ORIGINAL ARTICLE

Substrate use and postural behavior in free-ranging snub-nosed monkeys (*Rhinopithecus bieti*) in Yunnan

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Abstract

Extant colobines represent a predominantly arboreal primate radiation, but there are outliers such as some species of snub-nosed monkeys (*Rhinopithecus* spp.) that utilize both arboreal and terrestrial substrates. We quantified the degree of terrestriality and the distribution of individuals across canopy levels, the extrinsic and intrinsic determinants and constraints of strata association as well as use of postures in relation to behavior and food sources in a wild population of Yunnan snub-nosed monkeys (*Rhinopithecus bieti*) in the Samage Forest, China. The subjects spent 80.5% of the observation time in the trees and 19.5% on the ground. Ground use occurred most frequently in the context of travelling (61%) and less often in the context of feeding and resting (30% combined). Adult males frequented the ground significantly more often than other age–sex classes. Age–sex differences were also apparent in substrate preferences, which likely reflect body weight constraints. Adult males were significantly more associated with solid substrates and less with terminal branches than adult females and juveniles. Juveniles were seen more often on unstable ground (i.e. on thin and oblique branches) and in the upper canopy. Substrate use also varied with behavior: feeding was much more common in the upper stratum, outer canopy, on highly inclined and thin branches, as compared to resting. Severe weather also influenced canopy use in that tree crowns were used less often during periods of snowfall. The most frequently exhibited resting and feeding postures was sitting. Standing and suspensory postures were most often used in the context of feeding on lichens.

Key words: China, colobine, positional behavior, posture, terrestriality

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INTRODUCTION

Postural behavior and support use (ground use and use of various tree strata) in arboreal and semi-arboreal primates have been selected for optimal habitat exploitation and are the result of intrinsic (body size, morphology and dietary requirements) and extrinsic (resource

distribution, canopy features, phenology, temperature, predation pressure and conspecific threat) factors (Mendel 1976; Cant 1992; Bicca-Marques & Calegaro-Marques 1998; McGraw 1998a; McGrew & Bshary 2002; Youlatos 2002; Zhang *et al*. 2006; Kosheleff & Anderson 2009). Postural behavior is often considered to be the passive component of positional behavior, and locomotor behavior the active. Although most postural behavior demands lower levels of bone strain and muscle activity than locomotor behavior does, it is rarely ever a completely inactive state; passive activities such as resting and semi-passive activities such as feeding that involve posture occupy a substantial portion of an individual's activity budget (Prost 1965; McGraw 1998a; Fleagle 1999).

Descriptive accounts of primate postural repertoires have been obtained from field studies repeatedly (e.g. Ripley 1967; Mittermeier & Fleagle 1976; Schoen Ybarra 1984; Walker & Ayres 1996). Some studies also integrate ecological aspects, such as habitat structure, and support characteristics as well as dietary profiles (Morbeck 1977; McGraw 1998a). Among Old World monkeys, colobines usually sit while feeding, whereas more insectivorous/frugivorous cercopithecines tend to stand (McGraw 1998a). This is likely related to differences in the spatial distribution of preferred food items, with leaves being more universally distributed than fruits and insects in the canopy.

Yunnan or black-and-white snub-nosed monkeys [*Rhinopithecus bieti* (Milne-Edwards, 1897)] possess a variety of morphological and ecological peculiarities that make them interesting candidates for a study on positional behavior. They show pronounced sexual dimorphism in body mass (Jablonski & Pan 1995; Grueter & van Schaik 2009), they are among the heaviest of the non-ape primates (with *Rhinopithecus* males estimated to weigh up to 30 kg or more [Ren *et al*. 2004; Su & Jablonski 2009]), they make use of both arboreal and terrestrial supports (Kirkpatrick & Long 1994; Xiang *et al*. 2009) and they inhabit temperate mixed forests at relatively high altitudes and latitudes (Long *et al*. 1994; Li *et al*. 2008; Kirkpatrick & Grueter 2010). Their diet includes lichens as a staple and also young leaves and fruits as seasonal foods (Kirkpatrick 1996; Grueter *et al*. 2009b). Environmental constraints operating on their positional behavior are likely different from those in the tropics, because a large percentage of trees within the habitat are conifers, which differ in size and shape from

