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Habitat Use and Trophic Niche Overlap of Two Sympatric Colobines, *Presbytis potenziani* and *Simias concolor*, on Siberut Island, Indonesia

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Abstract According to ecological theory, the concept of niche differentiation is essential to our understanding of how sympatric species can limit competition over resources. We here examine ecological niche differentiation in 2 sympatric Asian langurs, *Presbytis potenziani* and *Simias concolor*, both endemic to the Mentawai Islands off the west coast of Sumatra. We collected data (home range size, canopy use, activity budgets, diet, and niche breadth and overlap) using GPS and scan/focal animal sampling methods on 2 groups of *Presbytis potenziani* and 3 groups of *Simias concolor* living in a mixed primary rain forest in northern Siberut. Results show that home ranges of the 2 species overlapped completely and that the home range size of *Presbytis potenziani* was *ca.* 4 times larger than that of *Simias concolor*. Lower canopy levels (<20 m) were used more often by *Simias concolor*, whereas *Presbytis potenziani* preferred the canopy >20 m. Apart from foraging and other activities, there was little difference in overall activity budgets of the 2 species. Regarding diet, although 60% of all food species examined were used by both langur species, they shared only 3 of the 10 most commonly eaten species. *Presbytis potenziani* fed more selectively on fruits, whereas *Simias concolor* fed predominantly on leaves. Levin's

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niche breadth indices revealed that the diet of *Simias concolor* is more general (0.34) than that of *Presbytis potenziani* (0.22). Based on a Pianka index of 0.32, we conclude that there is a relatively small food niche overlap between the 2 colobine species and that diet represents an important mechanism enabling their coexistence.

Keywords Activity budget · Diet · Habitat use · Mentawai islands · Niche separation · *Presbytis potenziani* · *Simias concolor*

Introduction

A niche is a region in the multidimensional hypervolume representing a combination of environmental factors necessary for growth, survival, and reproduction of a species (Hutchinson 1957; Tokeshi 1999). According to ecological theory, the niche concept and the concept of resource competition are central to our understanding of how sympatric species coexist. While the niche concept refers to all resources relevant for the existence of a species, competition theory posits that ≥2 species cannot coexist if they rely on the same resources, given that these are limited in supply (Gause 1934; Hutchinson 1957; Tokeshi 1999). Thus, in sympatric species, niche differentiation appears to have evolved as a mechanism to reduce resource competition to enable coexistence. In this context, 3 major niche dimensions — habitat type, temporal differentiation and food type— have been identified as being the principal determining factors (Schoener 1974).

Among sympatric primates, the importance of these 3 factors in defining ecological niches has been well demonstrated. For example, a study of 7 lemur species from the eastern of Madagascar demonstrated niche separation with respect to microhabitat characteristics and food chemistry; species occupying the same habitat chose foods with different chemical properties and those eating the same food showed differences in habitat use (Ganzhorn 1989). Data exist for a wide variety of other taxa —Agostini *et al.* (2010) on *Alouatta guariba clamitans* and *A. caraya*; Eckardt and Zuberbühler (2004) on *Cercopithecus nictitans* and *C. diana*; Heymann and Buchanan-Smith (2000) on *Saguinus labiatus labiatus* and *Callimico goeldii*; Heymann *et al.* (2000) on *Saguinus mystax* and *S. fuscicollis*; Mitani (1991) on *Cercopithecus neglectus* and *Colobus badius*; Reed and Bidner (2004) on *Colobus polykomos* and *Piliocolobus badius*; Singh *et al.* (2000) on *Macaca silenus* and *Presbytis johnii*; Vasey (2000) on *Varecia variegata rubra* and *Eulemur fulvus albifrons*— but to date most of the studies have concerned species that 1) have a wide geographic distribution, 2) show a parapatric (partly overlapping) distribution, or 3) are more stereotypically frugivorous than most colobines, or all of these.

