Evolutionary determinants of modular societies in colobines

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Modular societies are structurally characterized by nuclear one-male units (OMUs, or harems) embedded within larger relatively coherent social bands. Within the order Primates, modular societies are uncommon, found in only a few species, including humans. Asian colobines (Presbytini) principally form either unimale groups that forage independently and are often territorial, or modular associations, which range from tight bands composed of OMUs to loose neighborhoods of OMUs. A phylogenetic reconstruction of modularity in the Presbytini revealed that the single OMU pattern is probably the ancestral state while the modular pattern is derived. The selective forces favoring the evolution of modular societies have thus far been virtually unexplored. Although some ecological explanations cannot be ruled out at the moment due to lack of comparative and quantitative data, preliminary circumstantial evidence does not seem to support them. Instead, a social factor, bachelor threat, is consistent with many observations. This hypothesis argues that where the pressure from nonreproductive bachelor males is unusually high, OMUs aggregate as a means of decreasing the amount of harassment and the risk of takeovers and infanticide. A comparative test found an association between modular societies and bachelor threat, as proxied by sex ratio within social units. The concentration of modular systems in colobines may be due to their unusual ecology, which leads to unusually low intensity of scramble competition. Modular colobines rely more on nonlimiting ubiquitous resources than nonmodular ones and thus can afford to gather in bands. Moreover, by comparing the slopes of regressions between group size and daily travel distance for several groups of one modular and one nonmodular colobine, we found slopes in the nonmodular to be steeper by a factor 30, indicating that ecological constraints associated with scramble competition prevent higher level groupings in nonmodulars. Thus, modular sociality in Asian colobines may have arisen because both social benefits are substantial and ecological costs are relatively low. *Key words:* colobine, conspecific threat, ecological constraints, multilevel society, one-male unit, phylogeny, snub-nosed monkey. *[Behav Ecol 21:63–71 (2010)]*

Whereas in most animals living in stable and individualized social groups there are no levels of social organization beyond the social group, there are some exceptions, known as multilevel social systems or modular societies, which comprise 2 levels of distinguishable social grouping. They have been documented in several mammal species. Thus, African elephants (*Loxodonta africana*) regularly form large aggregations of stable subunits consisting of female bonded family groups (Moss and Poole 1983; Wittemyer et al. 2005). In plains zebras (*Equus burchelli*) and khulans (*Equus hemionus*), harems regularly join to form large, spatially cohesive herds (Feh et al. 2001; Rubenstein and Hack 2004). Other mammalian taxa with comparable multilevel social systems include sperm whales (*Physeter macrocephalus*; Whitehead et al. 1991), killer whales (*Orcinus orca*; Baird 2000), and prairie dogs (*Cynomys ludovicianus*; Hoogland 1995).

Among primates, a few species have been shown to have modular societies, for example, snub-nosed monkeys (*Rhinopithecus* spp.; Kirkpatrick 1998), proboscis monkeys (*Nasalis larvatus*; Yeager 1990), gelada baboons (*Theropithecus gelada*; Kawai et al. 1983), hamadryas baboons (*Papio hamadryas*; Kummer 1984), and humans (e.g., Chapais 2008). The foremost structural characteristics of primate modular systems are stable entities, usually one-male units (OMUs), which frequently or permanently associate, and thus form a higher grouping level, often termed the band (Grueter and Zinner [2004] and references therein) (Figure 1). Bands can be very large in size, with up to several hundred members (Grueter and Zinner 2004). Sociopositive and sexual behavior is largely restricted to the first tier, the OMU, whereas interunit interactions are limited (e.g., Dunbar RIM and Dunbar EP 1975; Zhang et al. 2006; Grueter 2009). Most modular taxa share other traits that distinguish them from the nonmodular ones: conspicuous sexual size dimorphism (Grueter and van Schaik 2009), prominent male adornments, large relative testes size (Grueter and Zinner 2004), large home ranges, and low population density (Grueter 2009).

In Asian colobines (Presbytini), 3 forms of social organization can be recognized: 1) separate, often territorial OMUs with little range overlap and few interunit encounters (and if so, rather aggressive) (e.g., *Presbytis hosei*, Mitchell 1994; *Trachypithecus vetulus*, Rudran 1973); 2) large coherent multimale–multifemale groups (only found in *Semnopithecus* spp., e.g., Borries 2000); 3) modular societies, with OMUs having large (>40%) range overlap, at times coordinating travel and occupying adjacent sleeping trees (Stanford 1991a, 1999b), or cofeeding in the same patch or adjacent patches (Mukherjee and Saha 1974; Bennett 1983), or OMUs exhibiting complete range overlap and forming tight cohesive bands that rarely split (e.g., *Rhinopithecus bieti*, Kirkpatrick et al. 1998). In modular societies, relations among units are generally rather neutral (e.g., Yeager 1992).

