. We primarily use descriptive statistics to present our results or use the day as the unit of analysis when comparing grooming bout rate, approach rate, and number of nearest neighbors. However, with such analyses, it is difficult to know what to consider an independent unit for analysis. By using day as independent units, we are likely inflating our sample size and have a problem with pseudoreplication (Hurlbert, 1984), thus the P values obtained should be viewed with caution. However, it is not clear what temporal unit would be appropriate as variables like grooming bout rate likely change slowly with changes in social relationships or group composition. To deal with this issue we take two approaches. First, we report the median and mean (±SD) grooming bout rate, approach rate, and number of nearest neighbors so that the magnitude of differences can be clearly evaluated. Secondly, we recalculate these variables for each of the two 4-day observation blocks per month. Since adult composition varied dramatically as a result of a take-over by an all male group and it would be inappropriate to pool these different conditions, we are limited in the statistical analysis that can be conducted using these observation blocks as independent units (i.e. the sample size is too small for some periods), but we again present the median and mean (±SD) so that the magnitude of differences can be assessed.

Wilcoxon Signed Ranks tests were performed for these comparisons. All tests were two-tailed and significance was set at $P < 0.05$. Statistical tests were done using SPSS.

RESULTS
Overall affiliation

Adult males and females spent 1.2% and 0.8% of time grooming in groups WW and B, respectively (P1 and P2 combined). The female-female grooming bout rate/individual was low in both groups (Table 3; and see Table 4 for comparison with other species).

Affiliation and group composition

In WW group, time spent grooming was mainly between adult females (Table 3). Considering day as the unit of comparison, the AF-AF grooming bout rate was approximately 30 times greater than the AF-AM grooming bout rate and the rates differed significantly (Wilcoxon Signed Ranks test, $z = -6.684$, $n_{AFAF} = 117$, $n_{AFAM} = 117$, $P < 0.001$). The AF-AF approach rate was greater than the AF-AM approach rate and a Wilcoxon Signed Ranks test indicated a significant difference ($z = -5.575$, $n_{AFAF} = 87$, $n_{AFAM} = 87$, $P < 0.001$). Female focals also had a greater number of female neighbors than male neighbors (Wilcoxon Signed Ranks test, $z = -6.801$, $n_{AFAF} = 82$, $n_{AFAM} = 82$, $P < 0.001$). These statistical trends were generally supported when the observation block was considered as the independent unit of comparison (Table 3).

In B group, in P1, (before the take-over by an all-male group), most grooming was between females (Table 3). The AF-AF grooming bout rate was approximately five times greater than the AF-AM grooming bout rate and differed significantly (Wilcoxon Signed Ranks test; $z = -2.345$, $n_{AFAF} = 49$, $n_{AFAM} = 49$, $P = 0.019$). Females

TABLE 4. Rates of grooming bouts (bouts/individual/h) across primate species

Social category	Species	AF-AF	AF/AM	AM-AM	Method of data collection	Reference
Resident-nepotistic	*Macaca mulatta*[a]	0.27	0.41	0.03	Scan	Teas, 1984
	M. nemestrina	0.04	0.03		*Ad lib.*	Oi, 1990
	M. fuscata	0.102			*Ad lib.*	Oi, 1988
	M. fascicularis					
	(1)	0.18			Focal	Wheatly, 1999
	(2)	0.17				
	(3)	0.16				
	M. cyclopsis					
	(FS)	0.03	0.006	0.0006	Scan	Birky and Hsiu Hui, 2005
	(KT)	0.006	0.012	0.003		
	Semnopithecus entellus[b]	0.32			Focal, *ad lib.*	Borries et al., 1994
Resident-nepotistic tolerant	*Cercopithecus mitis*[c]	0.071			*Ad lib.*	Rowell et al., 1991
		0.031			Focal, *ad lib.*	Cords, 2000
Resident-egalitarian	*Colobus guereza*					
	(K)	0.011	0.001	0	*Ad lib.*	Oates, 1977
	(C)	0.054	0.007	–		
Dispersal-egalitarian	*Papio ursinus*	0.20	0.58	0	Focal	Byrne et al., 1989
	Pan troglodytes (P3)	0.07	0.02	0.03	*Ad lib.*	Sugiyama, 1988
	Nasalis larvatus[d]	0.004			Scan	Yeager, 1990
	Piliocolobus badius	0.04	0.038		Focal	Korstjens et al., 2002
	P. temminckii	0.02		0.001	Scan	Starin, 1994
	Colobus polykomos[e]	0.11	0.01		Focal	Korstjens et al., 2002
	C. vellerosus[f]					
	(WW)	0.06	0.002		Focal	This Study
	(B)	0.02–0.07	0.01–0.03			