We here describe the mechanisms of coexistence in 2 sympatrically living colobines that are both specialized leaf eaters and that coexist across their entire distribution range. Among the 56 species of colobines in general and the Asian colobine taxa in particular, shared habitats over major portions of the geographic range are rare (Redmond 2008). For example, the distribution ranges of *Colobus guereza* and *Procolobus rufomitratus* overlap extensively in central Africa (Chapman *et al*. 2010) and for all other sympatrically living Asian colobines; i.e., *Semnopithecus entellus* and *Trachypithecus vetulus* on Sri Lanka (Napier 1985;

Oates and Davies 1994), *Presbytis rubicunda and Presbytis hosei* on the island of Borneo (Medway 1970), and *Trachypithecus obscurus* and *Presbytis (melalophos) femoralis* (Fleagle 1977) along the eastern Malaysian peninsula (Curtin 1980) distribution overlaps exist only partially (*ca.* 20–60%). In stark contrast, the Mentawaian colobines *Presbytis potenziani* and *Simias concolor* occur exclusively on a small archipelago (6000 km^2) off the west coast of Sumatra, where they coexist sympatrically across their entire distribution ranges.

Although several studies of the general ecology of the Mentawaian langurs exist (Tenaza 1987; Tilson 1977; Watanabe 1981), they are based on a very limited number of contact hours with individuals not habituated to human observers. Tilson and Tenaza (1982) described aspects of feeding and home range competition between *Presbytis potenziani* and *Hylobates klossii*, and more recent systematic studies of Mentawai langur socioecology are restricted to *P. potenziani* (Fuentes 1994; Sangchantr 2004).

Based on differences in morphology between the 2 langur species, certain predictions concerning niche differentiation can, however, be made. First, *Presbytis potenziani* has a slender body, with hind limbs that are much longer than the forelimbs (Oates and Davies 1994), whereas *Simias concolor* is of a stockier build, with hind and forelimbs of very similar length (Hadi *et al*. 2009a; Tenaza and Fuentes 1995). Consequently, we would predict that *Presbytis potenziani* has a greater ability to perform long-distance leaping, important in using higher forest canopy levels, and *Simias concolor* to be better suited to the use of lower canopy and ground levels. Second, important differences in the digestive systems between the 2 species exist. As do other members of the genus, *Presbytis potenziani* has a 3-chamber sacculated stomach (Bennett and Davies 1994), whereas the similarly locular stomach of *Simias concolor* possesses a presaccus as an additional compartment, thought to be a preliminary storage area that helps to ensure that there is always sufficient substrate available for fermentation (Caton 1998; Kuhn 1964). Thus, we expect a difference in diet composition to exist, whereby *Presbytis potenziani* feeds predominantly on low-fiber food, e.g., fruits, whereas high-fiber leaves form the major part of the diet of *Simias concolor.*

To test these predictions and investigate ecological niche differentiation between the 2 Mentawai langurs, we collected data on home range, canopy use, activity budgets, and diet from habituated individuals of both langur species living in a primary mixed rain forest in northern Siberut.

Methods

Study Site

We conducted the study in the Peleonan forest, located at 0°58′ and 1° 03′S (latitude) and 98°48' and 98° 51′E (longitude) in North Siberut, Mentawai, West Sumatra (Fig. 1). The forest represents the study area of the Siberut Conservation Programme (SCP: www.siberut-island.org) and encompasses *ca.* 5000 ha. The area is confined by coastal forest in the north and the Tateiku River in the south, while the western and eastern borders are formed by the Peleonan and the Sigep rivers, respectively.