In this paper, we examine the evolution of modular societies in Asian colobines. We first ask whether modular societies are derived in this taxon, as assumed by the hypothesis that follows. We then examine the conditions that led to the evolution of modular societies, focusing on social or ecological determinants in turn. The bachelor threat hypothesis (Rubenstein

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adult female

subadult female

infant

adult male

subadult male
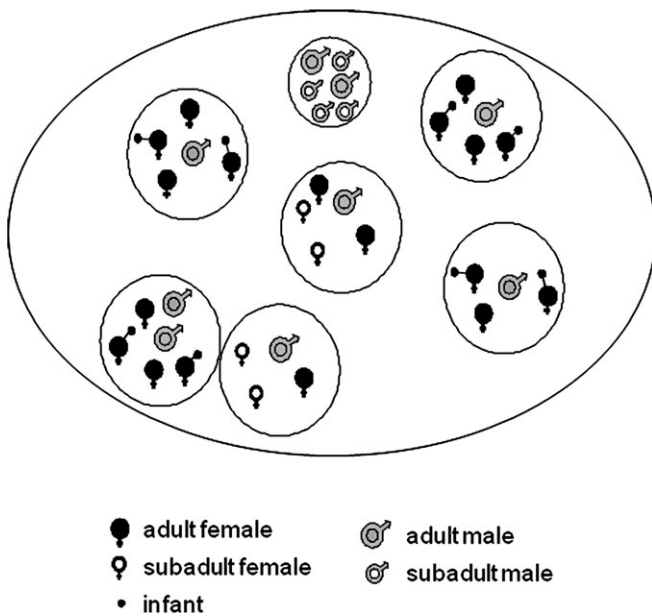
Figure 1
Structure of a modular system, exemplified by snub-nosed monkeys.
The illustrated hypothetical band consists of 5 OMUs and 1 AMU.

1986) posits that OMUs assemble and OMU males may form coalitions to decrease the amount of harassment, in particular the risk of takeovers and infanticide by nonreproductive bachelor groups. Rubenstein (1986) argued that bachelor threat is the most plausible scenario for the evolution of multilevel societies in plains zebras. He found that when coalitions form, female contact by bachelors was significantly reduced. OMU males thus benefit from a reduced risk of being ousted from their OMU, whereas females benefit from a reduced risk of infanticide. Sexual conflict, in the form of coercion and infanticide, may have been a critical selective factor shaping primate social systems (Smuts B and Smuts R 1993; van Schaik 1996; Sterck et al. 1997; Chapman and Pavelka 2005; Harcourt and Stewart 2007). Nonetheless, this hypothesis has not been applied to modular primate societies. Wrangham R, personal communication, Mori (1979), and Dunbar RIM and Dunbar EP (1975) noted that several gelada unit leaders sometimes engaged in a collective challenge to confront and chase invading all-male groups. A few comparative studies on primates living in other types of social organization also demonstrated that conspecific threat influences group size (Treves and Chapman 1996; Janson and van Schaik 2000).

To test the bachelor threat hypothesis, we developed the following prediction: across species, presence/absence of modularity (categorical), and home range overlap (as continuous proxy variable for modularity) are positively correlated with the number of bachelor males in the population (cf., Rubenstein and Hack 2004). Assuming an even male–female sex ratio at birth, the adult sex ratio (F:M) in mixed-sex units can serve as a proxy measure for bachelor threat. The higher the value, the more males are expected to be excluded from breeding units. That sex ratio is an accurate proxy for bachelor threat has been corroborated by the significant positive correlation between the actual number of nongroup males per bisexual group and sex ratio of bisexual groups in 19 groups of *Semnopithecus* spp. ($r_s = 0.596$, $P = 0.007$; data from Treves and Chapman 1996).

Many ecological benefits have been proposed to have favored group living in primates and other animals: localized resources (Altmann 1974), harvest efficiency (Cody 1971;

Altmann 1974; Cords 1987; Rodman 1988), predation avoidance (Alexander 1974; van Schaik 1983), between-group resource competition (Wrangham 1980; Yeager 1992), and thermal benefits (Bleisch and Xie 1998). Table 1 presents empirical and circumstantial evidence that these nonexclusive hypotheses are rather unlikely to explain why some Asian colobines evolved a tendency toward modularity. However, a more systematic assessment is needed once comparative data become available. Moreover, the predation hypothesis is not easy to characterize in quantitative terms and thus will be difficult to be ruled out completely. The localized resource hypothesis does not appear to be applicable to the strictly modular societies but may be an explanation for the loose neighborhoods found in some colobine species.