Information in brackets refers to different groups. Only non-captive studies were included. Social category following Sterck et al. (1997) except where further information states otherwise.
[a] *Macaca mulatta*, *M. nemestrina*, *M. fuscata*, *M. fascicularis*, *M cyclopsis*, have true nepotistic hierarchies; all other macaques have more egalitarian female relationships and should be placed in RNT (Matsumura, 2001).
[b] *Semnopithecus entellus* is placed in RN category because females form a linear hierarchy, although it is not nepotistic (Hrdy and Hrdy, 1976; Borries, 1993).
[c] *Cercopithecus mitis* is RNT because females form linear hierarchies (Cords, 2002).
[d] *Nasalis larvatus* is DE because both sexes disperse (Bennett and Sebastian, 1988).
[e] *Colobus polykomos* is placed in DE because females and males disperse (but females participate in between group contest; Korstjens and Schippers, 2003; Korstjens et al., 2005; Korstjens et al., in press).
[f] *C. vellerosus* is placed in DE because females disperse; however, we do not know if dispersal is frequent or occasional.

had a greater number of female neighbors than male neighbors and a Wilcoxon Signed Ranks test indicated a significant difference ($z = -4.409$, $n_{AFAF} = 47$, $n_{AFAM} = 47$, $P < 0.001$). The AF-AF approach rate was similar to the AF-AM approach rate (Wilcoxon Signed Ranks test, $z = -0.440$, $n_{AFAF} = 21$, $n_{AFAM} = 21$, $P = 0.660$). After the take-over, in P2, females continued to be more important social partners for females than males. Most time spent grooming was between adult females (Table 3) and the AF-AF grooming bout rate was approximately seven times greater than the AF-AM rate, which was significantly different (Wilcoxon Signed Ranks test; $z = -2.224$, $n_{AFAF} = 46$, $n_{AFAM} = 46$, $P = 0.026$). The AF-AF approach rate was greater than the AF-AM rate and the Wilcoxon Signed Ranks test indicated a significant difference ($z = -3.030$, $n_{AFAF} = 46$, $n_{AFAM} = 46$, $P = 0.002$). Female focals had an equal number of female and male neighbors (Wilcoxon Signed Ranks test, $z = -0.500$, $n_{AFAF} = 45$, $n_{AFAM} = 45$, $P = 0.617$). In P3, males seemed to be equally important social partners for females. Time spent grooming was equal between adult females and adult males (Table 3), the AF-AF grooming bout rate was similar to the AF-AM rate (Wilcoxon Signed Ranks test; $z = -0.135$, $n_{AFAF} = 31$, $n_{AFAM} = 31$, $P = 0.893$), and the AF-AF approach rate was similar to the AF-AM approach rate (Wilcoxon Signed Ranks test, $z = -0.385$, $n_{AFAF} = 25$, $n_{AFAM} = 25$, $P = 0.701$).

Although grooming bout rates were not significantly different between groups (Period 1 $z = -1.342$, $n_{AFAM} = 47$, $n_{AFAM} = 49$, $P = 0.180$; Period 2 $z = -0.535$, $n_{AFAM} = 40$, $n_{AFAM} = 46$, $P = 0.593$; Period 3 $z = -1.214$, $n_{AFAM} = 31$, $n_{AFAM} = 31$, $P = 0.225$), the approach (Period 1 $z = -2.336$, $n_{AFAM} = 24$, $n_{AFAM} = 21$, $P = 0.019$; Period 2 $z = -1.225$, $n_{AFAM} = 32$, $n_{AFAM} = 46$, $P = 0.221$; Period 3 $z = -2.760$, $n_{AFAM} = 31$, $n_{AFAM} = 25$, $P = 0.006$) and proximity rates (Period 1 $z = -3.492$, $n_{AFAM} = 44$, $n_{AFAM} = 47$, $P < 0.001$; Period 2 $z = -3.598$, $n_{AFAM} = 38$, $n_{AFAM} = 45$, $P < 0.001$) suggest AF-AM interactions were typically more common in B group (these rates control for the number of adults in each group in each time period). This suggests that AF-AM affiliation was stronger or more common in B group than in WW group.

Comparing the distribution of affiliative interactions using the blocks as the independent unit of analysis reveals differences in the same general direction with similar magnitudes, with the exception that the nearest neighbor differences for B group in period 1 were less distinct between AF-AF and AF-AM comparing blocks. In general, these comparisons support the statistical analysis and suggest that male-female relationships were stronger in B group than they were in WW group.