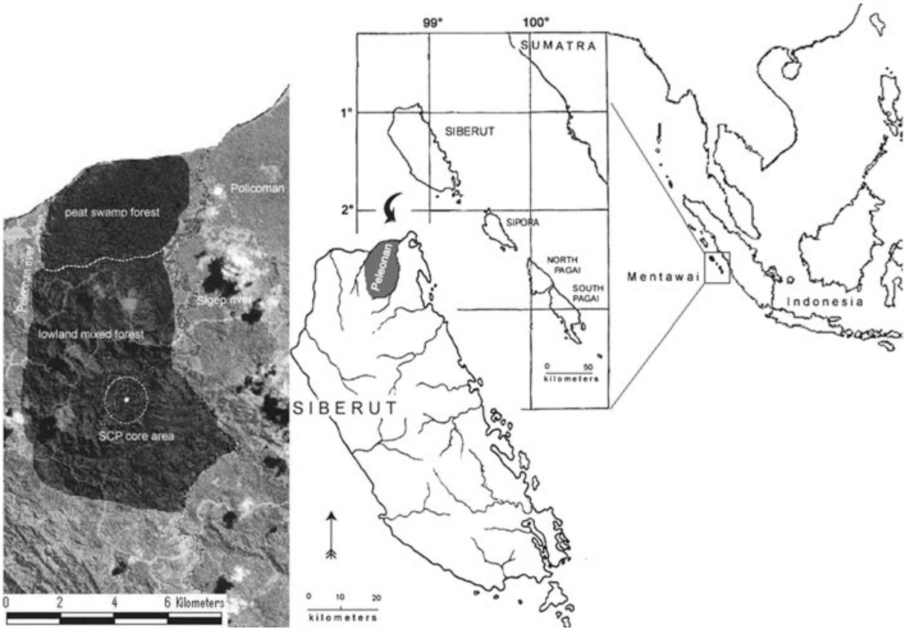

Fig. 1 Map of the study site, the Peleonan mixed rain forest in North Siberut.

The Peleonan forest consists partly of peat swamp forest, making up the northernmost part, as well as of mixed forest representing the much larger part toward the south. The study area, located in the center of this mixed forest, is composed of *ca.* 70 tree genera from 35 families, with Euphorbiaceae, Myrtaceae, Lauraceae, and Moraceae being the dominant taxa. The forest structure consists of >50% trees with diameter at breast height (DBH) between 21 and 40 cm, and 50% of trees 6–15 m high and 35% 16–30 m high (Hadi *et al.* 2009b).

The climate at the study site is typically equatorial, with high rates of precipitation throughout the year. The monthly rainfall from January through September 2008 varied from 120 to 568 mm, with fluctuation between months of low and high rates of precipitation being unpredictable. Temperatures recorded between March and December 2007 ranged between 20.6°C and 33.6°C (mean 25.6°C), with a mean relative humidity of 89.4%.

Focal Subjects

At the beginning of the observations, *Presbytis potenziani* group A consisted of 7 individuals, including 1 adult male and 3 adult females. The number of group members increased to 8 after a birth in 2008. Maximum group size from earlier studies in North Pagai (Fuentes 1996; Sangchantr 2004) was 6 individuals. We conducted focal animal sampling on 5 individuals of our study group (group A: 1 adult male, 2 adult females, 1 subadult male, and 1 subadult female).

For *Simias concolor* we collected data from individuals originally living in 2 groups, a 1 male–multifemale group (Aldran; here, we used 1 adult male and 1 adult female for focal animal sampling) and an all-male band (2 adult males used for focal animal sampling). In August 2008, 1 focal individual of the all-male band left to form a 1-male–multifemale group (Aldo group, 4 individuals in total). All individuals (of both species) were fully habituated to human observers.

We collected home range size data from *Presbytis potenziani* group A, and an adjacent group B, which was also habituated to human observers. For *Simias concolor*, we collected home range data from the 2 1 male–multifemale groups (Aldran and Aldo) and an adjacent *S. concolor* group B that was also habituated.

Data Collection and Analysis

We collected data daily between 06:00 h and 18:00 h from January 2008 to July 2009 during >4000 contact hours.

To determine home range sizes, we used a GPS to collect geographic positions of the groups. We collected GPS points at 30-min intervals, from a position at the spatial center of the group, i.e., at a position where the majority of group members gathered. Data collection in *Presbytis potenziani* group B and *Simias concolor* group B was sufficient to use the mimimum convex polygon (MCP) analysis, whereas in all other groups we collected additional data from March to July 2009 to use the fixed kernel contours (FKC) analysis also (Boyle *et al.* 2009; White *et al.* 2010), which provides additional information on the internal size structure of home ranges. This information allows identification of the most intensively used areas within a particular home range. We used GIS Quantum GIS 0.9.1 Ganymede and ESRI's ArcGIS, version 9.3 to convert GPS data points (fixes) into maps and the Hawth tool for ArcGIS to calculate the range size.

To assess the species-specific use of canopy, we collected height position data for individuals every 30 min using scan sampling. We measured absolute vertical heights using laser rangefinders and grouped them into 7 strata: 0–5 m, 6–10 m, 11–15 m, 16–20 m, 21–25 m, 26–30 m, and >30 m.