Even if there are no pervasive ecological benefits, however, the ecological conditions must permit the large groups associated with modular societies, and we will compare the extent of scramble competition, which is a direct function of group size (van Schaik and van Noordwijk 1988; Janson and Goldsmith 1995) among modular and nonmodular colobines. We would expect that modular colobines should be less ecologically constrained to form bands than nonmodular ones. Specifically, we predict a weaker effect of group size on foraging effort, as estimated by daily travel distance (DTD), in modulars. Comparing groups of different sizes of a given species provides the best test case to assess these ecological costs. We present intraspecific data for *R. bieti*, a modular taxon and *Presbytis thomasi*, a nonmodular colobine; these are the only species of Asian colobines for which data on several groups (>3) are available. Additionally, we predict that the percentage of "grazing" foods is higher in modular than nonmodular colobines, and DTDs are not substantially longer in modulars relative to nonmodulars. These latter 2 predictions are based on the assumption that in order for large groups to form at modest costs, the resource base must consist of superabundant and ubiquitous items such as mature leaves and lichens (Rodman 1988; Kirkpatrick et al. 1998), that is, grazing foods that reduce competition and would not force larger groups to exhibit longer DTDs to sustain per capita energy intake of group members (Janson and Goldsmith 1995; but see Snaith and Chapman 2008).

MATERIALS AND METHODS

The evolution of the trait modularity in the Presbytini was reconstructed in MacClade 4.07 (Maddison WP and Maddison DR 1992). We used different rules to reconstruct character evolution: parsimony, DELTRAN (resolving states that remain ambiguous when using parsimony so as to delay changes), and ACCTRAN (forcing ambiguous reconstructions to occur closer to the root and therefore reducing the number of transitions). In the cladogram of Figure 2, we consider the colobine social organization states ordered.

Information on the variables used here (i.e., social organization, home range overlap, sex ratio, % mature leaves/lichens in the diet, and DTD) was obtained from the published literature (and additional unpublished theses and personal communications) and is presented as Supplementary Material. Populations of colobines in extremely degraded and disturbed habitats (plantations, highly degraded secondary forest) were omitted from the analyses. If a population was represented by 2 data sets taken at different points in time, we used only the more extensive study. For the variable sex ratio, we used weighted species means, that is, means weighted by the number of groups studied, due to large differences in sample sizes. For the variables DTD and home range overlap in interspecific comparisons, we used means of population means. Different sample sizes across analyses are the result of missing data. For interspecific regression analyses, all

Table 1
Ecological hypotheses for band formation in Asian colobines

| Hypothesis	Description	Predictions	Applicability/evaluation
Localized resources	Highly localized essential or ephemeral food resources such fruit trees attract several OMUs or force OMUs to congregate at such places	Units should assemble only temporally when these resources are available or in spatially restricted places	Modular construction is a relatively persistent feature in at least the strictly modular colobines (e.g., Kirkpatrick et al. 1998; Zhang et al. 2006)
Harvest efficiency	Bands form because foraging as a band rather than separate units maximizes individual feeding efficiency by minimizing returns to depleted food patches	Individual net food intake should be higher in bands than in autonomous units or higher when living in groups than when foraging independently	Through theoretical modeling, it has been borne out that group foragers obtain food at lower rate than solitary foragers (Beauchamp 2005)
		Individual net food intake should be higher in bands than in autonomous units or higher when living in groups than when foraging independently	Subordinate units may experience less competition for access to dispersed profitable patches when separating from the band and foraging independently (Grueter 2009; sensu Harcourt and Stewart 2007)
		Modularity should be restricted to populations living in habitats with slowly regenerating and thus depletable foods (e.g., lichens) (cf., Kirkpatrick et al. 1998)	Band formation is not limited to species inhabiting habitats where food resource regeneration time is low
Predation avoidance	Protection from predators is an aggregative force for units	Groups should be sufficiently large to be buffered against predator attacks	A group size benefit (dilution, vigilance) from predation quickly saturates, so bands of several hundred seem unnecessarily large (Hamilton 1971; Pulliam 1973; cf., Kirkpatrick et al. 1998)
		Band formation should be more common in habitats with an intact predator community	Many tropical langurs live in small isolated OMUs despite the presence of arboreal feline predators (e.g., clouded leopards) in these habitats
Between-band resource competition	Units associate with other units to avoid displacement at resource sites	As a prerequisite for interband competition to be relevant, home range overlap among bands should be large	In the genus *Rhinopithecus* (modular), bands have no or little range overlap and interband competition does not seem to be strong (Chen et al. 1989; Bleisch and Xie 1998; Kirkpatrick et al. 1998)
Thermal benefits	Bands emerge because individuals in large bands have many partners for huddling and thus gain thermoregulatory benefits	The lower the mean annual temperature within the natural habitat of a given species is, the higher should be the prevalence of modular systems	By comparing average annual habitat temperatures of modular versus nonmodular colobine species, we found no statistical difference (t-test, $t = 1.54$, $P = 0.141$, df = 18) (this study)
		Modular societies should not exist in tropical climates, where animals would rarely if ever need to form big huddles to minimize heat loss	Modular societies are common in tropical climates
		Larger groups should form distinctively during the cold season	*Rhinopithecus bieti* (modular) live in a seasonally freezing climate, but the bands seem to be equally cohesive year round or even less cohesive during the cold season (Kirkpatrick et al. 1998; Grueter 2009)
		Huddling clusters should include members of other units	Because OMUs are discrete social entities, huddling does not involve more than one unit (Chen et al. 1989; Qi et al. 2004; Grueter 2009)

"Band" refers to a large social group composed of subunits. Arguments are given in disfavor of the hypotheses and references are listed of studies that have rejected the predictions.

variables (except % mature leaves) were ln-transformed prior to analysis to correct problems of unequal variances in non-phylogenetic analyses and to meet the assumptions of independent contrasts in phylogenetic trees.