Female-female coalitions

No female-female coalitions were observed in WW or B group during agonistic interactions over food. However, in B group, on three occasions in P2, two females joined forces to attack a male that had joined the group during

the take-over on his approach of the youngest immature. This immature had been injured during previous attacks by the extra-group males. The two females, one of which was the immature's mother, were sitting in close proximity to each other when they simultaneously rushed at the approaching male, vocalized, and grappled with him for several seconds, before he retreated (Saj and Sicotte, 2005).

Dispersal events

We observed one case of female transfer into B group. This female was observed returning with the all-male group after they had conducted a male incursion in her group (Sicotte and MacIntosh, 2004). This female stayed with B group until the field season ended two months later. On at least one occasion during her stay (*ad libitum* data), we saw her being groomed by one of the resident females of B group. She may also have copulated with one of the new males. There was no overt aggression between the new female and the resident females during or after her immigration into the group as indicated by aggression recorded in the focal and *ad libitum* records (Saj, 2005). Since this dispersal event was observed, four other females have been observed transferring between groups at this site (in 2004: J.A. Teichroeb pers. comm.). They represent two cases of dispersal; in one case a female transferred into a study group by herself, and in the second case, three females (one adult and two subadults) left their group together following a male incursion. These females were met with resident female aggression. The presence of an all-male group in 2001 (Saj and Sicotte, 2005), and another in 2004 (Sicotte et al., in press), and sightings of several solitary males indicate that male dispersal occurs.

DISCUSSION

A few cases of female dispersal were observed in our population. According to current socio-ecological thinking, if female dispersal is more predominant than female residency, this characteristic should be associated with low female-female affiliation, higher male-female affiliation than female-female affiliation, and an absence of female coalitions. Indeed, affiliation between adults occurred at low frequency in the two *C. vellerosus* groups. In comparison to other Old World monkeys, adult *C. vellerosus* (0.8–1.2%) spent a small proportion of time grooming. Sussman et al. (2005) reported a mean of 7% of time spent in affiliative interactions for Old World monkeys (range 1.8–27.5%), although they include affiliation by adults and immatures. We do have more comparable data from a previous study at this site, which temporally overlapped with this study by 4 months, in which we reported that affiliation by adults and immatures (grooming, copulations, and play) made up 2–4% of the overall activity budget in WW and B groups (Teichroeb et al., 2003). In accordance with our predictions, the female-female grooming bout rate/individual in *C. vellerosus* was also low, following the pattern found in most egalitarian species (e.g., "Resident-Egalitarian" and "Dispersal-Egalitarian" species: Sterck et al., 1997), although exceptions can be noted (e.g. *Papio ursinus* has a higher grooming rate than other egalitarian species; Table 4).

We also predicted higher male-female affiliation than female-female if female dispersal was more prevalent than female residency. However, grooming and approaches were predominantly between females and nearest neighbors were predominantly females. At this point, however, we are unable to determine if dispersal among females is occasional or frequent in our population (Steenbeek, 2000, Isbell, 2004). If it turns out that female residency is more predominant, it would explain our finding that female-female bonds are stronger than male-female bonds.

In between-group comparisons, inter-sexual affiliation was stronger in B group than WW. It might have been that females in B group needed male support as a buffer against infanticide. Among some species, females in one-male groups face a higher risk of infanticide than females in multi-male groups because the frequency of male take-over is higher (Newton, 1986; Robbins, 1995; Janson and van Schaik, 2000; van Schaik, 2000). However, the risk of infanticide can be reduced if the defeated resident male remains with the group and intervenes in infanticidal attacks (Smuts, 1985; Borries and Koenig, 2000; Palombit et al., 2000). To promote male protection, females may direct affiliative interactions towards the male(s) as a means of obtaining protection for their infant (Hrdy, 1979; Palombit et al., 1997, 2001). The direction of inter-sexual grooming in B group was primarily from the adult females to the adult male, which suggests females were more responsible in maintaining the relationship than the male was (Smuts, 1985). Although we have no evidence of a direct relationship between female grooming and male support in B group, the resident male remained with the group after the male take-over and intervened in attacks by the new males on the youngest immature, who survived (Saj and Sicotte, 2005).

We also predicted infrequent female coalitions over food. Indeed, there was no evidence that females formed within-group coalitions to gain access to or defend food resources in our two groups. However, females did apparently form coalitions in response to male attacks on an immature. For instance, we report 11 male aggressions towards an immature in Saj and Sicotte (2005). The mother of the infant retaliated aggression towards the male in eight of these cases, and was supported by another group female in three of these eight retaliations (Saj, unpublished data). In another case, a male was observed attacking an infant at least seven times in the 4 days prior to the infant's death. In three of these seven cases, between two and four females retaliated towards the male (Sicotte et al., in press). This phenomenon has been reported in several other primate species (Sommer, 1987; Smuts and Smuts, 1993; Korstjens et al., 2002) and suggests that the risk of conspecific threat may influence the nature of female alliances in some species (Treves and Chapman, 1996). It would seem that if food resources are not monopolizable or usurpable, agonism does not increase access to food, therefore it is not worthwhile to form coalitions with other females to access food. However, as suggested by van Schaik (1989), it appears that short-term coalitions between females to protect infants are valuable (i.e. in reducing harm to the infant), but it is probably not worthwhile to maintain these affiliative relationships in other circumstances.