To compare canopy use between *Presbytis potenziani* (N=5 individuals; 5502 scan data points) and *Simias concolor* (N=4 individuals; 3040 scan data points), we allocated all individual scan sampling data to 1 of 7 horizontal strata categories and standardized data samples for a given individual by dividing the total number of observations (events) of this individual in a certain height category by its total number of scans.

To obtain comparable behavioral data for activity budgets and food compositions, in total, we compiled 722 focal animal sampling protocols for *Presbytis potenziani* (based on 5 individuals) and 639 protocols for *Simias concolor* (based on 4 individuals). Each focal animal sampling protocol was composed of instantaneous sampling at 20-s intervals, covering a total length of 30 min, resulting in 90 data points (or events) per protocol.

To gain representative behavioral data, we generated 12 focal animal sampling protocols per individual per month, each representing a different hour of the daylight period (06:00–18:00 h).

The behavioral data collected include 6 activity categories: resting, feeding, foraging, traveling, social behaviour, and other (such as solitary play, autogrooming, agonistic and sexual behavior). We also recorded the food species and the parts of these species consumed, distinguishing leaves, flowers, fruits, and others (bark, fungi, lichen, animal matter). For further identification of plants used by primates, we collected herbarium samples, which we sent to the Herbarium of Andalas University, Padang and to the Herbarium Bogoriense, LIPI Bogor, Indonesia.

To obtain comparable standardized values for activity budgets and diet, we divided the sums of focal animal samples (events) for each category by the number of focal animal sampling protocols made. First we did this separately for each individual and month. Second we calculated the overall individual means by dividing the sum of monthly means by the number of observation months. Finally we summarized all these individual mean values for each category and divided them by the number of individuals observed in this species to obtain mean values for each category representing the species. Because all calculations are based on observation events taken from focal animal sampling protocols, representing a certain daylight hour each, we present the species-specific mean values as event/h.

The assumptions for normality were not met in our data set; thus we used the 2 tailed Mann–Whitney *U*-test to compare the values for canopy use, activity budget, and diet between *Presbytis potenziani* and *Simias concolor*. We determined significance at a p-level of ≤ 0.05.

We used the standardized Levin's index to calculate the values for niche breadth, applied to the proportions of food items consumed:

$$B = \frac{1}{\sum p_i^2}$$

where B is Levin's niche breadth and p_i is the proportion of a single resource category (food item) in relation to the overall consumption. Subsequently we calculated the standardized Levin's niche breadth (B_{sta}) by computing:

$$B_{sta} = \frac{B - 1}{B_{\max} - 1}$$

where B is Levin's niche breadth and $B_{\max}$ is the total number of food items recognized. The standardized Levin's index varies between 0 (minimal niche breadth) and 1 (maximal niche breadth) (Colwell and Futuyma 1971; Levins 1968).

Finally, to calculate trophic niche overlap between *Presbytis potenziani* and *Simias concolor*, we used Pianka's index with the formula:

$$Ojk = \frac{\sum pij\,pik}{\sqrt{\sum pij^2 \sum pik^2}}$$

where Ojk is the overlapping index between species j and k, and pi is the proportion of a single food item i in the diet of species j and k. Pianka's index varies between 0 (total separation) and 1 (total overlap) (Pianka 1973).

Results

Home Ranges

Home range sizes of *Presbytis potenziani* based on MCP and FKC analysis were 20.2 and 30.3 ha (N=2 groups) and were on average *ca.* 4 times larger than those of

Simias concolor (4.1–10.0 ha; *N*=3 groups; Table I). The internal size structure calculated via the FKC method showed that both species used their home range unevenly. The area covered by the FKC 50% probability contour indicated that *Presbytis potenziani* spent half of its activity in an area covering only 18% (5.5 ha) of their total home range. Similarly, the area used intensively (FKC, 50% probability contour) by *Simias concolor* represented 12% (1.2 ha, group Aldran) and 18% (1.0 ha, group Aldo) of the total home range (Fig. 2, Table I).

Although there was no intraspecific overlap of home ranges in *Presbytis potenziani*, *Simias concolor* home ranges overlapped on average by 5%. In contrast, the interspecific overlap of home ranges between *Presbytis potenziani* and *Simias concolor* was up to 100%. Because we collected data only on focal groups, it is not known to what extent home range overlap occurred with other groups.