tropical broadleaf trees. The locomotor repertoire of *R. bieti* includes quadrupedal walking, vertical climbing, leaping and, on rare occasions, suspensory behaviors (Wu 1993; Isler & Grueter 2006; Grueter & Xiao 2011). Previous work on use of tree strata and terrestriality has revealed that *R. bieti* are partly terrestrial, spending approximately two-fifths of their time on the ground (Xiang *et al*. 2009; but see Wu 1993 for a much higher value). The relatively high degree of terrestriality in *Rhinopithecus* as compared to most other colobines has been attributed to efficient inter-patch travel in relatively open terrain, and exploitation of terrestrial resources such as water and bamboo shoots (Kirkpatrick & Long 1994; Xiang *et al*. 2009). Virtually no data has been accumulated for postural behavior in snub-nosed monkeys and its relationship with feeding behavior.

This paper examines aspects of postural behavior and substrate use including ground use in a population of *R. bieti*, using the following predictions:

1. There are correlations between climate and substrate use. During inclement weather (snowfall, snowstorm), the monkeys will retreat to the lower canopy to escape exposure to wind and snow.

2. Monkeys show differences in strata use when 'feeding' *vs* 'resting'. Feeding is expected to be more common in terminal tree parts, and resting more common in inner (more stable) parts (see Doran 1993; McGraw 1998a).

3. There are differences in strata use among age–sex classes. As a result of their large body mass, adult males are expected to rest on large stable supports close to the tree stem, whereas other age–sex classes should be less constrained in their use of support types (see Cant 1992; Doran 1993).

4. There are differences in terrestriality among age–sex classes. Adult males are expected to be more terrestrial than other age–sex classes due to their greater weight (see Doran 1993; Zhang *et al*. 2006).

5. There are differences in terrestriality with regard to behavior types. Moving is expected to be more common on the ground, while resting and feeding are expected to be more common in trees (see Li 2007).

6. Postural behavior will vary with different activity states (see Rose 1978; Gebo & Chapman 1995).

7. Postural behavior will vary with different types of food items (i.e. lichens, buds/leaves and fruits) (see Bicca-Marques & Calegaro-Marques 1993).

MATERIALS AND METHODS

Site

We conducted this study in the Samage Forest (part of the extended Baimaxueshan Nature Reserve) in northwest Yunnan (27°34′N, 99°17′E). The forest is classified as a high-altitude (2600–4000 m) temperate mixed deciduous broadleaf and conifer forest. Li *et al*. (2008) identify 5 major vegetation zones, among which mixed deciduous broadleaf and conifer forest represents the main habitat type for *R. bieti*. Canopy cover ranges from approximately 50%–70% outside meadows, and tree height ranges from 15–19 m (depending on habitat type) (for more details on structural characteristics of trees and forest types, see Li *et al*. 2008). The climate at the study site is seasonal, with warm humid monsoon summers, cold arid winters (particularly at night) and 2 transition phases of fall and spring with moderate temperature and precipitation. The mean annual temperature within the habitat of the monkeys is approximately 10 °C and annual rainfall is approximately 1000 mm. The study group was composed of approximately 410 individuals; this number was established when the entire group crossed an alpine meadow in Jun 2007 (Grueter 2009).

Data collection and analysis

The protocol for this study was entirely observational and non-invasive. Data on positional behavior were collected on 116 days from Sep 2005 to May 2006, Aug 2006 to Nov 2006, and Jan 2007 to Jul 2007. Due to the fact that the study group was not fully accustomed to the presence of observers, we usually conducted our observations with a spotting scope (20–60× zoom) from prominent viewpoints, such as rocky outcrops, ridges or hillsides at a median distance of 200 m from the group. These distance observations ensured that the animals were behaving naturally and allowed us to obtain a better overview of the spatial distribution of the group members in different forest levels. Occasionally, close observations at 10–30 m also proved feasible (with or without optical devices).

