Research Article

Food Abundance Is the Main Determinant of High-Altitude Range Use in Snub-Nosed Monkeys

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High-altitude dwelling primates have to optimize navigating a space that contains both a vertical and horizontal component. Black-and-white or Yunnan snub-nosed monkeys (*Rhinopithecus bieti*) are extreme by primate standards in inhabiting relatively cold subalpine temperate forests at very high altitudes where large seasonal variation in climate and food availability is expected to profoundly modulate their ranging strategies so as to ensure a positive energy balance. A “semi-nomadic” group of *R. bieti* was followed for 20 months in the montane Samage Forest, Baimaxueshan Nature Reserve, Yunnan, PRC, which consisted of evergreen conifers, oaks, and deciduous broadleaf trees. The aim of this study was to disentangle the effects of climate and phenology on patterns of altitudinal range use. Altitude used by the group ranged from a maximum of 3550 m in July 2007 to a minimum of 3060 m in April 2006. The proportional use of lichen, the monkeys’ staple fallback food, in the diet explained more variation in monthly use of altitudes than climatic factors and availability of flush and fruit. The abundance of lichens at high altitudes, the lack of alternative foods in winter, and the need to satisfy the monkey’s basal energetic requirements explain the effect of lichenivory on use of altitudes.

1. Introduction

An adaptive way for endotherm animals in montane temperate areas to cope with pronounced seasonality in climate and resource availability is to change location along an altitudinal gradient, thereby following food or avoiding cold/snow and ultimately maintaining a positive energy balance. Terrestrial herbivores, especially cervids, have been known to migrate to lower altitudes in winter [1, 2]. Black-and-white snub-nosed monkeys (*Rhinopithecus bieti*) are semiarborescent colobine monkeys inhabiting subalpine temperate forests in Southwest China. Their association with such a highly seasonal, environmentally harsh, and primate-atypical environment has sparked investigations on how they utilize their three-dimensional habitat.

Contrary to the expectation, however, none of the systematic studies on altitudinal ranging patterns in this species has delivered evidence for use of lower altitudes in winter [3–6]; see also [7, 8] for the ecologically and phylogenetically close *Rhinopithecus brelichi* and *R. roxellana*, resp.). This peculiarity required explanation, and Quan et al. [6] have recently proposed a sunshine hypothesis which posits that solar radiation affects the altitudinal distribution (and microhabitat use) of this species, primarily because it reduces costs of thermoregulation. A test of this hypothesis in a population of *R. bieti* in Tibet has shown that solar radiation and sunshine hours increase with elevation in Tibet, and intensified solar exposure was seen as the main reason for the monkeys’ use of high altitudes in winter. However, Quan et al. [6] did not test a much more parsimonious

prediction, that is that the abundance of winter foods is the main determinant of use of altitudes. The authors argued that the “monkeys food resources decrease with increasing elevation and also decrease in winter compared to other seasons.” However, this statement is imprecise and misleading. It has been firmly established that at least for those populations of *R. bieti* that live at relatively high latitude, arboreal, and mainly fruticose lichens are a staple fallback food (*sensu* [9]), eaten throughout the year in large quantities and becoming an essential resource in winter when almost no fruit and no young foliage are available. At Xiaochangdu in Tibet, where the study of Quan et al. [6] was conducted, lichens make up 97% of the monkeys’ winter diet [10], while at the slightly more productive site at Samage ca 200 km to the south they are 82% [11].

At both sites, the monkeys exploit other seasonally available foods in addition to lichens: young leaves are preferentially consumed in spring and fruits in summer (although fruit availability is lower at the more marginal site Xiaochangdu). While it may be true that preferred food, such as, fruits become rarer at higher altitude (cf. [12]), this is demonstrably not the case for lichens. Grueter et al. [11] have previously shown that arboreal lichen load increases with altitude at Samage, and Li et al. [4] have argued that this may be the main reason why the animals stayed at moderately high altitudes in winter and did not descend to lower altitudes. This finding seems highly intuitive and seems to reflect an adaptive strategy, as gaining access to a sufficient amount of fallback foods strongly influences survival chances [13, 14]. Given their extreme reliance on one resource, it is therefore most prudent to assume that they use areas in winter where lichen density is highest.

In a previous paper, we compared use of altitude among seasons of one group of *R. bieti* over the course of one year [4]. Here we analyzed a larger data set (20 months) on range use, diet, phenology, and climate and tackle the question of determinants of altitude use in a multivariate way by simultaneously assessing the effects of several predictors (temperature, availability of seasonal foods, and dietary reliance lichens). Our results suggest that the relatively high abundance of lichens at high altitudes and the extreme dependence of the snub-nosed monkeys on these fallback foods determine their altitudinal patterns of winter ranging in a temperate habitat.