Canopy Use

We found both species most often (0.62–0.65 events per scan) in the 16–25 m canopy height range. We observed *Presbytis potenziani* more often at heights >20 m (21–25 m, 0.31 event/scan, MW U-test: $Z=-1.97$; $p=0.049$, $N=9$ and >30 m, 0.01 event/scan, MW U-test: $Z=-2.24$, $p=0.025$, $N=9$), whereas *Simias concolor* used the lower strata of the canopy including the ground level more frequently than *Presbytis potenziani* (16–20 m, 0.4 event/scan, MW U-test: $Z=-2.49$, $p=0.013$, $N=9$ and 0–5 m, 0.03 event/scan, MW U-test: $Z=-2.19$, $p=0.028$, $N=9$; Fig. 3).

Activity Budgets

Overall activity budgets for the 2 colobine species were similar. Both species devoted the majority of their average daily time budget to resting (45.7 and 49.8 events/h in *Presbytis potenzinai* and *Simias concolor*, respectively) and feeding (31.8 and 27.7 events/h in *P. potenzinai* and *S. concolor*, respectively). Traveling represented 6.2 and 5.6 events/h and social behavior 0.6 and 2.1 events/h in *Presbytis potenzinai* and *Simias concolor*, respectively. Although foraging (4.4 events in *Presbytis potenziani* and 2.2 events in *Simias concolor*, MW U-test: $Z=-2.2$, $p=0.03$, $N=9$) and other activities (1.3 events in *P. potenziani* and 2.5 events in *S. concolor*, MW U-test: $Z=-2.2$, $p=0.03$, $N=9$), differed between the species, we rarely observed these behaviors.

Table I Total number of fixes (GPS position records) per group studied and home range sizes based on MCP and FKC analyses

Group	Fixes	Home range area (ha)		
		MCP	FKC 95%	FKC 50%
Presbytis potenziani A	1411	30.53	30.31	5.47
P. potenziani B	403	20.24	–	–
Simias concolor B	432	4.1	–	–
S. concolor Aldran	553	8.4	9.96	1.2
S. concolor Aldo	370	4.9	5.59	1.01

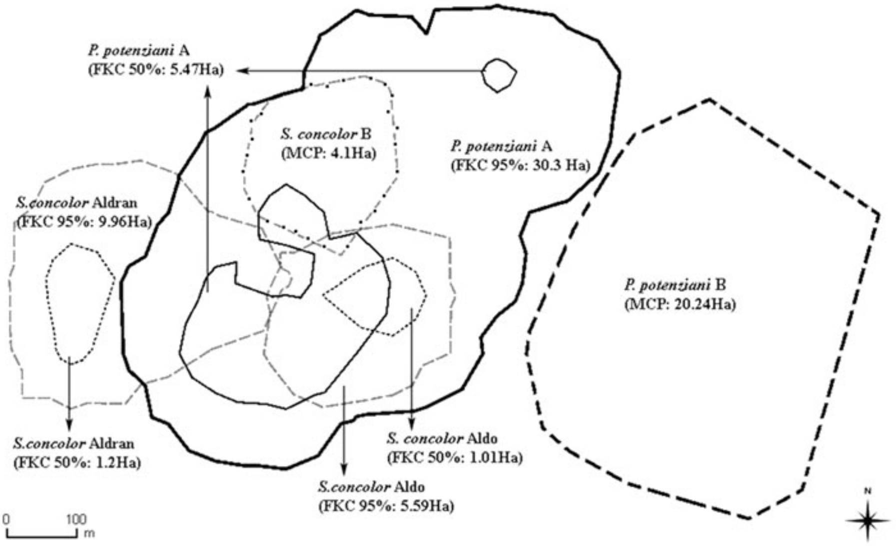

Fig. 2 GPS-mapped home ranges of *Presbytis potenziani* (N=2) and *Simias concolor* (N=3) based on minimum convex polygons (MCP) and fixed kernel contours (FKC) 95% and 50% analyses. Bold line=FKC 95% of *Presbytis potenziani*; thin line=FKC 50% of *P. potenziani*; bold dashed line=MCP of *P. potenziani*; thin dashed line=FKC 95% of *Simias concolor*; dotted line=FKC 50% of *S. concolor*; dashed-dotted line: MCP of *S. concolor.*