Scans of all visible animals were taken at 15 min (dataset DS-15) or 30 min (DS-30) intervals and dictated into a tape recorder. Group members were often spread out over large distances (median 90 m) in the forest and across forest strata, precluding data collection on all members of the group during a single scan. If a large number of monkeys (usually >20) was in view, we chose 30 min scans (*n* = 225); if only a relatively small number (usually <20) was visible, we conducted 15 min scans (*n* = 1372). For every scan, we noted the date, time and weather conditions, and whether the ground was poorly visible, moderately visible or highly visible. For every subject scanned, we recorded age (adult, subadult, juvenile or infant), sex (but not for juveniles and infants), activity (rest, groom, move, play, feed, vigilance, aggressive and miscellaneous). For every feeding and resting record, we attempted to record the posture, support type (size and inclination) and canopy level. However, it was often not possible to record all positional/postural variables in a scan (sample sizes are given in the Results section). We collected data on canopy use only when the whole canopy of a tree was visible.

The following postures were distinguished based on Dagosto and Yamashita (1998), Dasilva (1993), Fleagle (1978), Gebo and Chapman (1995) and Rose (1978), with some modifications. Sitting: animal rests on its haunches, with feet in toward the mid-line of the body or spread outward, or with feet above the head; feet may be grasping or hanging over the support or propping the body up with midfoot or heel touching the support. Vertical clinging: animal clings to a vertical or strongly oblique support without sitting on a branch. Suspensory: tripedally/quadrupedally (body of an animal is suspended underneath a support), bimanually (suspended by arms) or hindlimb (suspended by legs). Standing: animal stands quadrupedally. Reclining: animal lies down on its ventrum, side or back. Crouching (for resting only): ventral surface in contact with substrate, but weight resting on limbs. Hunching (for resting only): spine curved, chin dropped (head bowed), limbs close to body (huddling is always done in a hunching position). Other: for example, bipedal stand.

Location was divided into the following categories: ground, lower canopy (lower third of crown), mid-canopy and upper canopy (upper third of crown). The following support sizes were distinguished (see Gebo & Chapman 1995): very large (size 4), more than 40 cm in circumference; large (size 3), 25–40 cm in circumference (boughs); medium-sized (size 2), between 6 and 25 cm in circumference (branches); and small (size 1), less than 5 cm in circumference (twigs). Support inclination was defined as follows: horizontal, 0–15 degrees to the horizontal; oblique support, between 15–45 degrees to the horizontal; and steep, from 45–80 degrees to the horizontal. We differentiated among the following locations on branches: fork (within 1 m of the central tree trunk), mid-branch and terminal branch.

For the analysis of data on postural behavior and substrate use, we used a subset of the data including only

weaned individuals above the age of infants (>1 year). For the analysis of the proportion of terrestriality, we used only data collected when the ground was moderately or highly visible; otherwise data would have been severely biased against animals under the canopy. We first calculated frequencies of strata/support/ground use separately for DS-15 and DS-30, and then averaged values derived from the 2 datasets. For the comparisons between behavior/age–sex class and strata/support use, DS-15 and DS-30 were lumped together. Data were analyzed using χ^2 contingency analysis ($r \times c$ contingency tables) and χ^2 goodness of fit tests.

RESULTS

Postures

Sitting was the most common posture shown while resting (74%), followed by hunching (22%) (Fig. 1b). Sitting was also the most common feeding posture (84%), followed by standing (7%) and suspensory (6%) (Fig. 1a). Other postural behaviors, such as lying and vertical clinging, were seldom used while feeding.

Standing and suspensory postures were more often used in the context of feeding on lichens than in the context of feeding on buds/leaves and fruits. Sitting was more often used when feeding on buds/leaves and fruits than when feeding on lichens (Table 1). Contingency analysis revealed a significant association between postural categories and food items ($\chi^2 = 22.99$, $P < 0.001$).