We excluded *Semnopithecus* from tests of the bachelor threat hypotheses because a previous analysis has already dealt with the effect of conspecific threat on size and composition of *Semnopithecus* groups (Treves and Chapman 1996). *Semnopithe-cus* represents the only taxon of Asian colobines that exhibits a variable social system: mostly large multimale–multifemale groups (mean group size: 27) and some unimale groups. There are no modular populations in this taxon, which makes it methodologically difficult and biologically unjustified to include *Semnopithecus* in the analysis, although large multi-male–multifemale groups may be functionally analogous to modular societies.

Figure 2
Colobine phylogeny, indicating the distribution of the 3 character states as defined in the text. Phylogeny is based on Bininda-Emonds et al. (2007), with terminal branches having been modified after Wang et al. (1997), Zhang and Ryder (1998), Nadler and Roos (2002), Li et al. (2004), Sterner et al. (2006), Osterholz et al. (2008), and Geissmann, unpublished data where necessary. Note that the phylogenetic relation of the *Nasalis–Simias* branch with regard to the other colobines differs between the composite estimate of Purvis (1995) and the supertree of Bininda-Emonds et al. (2007).
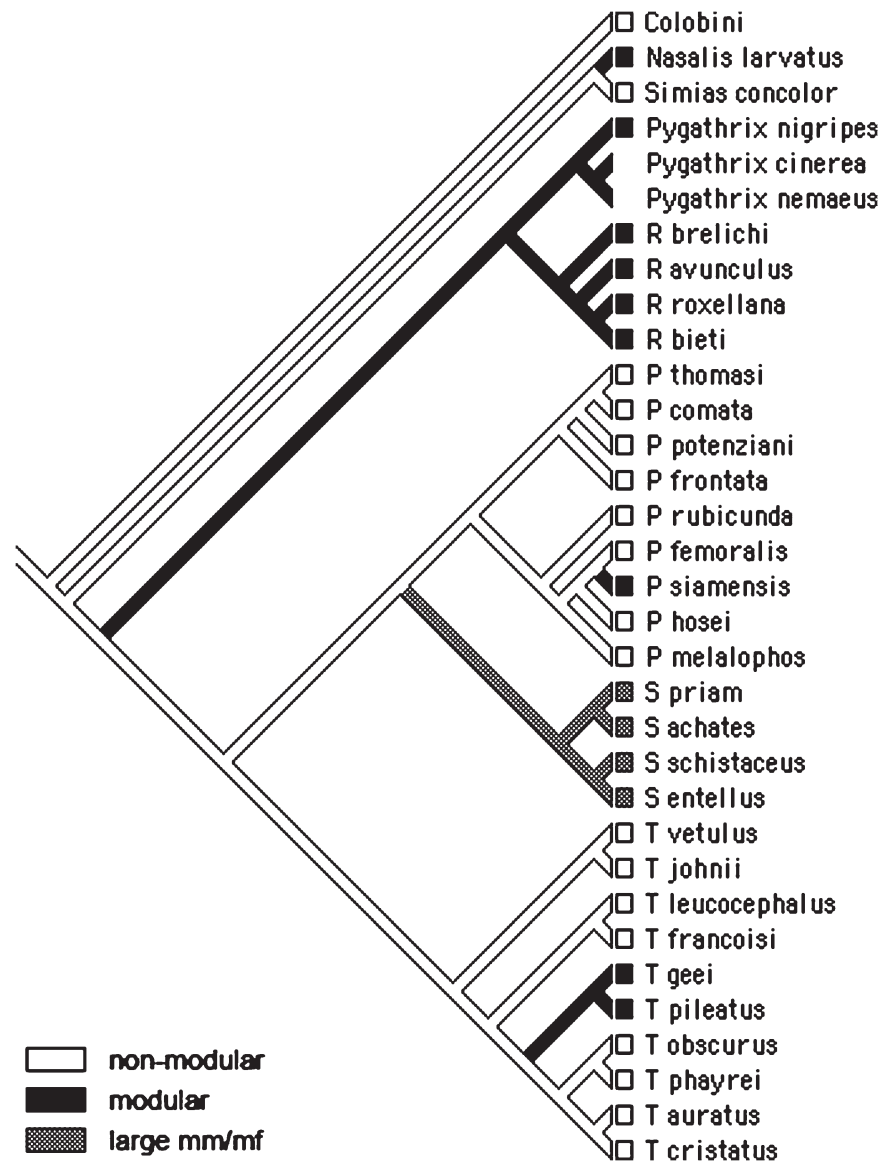
Because all species with modular systems also show substantial home range overlap, we used home range overlap as a continuous proxy measure for modularity. Such a continuous variable is better suited for testing comparative predictions than a categorical variable because it provides more fine-grained variation and is more likely to meet parametric statistical assumptions (Nunn 1999; Nunn and Barton 2001). Between-group encounter rate was found to be correlated with home range overlap in this sample of Asian colobines (Spearman $r_s = 0.935$, $P < 0.001$, $n = 11$), so there was no need to include encounter frequency as an additional variable (contra van Schaik et al. 1992).