Diet

Based on both identified and unidentified taxa, *Presbytis potenziani* and *Simias concolor* ate 118 and 99 plant species respectively, with 62 species being used by both. While this overlap in food species composition represents >50% for both langurs, our analysis of 1) the top 10 food species used and 2) food preferences with

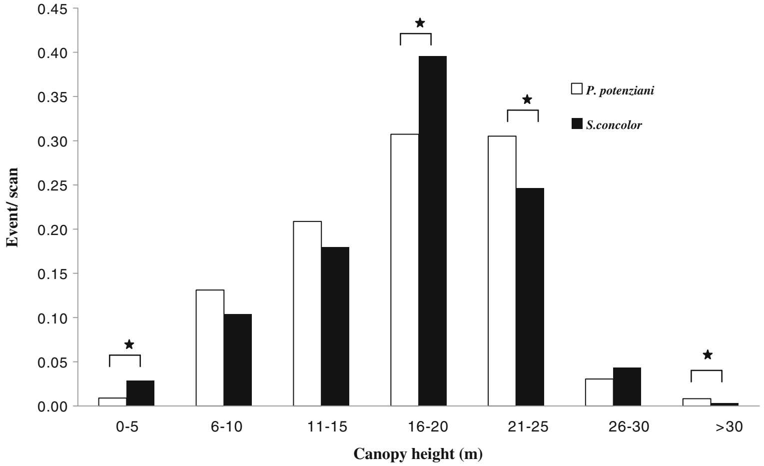

Fig. 3 Distribution of the use of canopy levels (event/scan) for *Presbytis potenziani* (N=5 individuals) and *Simias concolor* (N=4 individuals).

regard to leaves, flowers, fruits, etc. for each individual showed differences between the species.

The top 10 food species used by *Presbytis potenziani* and *Simias concolor* accounted for 41% and 48% of their overall diets. Of the top 10 food species, only 3 were used by both primate species (Table II).

Mean values for food preferences for certain parts of food species indicated that *Presbytis potenziani* fed predominantly on fruit (17.3 events/h), followed by leaves (10.8 events/h), flowers (1.6 events/h), and other items (1.5 events/h). In contrast, *Simias concolor* mainly fed on leaves (15.8 event/h, MW U-test: $Z=-2.2$, $p=0.027$, $N=9$), followed by fruits (6.3 events/h, MW U-test: $Z=-2.45$, $p=0.014$, $N=9$), flowers (4.9 events/h, MW U-test: $Z=-2.45$, $p=0.014$, $N=9$), and other items (0.6 events/h; MW U-test: $Z=-2.2$, $p=0.027$, $N=9$).

Detailed analysis of all food items (including all parts of different plant species eaten) revealed 256 food items in total, 176 and 143 of which were eaten by *Presbytis potenziani* and *Simias concolor*, respectively. Of these, 63 items (36% in *Presbytis potenzinai* and 44% in *Simias concolor*) were used by both species (see Table SI in electronic supplementary material [ESM]). Based on these different compositions in their overall diet, calculated niche breadths (Levin's index) were 0.22 for *Presbytis potenziani* and 0.34 for *Simias concolor*. Finally, the Pianka's index, describing the dietary overlap between the 2 langur species, was 0.32.

Table II Ranked proportions (event/h) of the top 10 food plant species used by *Presbytis potenziani* and *Simias concolor*

Food species	Life form	Event/h and rank for *Presbytis potenziani*	Event/h and rank for *Simias concolor*
Xanthophyllum vitellinum	Tree	2.23 (1)	–
***Argyreia* sp.**	**Liana**	**1.73 (2)**	**1.72 (5)**
Bhesa paniculata	**Tree**	**1.55 (3)**	**2.49 (1)**
Artocarpus integer	Tree	1.48 (4)	–
Antidesma velutinosum	Tree	1.26 (5)	–
Chisocheton divergens	Tree	1.13 (6)	–
Syzygium palembanicum	**Tree**	**1.11 (7)**	**1.95 (4)**
Gnetum latifolium	Tree	0.85 (8)	–
Palaquium gutta	Tree	0.71 (9)	–
Mangifera macrocarpa	Tree	0.68 (10)	–
Mallotus subpeltatus	Tree	–	2.43 (2)
Arenga obtusifolia	Palm	–	2.08 (3)
Endospermum malacense	Tree	–	1.67 (6)
Artocarpus dadah	Tree	–	1.28 (7)
Poikilospermum suaveolens	Tree	–	1.05 (8)
Carallia brachiata	Tree	–	0.93 (9)
Durio zibethinus	Tree	–	0.85 (10)
Total event/h (Proportion in overall diet)		12.82 (41.01%)	16.45 (47.96%)

Plant species used by both langurs are indicated in bold.