Strata and support use

Of the scanned individuals in trees, 53% were found in the middle canopy, 32% in the lower canopy and 15% in the upper canopy ($n = 4378$). This allocation to strata was different from a homogenous distribution ($\chi^2 = 949.94$, $P < 0.001$). There was a significant difference in the frequency of use of branch positions ($\chi^2 = 546.13$, $P < 0.001$). Among locations on branches, the fork was the most frequently used location (44%), followed by mid-branches (42%) and terminal branches (14%) ($n = 3131$). There was a significant difference in the use of both substrate sizes ($\chi^2 = 680.49$, $P < 0.001$) and substrate inclinations ($\chi^2 = 176.32$, $P < 0.001$). The subjects were recorded mostly on size 2 branches (62%), followed by size 3 branches (23%). Very thin and very thick branches were used less often (size 1, 9%; size 4, 6%) ($n = 1144$). Horizontal branches made up 57% of all scanned records, followed by moderately inclined
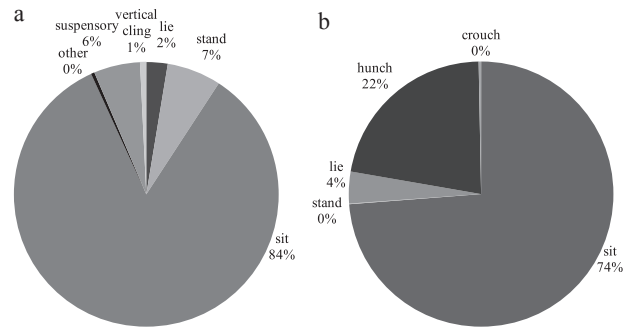

Figure 1 (a) Frequencies of feeding ($n = 1600$) postures by Yunnan snub-nosed monkeys; (b) frequencies of resting postures ($n = 1318$).

Table 1 Postures used in relation to foraging context

	Buds/leaves (%)	Fruits (%)	Lichens (%)
Stand	3.9	0.0	7.3
Sit	93.4	94.5	84.1
Lie	0.4	2.0	2.5
Suspensory	2.3	3.5	6.1

$N = 1101$ postural records for which both posture and food item were known (mean of 15 and 30 min scans).

branches (31%) and steep branches (12%) ($n = 576$).

There was a highly significant association between behavioral categories and canopy level ($\chi^2 = 205.02$, $P < 0.001$, $n = 3649$) and between behavioral categories and branch position ($\chi^2 = 449.50$, $P < 0.001$, $n = 2909$). Substrate size and behavior were significantly related ($\chi^2 = 90.76$, $P < 0.001$, $n = 380$), as was inclination and behavior ($\chi^2 = 70.57$, $P < 0.001$, $n = 530$) (Table 2).

Age–sex categories were significantly associated with canopy levels ($\chi^2 = 22.74$, $P < 0.001$, $n = 3135$) and branch positions ($\chi^2 = 242.84$, $P < 0.001$, $n = 2561$). There was also a significant association between substrate size and age–sex class ($\chi^2 = 22.88$, $P < 0.001$, $n = 1040$), but not between inclination and age–sex class ($\chi^2 = 3.60$, $P = 0.462$, $n = 483$) (Table 3).

Snowfall influenced the use of canopy levels ($\chi^2 = 7.56$, $P < 0.05$, $n = 208$ strata records on snowy days). The upper canopy was used less (7% *vs* 15%), while the lower canopy was used more often during snowfall (42% *vs* 32%). The proportional use of the middle canopy remained the same (50% *vs* 53%).