Due to their shared ancestry, species values are often not considered to represent independent data points in comparative analyses of cross-species patterns (Harvey and Pagel 1991; Martins and Hansen 1996; Abouheif 1999). This phylogenetic nonindependence increases Type I error rates because the degrees of freedom (df) are not properly partitioned (Pagel 1993). We thus controlled for phylogeny by means of the independent contrasts method (Felsenstein 1985), as implemented by the PDAP module (Garland et al. 1999) of the program Mesquite (Maddison WP and Maddison DR 2005).

The phylogeny used was primarily based on a molecular supertree containing estimates of divergence dates for various nodes (Bininda-Emonds et al. 2007). Because the topology is not fully resolved for Asian colobines, additional species (for which data on the variables of interest were available) were added to the tree based on phylogenetic information obtained from other sources (Wang et al. 1997; Zhang and Ryder 1998; Nadler and Roos 2002; Li et al. 2004; Sterner et al. 2006; Osterholz et al. 2008). If unequivocal information on divergence dates from these additional sources could not be extracted, we arbitrarily spaced nodes evenly along branches (cf., Plavcan 2004).

Because the independent contrast method is relatively robust to inaccuracies in the available phylogenetic information (branching sequence and branch lengths) and because mostly terminal branches were unresolved, such ambiguities have been found to hardly affect the outcome of the analysis (Martins and Garland 1991). When repeating the contrast analysis under a "punctuated evolution" model, that is, setting all branch lengths equal to 1, the results did not differ in the level of significance from the ones presented here. Absolute contrasts were also standardized by dividing them by the

square root of the sum of the branch lengths. This was done because the further back on the roots of the tree, toward the most primitive character states, the contrasts are more and more removed from the observed values and are estimated through an averaging process. Thus, the estimated primitive characters states were given less weight than the topmost states (Garland et al. 1999; cf., Barrickman et al. 2008). Contrasts were statistically analyzed with least squares regression, and following standard practice, contrasts slopes were forced through the origin (Garland et al. 1992).

Comparative analyses were also performed using species data, that is, without controlling for phylogeny. Both nonphylogenetic and phylogenetic results are reported. We used model I linear regressions to test for relationships between a dependent and an independent variable. Analyses were run in JMP 7 and SPSS 16.0. All probabilities reported are for 2-tailed tests. Statistics were considered significant at $P < 0.05$.
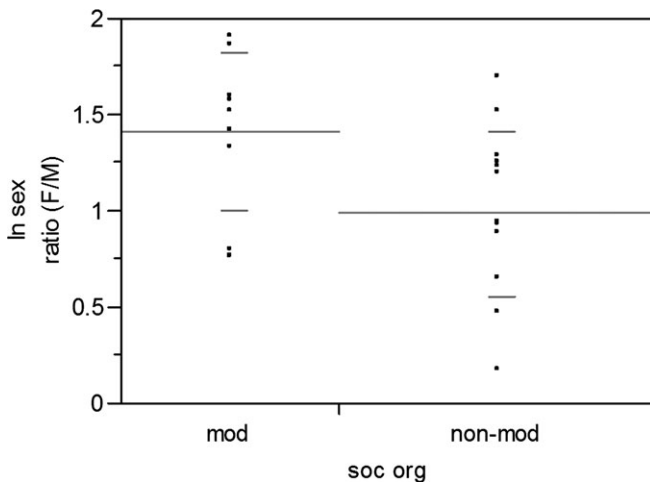
RESULTS

Historical origins of modularity

Reconstruction of the social organization of the Presbytini (with Colobini as an outgroup) confirms that a nonmodular system was ancestral and modularity is a derived feature (Figure 2). DELTRAN, ACCTRAN, and parsimony all yielded the same pattern. Modularity evolved 3 or 4 times independently in the Presbytini: twice in the odd-nosed colobines (only once if we assume a monophyletic relationship for the odd-nosed colobines [Sterner et al. 2006]), once in *Presbytis* (*Presbytis siamensis*), and once in *Trachypithecus* (*Trachypithecus geei* and *Trachypithecus pileatus*). Modularity was likely lost secondarily in *Simias*, which has a tiny geographical distribution on the Mentawai Islands, possibly because its groups are very small due to the absence of feline predators or because recent anthropogenic infiltration and hunting on the Mentawai Islands has reduced population numbers of this species to a level where modularity cannot be expressed anymore (cf., Watanabe 1981). Strict modularity is phylogenetically confined to the odd-nosed colobines.