As we pointed out in the introduction, we could not establish dominance relationships among females, and this impedes our ability to draw firm conclusions at this point about this important aspect of female social relationships. The fact that the food resources were non-

monopolizable and non-usurpable (Saj and Sicotte, in press a) in association to the low rate of agonistic interactions (Saj and Sicotte, in press b) may be indicative of egalitarian relationships (although see Sussman et al., 2005).

The combination of social characteristics that we report here is largely congruent with the spatial and temporal distribution of food resources at BFMS and the related female competitive regime reported elsewhere. In Saj and Sicotte (in press a), data are presented that indicates the potential for monopolizability and usurpability of high-quality food resources among *C. vellerosus* was low. This pattern implied the potential for direct within-group feeding competition among *C. vellerosus* was low, and thus agonistic interactions over food would not be expected. Indeed, the behavioral data confirmed that agonism over food was extremely rare (Saj and Sicotte, in press b). Our data also suggests that females rarely participated in between-group competition (Sicotte and MacIntosh, 2004; Saj, 2005). In this article, we present the third piece of the puzzle necessary to investigate the socio-ecological model by connecting the ecological conditions and associated female competitive regime with the associated social structure of *C. vellerosus,* which is characterized by low levels of female affiliation, a lack of female-female coalitions over food, and female dispersal (van Schaik, 1989; Sterck et al., 1997). These characteristics describe the "Dispersal-Egalitarian" category of the model proposed by Sterck et al. (1997). However, as we discussed earlier, we also observed greater female-female affiliation compared to male-female affiliation, which may be more indicative of a female resident species (Wrangham, 1980; van Schaik, 1989). This observation is difficult to interpret in combination with our other social data, unless future research demonstrates that female residency is a more predominant pattern than female dispersal for *C. vellerosus.*

Unlike the folivores listed in Table 1, our species mostly fits the predictions of the socio-ecological model. This leads us to ask why some species fit the predictions of the model and why some do not? One interesting avenue to examine is the occurrence of female dispersal (a trait exhibited by the species in Table 1). Female dispersal has often been inferred in species on the basis of few instances. However, unless such data is matched with data on female residence (i.e. female reproduction in their natal group), it is not possible to ascertain which trait is more predominant. Hence, species may be misclassified. Furthermore, female dispersal may be occasional or facultative in some species (Moore, 1993; Strier, 1994; Isbell and Van Vuren, 1996; Steenbeek, 2000; Isbell, 2004), which is not predicted by the current socio-ecological model (Sterck et al., 1997). If this is the case, association between traits are not as easy to predict. For example, high female participation in inter-group encounters co-occurred with female dispersal in *Colobus polykomos* (Korstjens et al., 2005; see other references in Table 1). Some authors have suggested de-linking female dispersal and some social traits (Isbell, 2004; Koenig et al., 2004). However, we argue that before de-linking, we need to better understand the pattern of female relatedness in groups in which female dispersal occurs. For instance, it might turn out that although female dispersal occurs, it is occasional, thus most females in a group are related, and therefore it is not contradictory that females participate in between group encounters or form a linear dominance hierarchy.

Such flexibility is likely to occur in species where the ecological and social costs of dispersal are rather low, and where the benefits of residency are perhaps also not dramatically high. Females in such species would have a larger range of dispersal/residence options which would cause stochastic variation in group composition (particularly in the number of related females) and ultimately in the resulting social structure.

CONCLUSIONS

In conclusion, our data suggests there is good reason to focus on "competition modeling" to explain primate social structure, even in a species which has very little direct competition (contra Sussman et al., 2005). This paper is the third in a series of papers (Saj and Sicotte, in press a,b) in which we investigate the link between food distribution and abundance, competitive regime, and social structure. Here, we present data showing that female affiliation in *Colobus vellerosus* is low, female coalitions over food are absent, and female dispersal occurs, which are correctly associated with our other data which indicates female-female agonism over food is low and that food resources are not monopolizable or usurpable. Taken together, these data suggest the current socio-ecological model is correct to link food distribution and female feeding competition to explain primate social structure.

ACKNOWLEDGMENTS

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