Table 2 Use of positions within canopy and substrate types, stratified by activities

Activity	Branch position (%)			Canopy (%)			Inclination (%)			Substrate size (%)			
	Fork	Mid-branch	Terminal branch	Mid-canopy	Lower canopy	Upper canopy	Horizontal	Oblique	Steep	1	2	3	4
Rest and groom	55.0	41.0	4.0	52.1	39.1	8.8	68.6	27.8	3.6	5.3	55.8	30.3	8.6
Feed	27.1	44.6	28.3	57.7	20.1	22.2	45.2	33.6	21.2	16.3	66.2	16.8	0.7

Table 3 Use of positions within canopy and substrate types, stratified by age–sex class

Age–sex class	Branch position (%)			Canopy (%)			Inclination (%)			Size (%)			
	Fork	Mid-branch	Terminal branch	Mid-canopy	Lower canopy	Upper canopy	Horizontal	Oblique	Steep	1	2	3	4
Male (adult, subadult)	61.4	31.8	6.8	57.9	28.1	14.0	55.5	32.9	11.6	3.4	61.5	29.9	5.2
Female	37.0	47.5	15.5	52.2	33.6	14.2	49.3	37.2	13.5	9.5	62.4	22.2	5.9
Juvenile	29.5	47.1	23.4	49.5	29.1	21.4	54.7	28.3	17.0	15.8	65.2	14.0	5.0

Ground use

The subjects spent 80.5% of the observation time in the trees and 19.5% on the ground (mean of combined datasets, $n = 2717$) (Fig. 2). Moving accounted for 61% of terrestrial activities, resting 15%, feeding 15%, grooming 7% and playing 2% ($n = 900$). Of all ground use records with identified age–sex class, 37% were of males, 34% were females, 25% were juveniles and 4% were non-dependent infants ($n = 568$). The frequencies of ground use records differed significantly among the age–sex classes (χ^2 goodness of fit test, $\chi^2 = 233.1$, df = 3, $P < 0.001$; expected frequencies were calculated based on the proportional representation of a particular age–sex class in the group).

DISCUSSION

Yunnan snub-nosed monkeys demonstrate some unusual ecological and morphological features that deviate from 'typical' colobines. They have extreme sexual dimorphism in body mass, and most populations live in mixed temperate forests at high altitudes with a large percentage of coniferous trees where they feed extensively on lichens. We discuss the adaptive significance of their postural behavior and substrate use in light of these environmental and anatomical constraints.

Postures

Sitting was by far the most frequent postural state while feeding, as has been demonstrated for other colobines (Rose 1978; Gebo & Chapman 1995; McGraw 1998a). Suspensory behavior was shown as a means of

Figure 2 Yunnan snub-nosed monkeys travelling terrestrially in the Samage Forest, Yunnan.

acquiring food, and permitted exploitation of food from terminal branches (see Grand 1972; Wright *et al.* 2008). Forelimb suspension is also commonly used in both locomotion and postures in the congeneric Tonkin snubnosed monkey (*Rhinopithecus avunculus* Dollman, 1912) from subtropical karst forests in northern Vietnam (Covert *et al.* 2008).

Little is known about how food types influence postures in wild primates. A study on black spider monkeys [*Ateles paniscus* (Linnaeus, 1758)] found no support for the prediction that body postures would differ in connection with the consumption of fruit and leaves (Youlatos 2002), whereas a study on black howler monkeys [*Alouatta caraya* (Humboldt, 1812)] found sitting to be more common during feeding bouts on leaves than when feeding on fruits/seeds (Bicca-Marques & Calegaro-Marques 1993). We documented a significant association between postural behavior and food items. This significant effect is likely because of the unusual staple food of lichens for *R. bieti*, which requires standing and suspension for efficient acquisition.

McGraw (1998a) studied postural aspects in several sympatric species of African cercopithecines and colobines and notes that colobines engaged most often in reclining behavior, both during feeding and resting, and that this was almost certainly related to their high fiber, low energy diet. McGraw also suggests that lying supine is a strategy by which heat can be dissipated from the body during periods of high temperature. We found that lying was not a very common posture in *R. bieti*. Infrequent lying behavior might be related to either a different resource base or, more likely, to thermoregulatory constraints; that is, the higher energy diet of *R. bieti* (lichens and fruits) means that it is not necessary for them to recline or the often prevailing cold requires a more energy-conserving posture, such as hunching. Dasilva (1993) demonstrate that sitting 'hunched' occurs more often during phases of cool, wet weather and low energy intake, and concludes that this posture is designed to reduce heat loss. Grey-shanked douc langurs [*Pygathrix cinerea* (Nadler, 1997)] were also found to engage significantly more often in a hunched resting position in the wet season (Ha *et al.* 2010). This assertion remains untested for *Rhinopithecus*.