Bachelor threat hypothesis

As shown in Figure 3, there was a significant difference in sex ratio of bisexual groups (proxy measure for bachelor threat)

between the categorical variables modular versus nonmodular (t-test, $t = -2.353$, $P = 0.0290$, df = 20). When using home range overlap as a continuous proxy measure for modularity, sex ratio of bisexual groups showed a significant positive correlation with home range overlap ($F_{1,16} = 5.835$, $P = 0.0280$, $R^2 = 0.267$, R^2 adjusted $= 0.221$). The regression equation would be:

$$\ln \text{home range overlap} = 1.87 + 1.24 \times \ln \text{sex ratio (Figure 4a)}$$
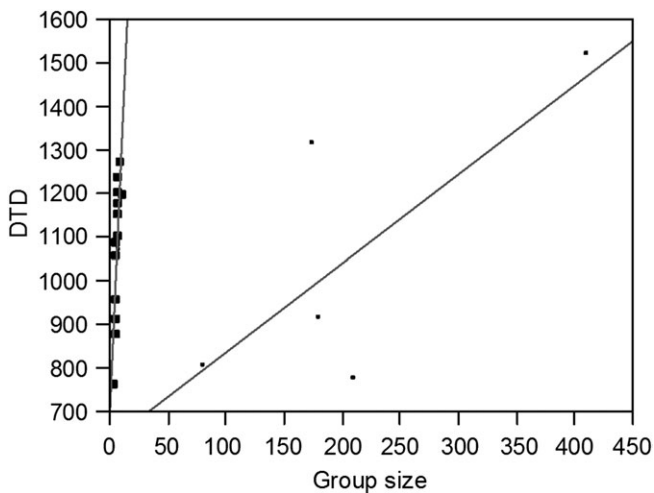
After removal of phylogenetic dependence, this relationship became highly significant ($F = 18.573$, $P = 0.0005$) (Figure 4b).

Ecological constraints on band formation

We investigated the effect of group size on DTD for several groups of *R. bieti* and *P. thomasi*, respectively (Figure 5). We found a significant positive linear relationship for *P. thomasi* ($F_{1,12} = 17.57$, $P = 0.0013$, $R^2 = 0.594$, R^2adj. $= 0.560$), whereas DTD tended to increase with group size in *R. bieti* but not significantly so ($F_{1,3} = 3.73$, $P = 0.1490$, $R^2 = 0.554$, R^2 adj. $= 0.406$) (see Figure 5 for data sources). An analysis of covariance was then performed with both species to test if the 2 slopes were significantly different. The effect of group size on DTD was found to be higher for *P. thomasi* than for *R. bieti* ($F = 7.68$, $P = 0.0143$, df = 1). The 2 slopes differed by
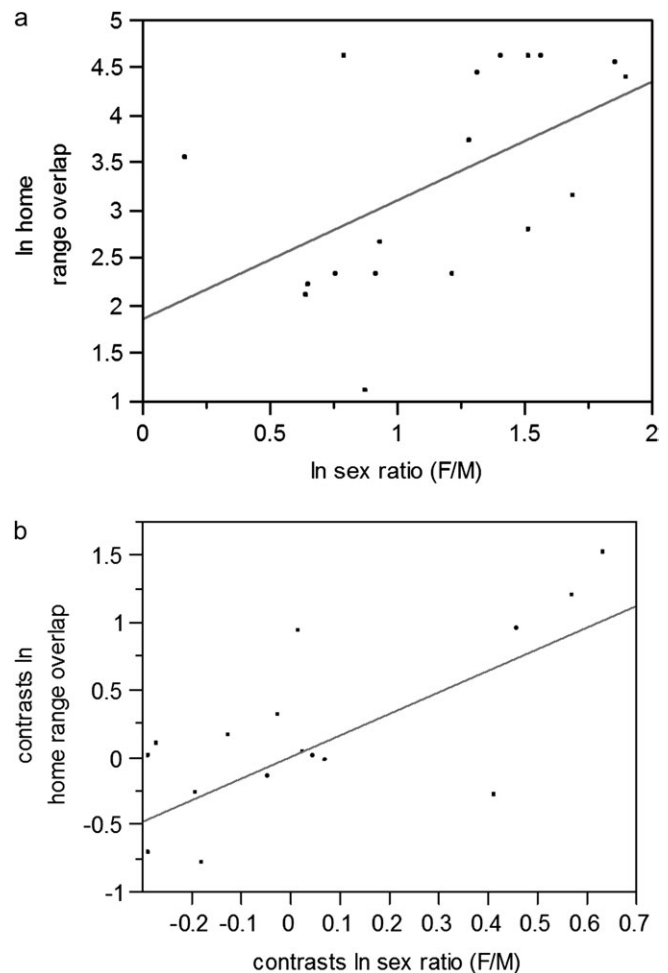
Figure 4
Association between home range overlap and sex ratio (F:M) in Asian colobines. (a) Species data and (b) independent contrasts.