Discussion

Our data on ecological niche differentiation in the Mentawaian colobines show that within the relatively undisturbed habitat of our study area, home ranges of *Presbytis potenziani* are *ca.* 4 times larger than those of *Simias concolor*. This finding is similar to that reported earlier by Watanabe (1981) for nonhabituated individuals in a secondary forest in Eastern Siberut. Other data from the literature also suggest home ranges to be larger for *Presbytis potenziani* than *Simias concolor*, although actual size varies considerably according to habitat quality (Fuentes 1994; Sangchantr 2004; Tenaza and Fuentes 1995; Tilson 1977).

Our results indicate very little intraspecies overlap of home ranges for *Simias concolor* and none for *Presbytis potenziani*, a finding supported by our observations of a high degree of aggression and vocalization behaviors in intergroup encounters for *P. potenziani*, but a much lower level for *S. concolor* (*unpubl. data*). In contrast, the degree of overlap between the 2 species was almost complete. However, although living in close sympatry, the Mentawai langurs do not form stable polyspecific associations as observed, e.g., in *Cercopithecus nictitans* and *Cercopithecus diana* (Eckardt and Zuberbühler 2004), probably due to differences in home range size requirements and a much lower natural predation pressure on the Mentawai islands. However, the low levels of interspecific agonistic behavior, frequently observed during group encounters, are in line with results from a study of lion-tailed macaques (*Macaca silenus*), bonnet macaques (*M. radiata*), and Hanuman langurs (*Semnopithecus entellus*) living sympatrically in the Western Ghats of SW India (Singh *et al.* 2011), and in contrast to observations in sympatrically living frugivorous primates such as blue monkeys (*Cercopithecus mitis*) and red-tailed monkeys (*C. ascanius*) (Houle *et al.* 2006).

Our finding of low competition over resources among the Mentawai langurs is further supported by our results on species-specific habitat use. Although home ranges of *Presbytis potenziani* and *Simias concolor* overlap completely, their species-specific use of the forest canopy shows differences. Thus, in contrast to *Presbytis potenziani*, which showed preferences for elevated strata and avoided extremely low positions, *Simias concolor* was more often found in lower strata and at ground level (Fig. 3), where it foraged on mushrooms growing on decaying wood and in scrub vegetation. The canopy use of *Presbytis potenziani* corresponds well with data for this species collected previously by Fuentes (1996) and has also been described for other members of *Presbytis* and *Trachypithecus* (Bennett and Davies 1994; Curtin 1976; Davies 1984; Ruhiyat 1983).

The differences in canopy use and the accompanying locomotive behavior support our hypothesis relating these behaviors to the morphological differences between the species (Ankel-Simons 2000). Whereas the relatively slender body of *Presbytis potenziani* with longer hind limbs supports long-distance leaping and traveling in the upper canopy to explore widely scattered and patchy food resources, i.e., fruiting trees, the stockier (macaque-like) body of *Simias concolor*, in which hind and forelimbs are similar in length, is better suited to a more intensive use of the lower canopy, including the ground level. In this regard, it is of interest to note that *Simias concolor* was repeatedly observed by local inhabitants crossing creeks by wading and swimming (Hadi *pers. comm.*), a behavior somewhat unusual for langurs, but that has also been described for the closely related proboscis monkeys (*Nasalis larvatus*: Bennett and Davies 1994; Bennett and Sebastian 1988; Yeager 1993).