Use of forest strata and support types

In golden snub-nosed monkeys (*Rhinopithecus roxellana* Milne-Edwards, 1870) at Shennongjia, the middle stratum made up three-quarters of all positional records, followed by the upper stratum (Li 2007). The high per-centage staying in the mid-stratum found in our study is consistent with the findings of Li (2007), but two-thirds of our records fell into the lower stratum. In line with our results, Zhang *et al.* (2006) found that golden snubnosed monkeys at Zhouzhi spent more than 50% of their time in the low stratum. Tonkin snub-nosed monkeys also frequently rest on lower branches (Dong & Boonratana 2006). In the study of Ren *et al.* (2001), golden snub-nosed monkeys were more or less equally distributed across the low stratum, the middle stratum and 'canopy'. The variation observed is probably linked to the availability and abundance of tree species (pyramidal conifers *vs* more rounded broad-leaved trees) and local weather conditions. We found weather to have an effect on use of tree levels: during periods of snowfall, the monkeys avoided tree crowns and tended to rest closer to the ground where they were likely better protected.

The apparent preference for tree forks as resting places is likely attributable to greater stability near the tree stem. We found that the monkeys made use of solid medium-sized to (very) large supports for recreational activities such as grooming and resting (see Doran 1993; McGraw 1998a). Small branches and terminal branches were used considerably more often during feeding as opposed to resting. Stability seems to be the main determinant of support utilization patterns during resting, whereas food distribution determines support use patterns while feeding (Doran 1993).

Resting was uncommon in the upper stratum, possibly because of greater exposure to raptors (see Li 2007). In line with Li (2007), feeding was much more common than resting in the upper stratum. The core sections of trees are often considered to contain less or lower quality food than more peripheral sections (Hunt 1992; Houle *et al.* 2007), but this remains unsubstantiated for the temperate mixed forest at our study site. Males and females showed differences in strata use, but their diet does not consistently diverge (Grueter *et al.* 2009b). Hence, the difference between males and females is most parsimoniously explained with differences in body weight constraining strata use. Due to their larger body mass, males were also constrained from using very small support sizes as compared to females and especially juveniles (see Cant 1992; Doran 1993; Remis 1995; Myatt & Thorpe 2011; but see Gebo & Chapman 1995).

Terrestriality

Through this and previous studies it has become firmly established that Yunnan snub-nosed monkeys

are more terrestrial than most other modern Asian colobines. The only other extant Asian colobines that do not spend a substantial amount of time in trees are Hanuman langurs (*Semnopithecus* spp.) (Sugiyama 1976; see also Kirkpatrick & Long 1994), golden snub-nosed monkeys, and also limestone langurs on rocky surfaces [*Trachypithecus leucocephalus* (Tan, 1955) and *Trachypithecus delacouri* (Osgood, 1932)] (Huang & Li 2005; Workman & Schmitt 2012). A majority of ancient colobines from the Miocene, Pliocene and Pleistocene (including European taxa like *Mesopithecus* and *Dolichopithecus*, and African taxa like *Cercopithecoides* and *Rhinocolobus* were likely either semiterrestrial or exclusively terrestrial (Leakey 1982; Delson 1994; Youlatos & Koufos 2010). Locomotor flexibility allowed them to occupy mixed habitats and to exploit a range of food resources within those habitats.