Figure 3
Adult sex ratio (F:M) of bisexual groups compared between modular and nonmodular colobines.

Figure 5

Regressions of group size against DTD for several groups of *Rhinopithecus bieti* and *Presbytis thomasi*. Group size refers to band size in *R. bieti*. The small squares designate *R. bieti*, the large ones *P. thomasi*. The following equations were obtained: *R. bieti*: DTD = 631 + 2.04 × group size; *P. thomasi*: DTD = 666 + 60.17 × group size. Data for *P. thomasi* were taken from Steenbeek and van Schaik (2001), data for *R. bieti* from Kirkpatrick et al. (1998), Liu et al. (2004), Xiang (2005), Ren et al. (2009), and Grueter CC, unpublished data.

a factor of 29.5; whereas *P. thomasi* have to travel another 60 m per additional individual added to the group, DTD increases by only 2 m per individual in *R. bieti*. The relative ranging cost (RRC) (Janson and Goldsmith 1995), which measures the increased ranging cost of an additional group member scaled relative to the DTD of a hypothetical group of 1, is 0.083 for *P. thomasi* and 0.003 for *R. bieti*.

DTD did not differ significantly between modular and non-modular colobines ($t = -1.101$, $P = 0.2909$, $df = 14$). The difference between modular and nonmodular species in the percentage of low-quality foods in the diet (mature leaves and lichens) was significant ($t = -2.240$, $P = 0.0432$, $df = 14$).

DISCUSSION

The correlations between the suspected number of bachelor males and the prevalence of modularity confirm the prediction of the bachelor threat hypothesis for Asian colobines. In addition, there is also ample circumstantial evidence that incursions by bachelors pose a real and significant threat to colobine unit leaders and also females. First, infanticide is a common male reproductive strategy among primates (van Schaik and Janson 2000) and also pays in seasonally breeding colobines via reduction of interbirth interval of the mother (e.g., Borries 1997; Cui et al. 2006). Second, take-over and infanticide by putative bachelor males has been documented in several modularly organized colobine societies (e.g., Agoramoorthy and Hsu 2005; Xiang and Grueter 2007; Qi et al. 2008). Third, all-male units (AMUs) are an influential part of modular societies and habitually follow the mixed-sex bands and associate with them (Bennett and Sebastian 1988; Yeager 1990; Stanford 1991a; Kirkpatrick 1998; Grueter and Zinner 2004; Hoang 2007). Fourth, males respond differently to other OMU males than AMU males. Although encounters between reproductive units and nonre-productive units are often characterized by high levels of ten-sion, encounters between OMUs evoke more casual responses (Stanford 1991a; Boonratana 1993; Grueter CC, personal observation). Fifth, OMU males exhibit nonaggressive rela-

tions with extra-unit males that are known to them, that is, encountered on a regular basis (Stanford 1991a). In *R. bieti*, males of different OMUs are consistently in close proximity and tend to be neutral toward each other most of the time unless a male encroaches on another male's space (Grueter 2009).

The explanatory power of the bachelor threat hypothesis for modular colobines is further bolstered by observations of unit holders actually collectively defending the group against incur-sions by bachelor males (cf., Rubenstein and Hack 2004). Cases of OMU leaders collaboratively attacking intruding AMU males have recently been reported for a habituated group of *Rhinopithecus roxellana* (Zhao and Li 2009). The rea-son why such cases are not more widely reported in the colobine literature may be due to the extremely difficult ob-servation conditions that characterize most study sites (poor habituation, dense foliage etc.), and the fact that modular colobines have been the focus of relatively few field studies.

Even if male cooperation is uncommon in some modular colobine societies, this does not necessarily invalidate the bach-elor threat hypothesis. First, it is possible that males of different units do not need to show deliberate coordination against bachelors. Sterck and van Hooff (2000) mention that male Asian colobines "seem neither to check the actions of other males nor to coordinate their behavior with other males ac-tively, but they may well act in parallel because similar behav-ior is triggered by the same stimulus (e.g., Curtin 1980, for banded langurs)." Second, even if intentional cooperation is not exhibited by males in bands, a benefit for males may accrue simply for numerical reasons: the probability of being targeted and ousted by bachelors is supposed to decline as units gather in larger bands. This is analogous to the dilution effect, a supposedly adaptive response to predation (Pulliam and Caraco 1984; Caro 2005).