Activity budgets for both species follow patterns observed in other folivorous monkeys in Africa, e.g., *Colobus guereza*, *C. satanas*, and *Procolobus badius* (Rowe 1996; Struhsaker and Oates 1975) and in other Asian colobines such as *Presbytis comata* (Ruhiyat 1983), *P. thomasi* (Gurmaya 1994), *Trachypithecus cristatus* (Brotoisworo and Dirgayusa 1991), *T. leucocephalus* (Li and Rogers 2004), *T. pileatus* (Islam and Husain 1982), and *Nasalis larvatus* (Matsuda *et al.* 2009), in which only small proportions of time are spent on social behavior, but >80% of mean daily activity is devoted to resting and feeding. This activity pattern is typical for colobines that consume diets largely based on leaves, seeds, and unripe fruits, which require prolonged periods of resting to support digestion (fermentation) in their sacculated stomachs (Folk 2000; Kuhn 1964; Oates and Davies 1994). The interspecific differences in time spent foraging found here can be explained by the more efficient use of abundant food resources such as leaves and flowers by *Simias concolor*, compared to the extensive foraging on scattered fruit resources by *Presbytis potenziani*.

Our findings on dietary separation between the 2 Mentawai langurs agree well with those on other sympatric Asian colobines: Among the colobines of Malaysia, for example, *Trachypithecus obscurus* prefers to feed on leaves, whereas *Presbytis femoralis* feeds more on fruits (Curtin 1980; Davies *et al.* 1988) and in Kalimantan, *P. hosei* feeds predominantly on leaves (Mitchell 1994), while *P. rubicunda* prefers fruits (Davies 1991). Likewise, *Trachipithecus vetulus* feeds much more on leaves (60%; Hladik 1977) than *Semnopithecus entellus* (39%), both living sympatrically on Sri Lanka (Bennett and Davies 1994). Thus, collectively the data suggest that feeding on a leaf- or fruit-based diet represents an ecological tradeoff among sympatrically living colobines generally. The digestion of a predominantly leaf-based (high-fiber) diet may be supported by the presence of a presaccus, which is thought to function as a preliminary storage area, ensuring that there is plenty of substrate continuously available for fermentation (Caton 1998; Kuhn 1964). This specific anatomical characteristic can be found in *Simias concolor* but not in *Presbytis potenziani*, which accordingly prefers a fruit-dominated diet, as predicted by our hypothesis.

In total, we identified 118 and 99 food species as being eaten by *Presbytis potenziani* and *Simias concolor*, respectively, of which 62 species (>50% for each) were used by both langur species. This degree of dietary overlap is roughly similar to that of 43% reported for the African colobines *Procolobus badius* and *Colobus guereza* living sympatrically in the Kibale National Park (Chapman and Pavelka 2005). However, in the present study, when only the 10 most frequently consumed items are considered, the overlap is lower (30%). Further, when leaves, fruits, flowers, etc. of the same food plant species are considered as separate items (see ESM Table SI), a clear separation of food preferences becomes visible, with only *ca.* 25% of all food items recorded being used by both species. This small degree of overall dietary overlap is reflected by the relatively low values of Levin's (niche breadth) and Pianka's (niche overlap) indices for the Mentawai langurs. The slightly higher Levin's index in *Simias concolor* than in *Presbytis potenziani* reflects a more even use of food items compared to the latter. Hence, *Simias concolor* seems to be able to exploit a greater variety of food items within their smaller home ranges vs. *Presbytis potenziani*, which spend more time for traveling and foraging to assort their diet.

In a similar study on sympatric howler monkeys (*Alouatta guariba clamitans* and *A. caraya*) in the Atlantic forests of northeast Argentina, a trophic overlap index of 0.6 was obtained. This represents a much higher proportion of dietary overlap than that found in the present study and may play an important role in maintaining the essentially parapatric distribution of howler species throughout the Neotropics (Agostini *et al.* 2010). Similarly, Sushma and Singh (2006) found a dietary overlap value of 0.56 between *Macaca silenus* and *M. radiata* in the rain forests of the Central Western Ghats, South India, combined with behavioral intolerance between these species. In contrast, the relatively low trophic niche overlap index (0.32) calculated for the 2 colobines in this study confirms our initial assumption that the ecological niche separation, allowing a sympatric distribution of *Presbytis potenziani* and *Simias concolor* on the Mentawai islands, is determined predominantly by the species-specific diet.

In summary, the present study shows that home ranges of the sympatric langurs *Presbytis potenziani* and *Simias concolor* differ markedly in size and overlap completely. Although their overall daily activity budgets are quite similar, we identified the species-specific differences in diet (food species, food preferences, and food items), as reflected by a relatively low dietary overlap value, linked with a differential use of the canopy/home range, as the main mechanisms by which ecological niche separation of the 2 langur species is achieved.

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