Body size differences across species can lead to differences in positional behavior (Fleagle & Mittermeier 1980; Remis 1998). Hanuman langurs and snub-nosed monkeys are among the heaviest langurs, and their higher levels of terrestriality may be explained by the limited capacity of arboreal supports to sustain large animals (see Fleagle 1999). The high proportion of terrestrial behavior of *R. bieti* may also be related to their manual and pedal morphology. The short fingers and toes of the species are probably related to the seasonally cold conditions under which they live; in this way, they appear to follow Allen's rule. Thus, the inability of the animals to navigate narrow arboreal substrates, especially as large-bodied adults, may be at least partly due to the shortness of their fingers and toes, and their inability to gain secure purchase on branches while climbing.

Our research has shown that all age–sex classes can dwell in trees, but that adult males are constrained from utilizing fragile supports. Ground use was especially frequent in males, as has been found in other studies on *Rhinopithecus* (Kirkpatrick *et al*. 1998; Ren *et al*. 2001; Zhang *et al*. 2006; Li 2007; Xiang *et al*. 2009). The males' higher propensity to stay on the ground seems to be associated with their larger body size, which is in line with studies showing that body size differences can produce variation in positional behavior (Sugardjito & van Hooff 1986; Doran 1993).

When structurally different habitats do not result in substantial variation in positional profiles, phylogenetic conservatism can be inferred (e.g. Doran & Hunt 1994; McGraw 1998b). In contrast, site-specific variability in positional behavior indicates a proximate response to heterogeneity in habitat structure and availability of supports (Gebo & Chapman 1995; Dagosto & Yamashita 1998). The terrestriality value reported here (approximately 20%) compares well with Xiang *et al*. (2009) (18%) and Kirkpatrick and Long (1994) (19%), indicating that *R. bieti* can be considered a partly terrestrial species across populations, and that its terrestrial lifestyle is an evolved or morphologically driven propensity, and not a proximate response to the environment. (However, note that the estimates of terrestriality presented here should be viewed with some caution, as an unbiased and fully reliable estimate cannot be derived. Poor conditions for observing terrestrial behavior due to thick canopy cover in some areas may have yielded observational biases. However, because all studies on terrestriality in *Rhinopithecus* were more or less equally affected by low visibility due to similar methods of collecting data, data comparability is still valid.) Quantitative data on forest physiognomy across sites would allow the phylogentic inertia model to be tested.

The ecologically and phylogenetically closely related *R. roxellana* and *R. bieti* share a tendency for terrestriality, but actual frequencies differ across studies: Ren *et al*. (2001) and Zhang *et al*. (2006) report values of approximately 14%–15% for *R. roxellana* at Zhouzhi. Kirkpatrick and Gu (unpubl. report) state that their working estimate was that monkeys were terrestrial between 30% and 70% of the time. Li (2007), however, reports that *R. roxellana* at Shennongjia spent only approximately 3% of the time on the ground. This conspicuous intraspecific variability could be methodological, but is probably at least partly contingent on variation in the openness of the terrain. The relatively closed canopy at Shennongjia may be more conducive to arboreal travel (see Li 2007). No quantitative data on ground use are available for the other *Rhinopithecus* species, but it has been observed that Tonkin snub-nosed monkeys (*R. avunculus*) are occasionally also terrestrial (Dong & Boonratana 2006). Guizhou snub-nosed monkeys [*Rhinopithecus brelichi* Thomas, 1903)] have been described as mostly arboreal (Bleisch *et al*. 1993).

Yunnan snub-nosed monkeys seem to move efficiently on the ground as well as in the trees, as would be expected from a semi-arboreal primate. Ground use most often occurred in the context of travelling (see also Ren *et al*. 2000; Li 2007). All age–sex classes, including heavy full-grown males engage in long distance leaping often when moving from tree to tree. Nevertheless, long distance travel habitually takes place on the ground, even when the canopy is unbroken (C. C. Grueter, pers. observ.), indicating that ground travel is more energy-

conservative than tree-to-tree jumping (see Zhang *et al.* 2006). Terrestriality can be seen as an adaptation to efficient foraging between prolific patches of food in a mosaic habitat, such as that inhabited by *R. bieti* at Samage, where preferred mixed broadleaf and conifer forest is interspersed with meadows and pine forest (see Grueter *et al.* 2008; Li *et al.* 2008). Terrestrial travel is also related to a relatively open habitat where a discontinuity in the canopy has selected against arboreal travel (see Zhang *et al.* 2006). Those colobines that exhibit a substantial degree of terrestriality, namely *R. roxellana*, *R. bieti* and *Semnopithecus* spp., tend to inhabit relatively open areas.