The principle of OMU leaders gathering together for safety reason is similar to the acceptance of "follower" males, as found in some OMU-based equid and primate societies. In some equids, male followers at times also help dominant stal-lions to protect females against harassment by outside males and to hold off outside males from matings with band females (Miller 1981; Stevens 1990; Feh 1999 but see Linklater et al. 1999). In mountain gorillas, follower males can participate in interunit encounters and aid the dominant male in defending the group from potentially infanticidal external males (Robbins 2001; Sicotte 2001; Harcourt and Stewart 2007). In hamadryas baboons, there is some evidence that males be-longing to a clan cooperate to prevent nonclan males from kidnapping females (Sigg et al. 1982). In chimpanzees, males cooperatively defend estrous females from mating with other males when the number of group males reaches a certain threshold and single males are no longer able to monopolize the females on their own (Watts 1998). In gelada baboons, Dunbar (1984) has suggested that by allowing an extra male to join the harem as a follower, the current leader may reduce the chances of his unit being the target of a takeover attempt by a bachelor male and may thus prolong his tenure as a breeding male. Dunbar (1984, p. 177) explains that "the benefits that unit holders derive from accepting a follower have nothing to do with the latter's playing any active role in supporting the unit leader during takeover attempts by rival males. It seems to work, however, because harems with followers reduce the 'effective' size of the units (i.e., the num-ber of unit females actually bonded with the harem male), thus increasing the females' loyalty to the leader and reducing the probability of being evicted by other males." The same reasoning may be appropriate for a modular colobine system.

Another factor possibly affecting the formation of bands is kinship among units. A network of (male) kin among those

units may facilitate OMUs keeping closer together (cf., Bradley et al. 2004). In proboscis monkeys and capped langurs, OMUs form differentiated relationships in which they tolerate some groups but not others (Yeager 1989, 1991; Stanford 1991a, 1991b). Investigating such kinship factors among units in a modular colobine society would lead to a better understanding of how these complex societies operate.

The question arises as to whether the multimale–multifemale groups of *Semnopithecus* represent an alternative solution to the same fundamental evolutionary stimulus, namely conspecific threat? Treves and Chapman (1996) found partial support for this idea, that is, when the risk of infanticidal attack from all-male bands was high, groups of *Semnopithecus* were larger and contained proportionately more adult females but not males. However, other hypotheses have been proposed and no consensus as to the functional significance of the dichotomous social organization of *Semnopithecus*—with some populations showing unimale and others multimale groups—has been reached (Koenig and Borries 2001). Whereas habitat does not appear to have power to explain social structure (Newton 1988), other potentially determining factors have been invoked, namely population density (Moore 1999; but see Newton 1988), the risk of predation (Treves and Chapman 1996; but see Newton 1988), and male monopolization potential of females (Newton 1988; Srivastava and Dunbar 1996), the latter being dependent on length of breeding season (Srivastava and Dunbar 1996; Moore 1999). It is also conceivable that these large multimale–multifemale groups are phylogenetically constrained in the *Semnopithecus* clade.

Resource distribution and availability do not appear to have a constraining effect on modularity, but several lines of evidence demonstrate that costs of assembling may be reduced in modular colobines relative to nonmodulars. First, modulars include a higher percentage of abundant staple foods of low quality, such as lichens and mature leaves, into their diet than nonmodulars. Second, there was no significant difference in DTD between modular and nonmodular colobines, despite big differences in mean group size, which is compatible with lower RRCs for species that became modular. Third, intraspecific regressions of DTD on group size for the only 2 species with the relevant information showed that modulars faced much lower scramble competition costs than nonmodulars (Figure 5). This does not mean that modular colobines do not face scramble competition because the correlation between group size and DTD in *R. bieti* was still positive, but rather that the scramble is so weak that even the largest groups of *R. bieti* have only marginally higher DTD than the largest *P. thomasi* groups, despite being nearly 40 times larger. This finding is especially compelling because the ratio of females to males in *P. thomasi* is at the upper range of nonmodulars, that is, *P. thomasi* would benefit from band formation due to high bachelor pressure, but ecological costs seem to prevent modularity. However, it has to be kept in mind that these conclusions are founded on an analysis of 2 species only and thus have to be considered provisional. Resource competition in modular colobines is probably more pronounced on ephemeral foods than staple foods but does not seem to be strong enough to limit group size (Grueter et al. 2009). The predominance of modular societies in other grazers such as plains zebras and gelada baboons may also be permitted by low levels of feeding competition.

In sum, modular societies in Asian colobines originate from autonomous OMUs that sought aggregation. At least one ecological benefit, namely thermal benefit, did not determine the formation of bands in Asian colobines. Although this study did not discount the other ecological theories such as predation avoidance and harvest efficiency on empirical grounds, there is no compelling evidence in favor of them. Nevertheless, more rigorous testing is needed once comparative data become available. We considered the threat of bachelor males as a plausible alternative scenario, which was found to be consistent with all known facts but needs to be strengthened by further in situ observations. This finding adds to a growing body of evidence showing the importance of conspecific threat as a constraint in driving the evolution of mammalian societal patterns and social strategies (Nunn and van Schaik 2000; Arnqvist and Rowe 2005; Pradhan and van Schaik 2008; Muller and Wrangham 2009). Furthermore, the modular colobines were better able to respond to bachelor threat than nonmodulars because the abundant and nonlocalized resource base of the former keeps foraging costs low and permitted the formation of bands in the first place.

SUPPLEMENTARY MATERIAL

Supplementary material can be found at http://www.beheco.oxfordjournals.org/

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