Availability of food sources on the ground is probably higher in such open habitats as opposed to closed canopy forests with limited ground vegetation. While Yunann snub-nosed monkeys feed predominantly on arboreal foods at Samage, some items are harvested terrestrially: for example, terrestrial herbaceous vegetation, mushrooms, underground storage organs and bamboo shoots (Ren *et al.* 2008; Grueter *et al.* 2009a; see also Ding & Zhao 2004). Xiang *et al.* (2009) also note that terrestrial behavior often occurs in the context of foraging for grasses and invertebrates. Ren *et al.* (2001) also argue that ground use opens up new foraging possibilities, such as pine seeds. In addition, descents to the ground are sometimes intended for drinking at water pools (Liu *et al.* 2007; see also Mourthe *et al.* 2007 for a non-*Rhinopithecus* example).

The semi-terrestrial habitus of Yunnan and golden snub-nosed monkeys might indicate reduced ground predator pressure (Ren *et al.* 2001). One-quarter of the ground records involved 'non-essential' activities, such as resting, playing and grooming, which may be a sign of relaxed predation risk. Li (2007), however, found that social and inactive behavior in golden snub-nosed monkeys was confined to the canopy, with more than 99% of the ground records happening in the context of travelling and foraging. The higher degree of terrestriality in adult males may also reflect their lower suceptibility to predators (see Ren *et al.* 2001; Li 2007; Xiang *et al.* 2009). Predation has often been suggested to be a key determinant of strata use, but we lack information on predator densities and predation rates for this site, thus precluding a firm judgment on the explanatory value of this theory at this time. If predation was the main determinant of substrate use, we would expect juveniles to avoid upper tree crowns where they are exposed to aerial predators. However, juveniles were the age–sex class that spent the most time in the canopy.

Another reason why the snub-nosed monkeys descend to lower strata or the ground might be to escape heat and direct exposition to solar radiation, especially in the summer, but also in winter. Despite overall cold winter temperatures, the intense sun and cloudless sky might force the monkeys to move to lower tree strata (sun exposure is magnified due the partially leafless forest canopies in winter). In chimpanzees, terrestriality is positively correlated with temperature in the sun (Kosheleff & Anderson 2009). Detailed measurements of ambient temperature and solar radiation need to be taken to examine this hypothesis.

How snow coverage affects the snub-nosed monkeys' ability to progress on the ground has yet to be investigated. As evidenced from prints, they continue walking on the ground if there is medium snow cover (approximately 10–20 cm). However, during periods of intense snowfall, they are expected to progress more in the canopy instead of the ground because snowfall increases the transportation costs (Telfer & Kelsall 1984). In line with this prediction, Japanese macaques spend less time moving on the ground when snow depth increases (Watanuki & Nakayama 1993).

CONCLUSION

Yunnan snub-nosed monkeys exhibit some similarities to other colobines in terms of their postural behavior (e.g. sitting being the most frequent postural state while feeding). Thermoregulatory constraints in their temperate habitat may explain some of the observed differences (e.g. rare instances of reclining). In terms of canopy use, Yunnan snub-nosed monkeys differ from most other colobines by devoting a relatively large proportion of their time to terrestrial behavior, which appears to be an adaptive function for efficient travelling/foraging. However, additional data from different populations is necessary to validate this assertion. In line with a variety of primate taxa, their use of trees depends primarily on their body size and shows activity-related variation (such as a predominance of feeding in the upper canopy).

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