2. Methods

Field work was conducted on a large free-ranging group of snub-nosed monkeys ($n = 407$ members) in the Samage Forest (Baimaxueshan Nature Reserve) in Yunnan province, PRC (27°34'N, 99°17'E), between September 2005 and July 2007. The site consists of evergreen conifers, oaks, and deciduous broadleaf trees. The study group occupied a wide range of altitudes, from 2600 m in the valley bottom to 4000 m near the summits of the mountains (Figure 1). Total annual rainfall (average of 2005/06 and 2006/07) was 1004 mm, and mean annual temperature was 14.3°C at the research station at 2450 m (estimated to be around 10°C

FIGURE 1: Study site Samage near the village of Gehuaqing in the Baimaxueshan Nature Reserve, Yunnan, China. The highest peak is Mount Samage (4166 m).

within the core area of the range of the study group at 3200 m). Temperature and precipitation varied markedly with seasons (for details on climate, see [11]). Several habitat types have been identified at the study site, ranging from subtropical evergreen forest in valleys, pine forest on lower slopes, mixed deciduous, and evergreen conifer forest, with bamboo and rhododendron featuring in the shrub layer. Pure fir forest tends to take over from mixed forest (with spruce, hemlock, and firs as the dominant gymnosperms) above ca 3500 m [4]. Parts of the Samage Forest have been selectively logged, and various human activities, such as, grazing of cattle and goats and harvest of nontimber forest products were still taking place inside the reserve when this research was carried out.

Over the course of the study, we obtained a total of 1900 location records (altitude and geographical coordinates) of the group’s center every 30 min using a GPS receiver (Garmin eTrex Summit). The group’s center was determined by visually estimating the spread of the group and taking the midpoint. Climate data collection is described in Li et al. [4]. Phenology data were collected by inspecting 157 food trees for the presence or absence of fruits and young leaves on a monthly basis (for details see [4]). We visually assessed lichen biomass of trees in 67 400 m² plots, and each tree was assigned a lichen load factor ranging from 0 (none) to 4 (heavy) (see [4]). Data on monthly dietary composition was gathered via instantaneous group scans at 15 or 30 min intervals. For each scanned individual that was feeding, we recorded the food type, namely, lichens, young leaves, mature leaves, buds, flowers, fruits/seeds, and others (for details, see [11]).

We constructed a general linear model with mean monthly group altitude used as the response and dependence on lichens (as measured by the percentage of lichen in diet) as the main predictor and ambient temperature at research site, fruit, and young leaf availability as control predictors. Mean monthly temperature and total monthly rainfall were rather strongly correlated ($r_p = 0.72$), so we excluded rainfall from model. Linear models were run in JMP, and correlations were conducted using the function `cor.test` in R [15].

FIGURE 2: Lichen load per 400 m² plot correlated with altitude (in m above seal level).

TABLE 1: GLM with monthly use of altitude as the response and temperature, fruit availability, young leaf availability and the reliance on lichen as predictors (whole model test: $F = 3.5173$, $R^2 = 0.484$, $P = 0.0324$).

Predictors	Estimate	<i>t</i> ratio	<i>P</i>
Temperature (°C)	0.0010141	0.78	0.4490
Fruit availability	0.0003114	1.39	0.1845
Young leaf availability	0.0002704	1.46	0.1661
% lichen in diet	0.0004584	2.54	0.0229

3. Results

Lichen load of trees was significantly higher at higher altitudes (Kendall's τ , $\tau = 0.5348714$, $z = 6.3229$, P value = $2.567e-10$; Figure 2), where the proportion of conifer to broadleaf trees is more biased [4].

The mean monthly altitude used by the focal group was 3270 m (SD 129 m). The monthly minimum was 3060 m in April 06 and the monthly maximum was 3550 in July 07. Neither climatic factors nor the availability of flush and fruit had an effect on the monthly use of altitudes. The monkeys' degree of dependence on lichen was the only predictor that had a significant effect on the monthly use of altitudes (Table 1).

4. Discussion

There has been no compelling evidence for an effect of climate on the use of altitudes in snub-nosed monkeys inhabiting montane forests in the north-temperate zone [3–8]. Black-and-white snub-nosed monkeys are unusual among primates in their colonization of marginal habitats and unique in their dietary specialization [11, 12]. The ability to digest lichens and extract energy from them enables them endure winter when there is a severe shortage of plant foods

[11]. The present findings show that the degree of lichen use best explains the pattern of altitudinal ranging and resolves the paradox of lack of downward migration in winter, as lichen abundance linearly increases with altitude. The fact that lichens are rich in nonstructural carbohydrates [12] may counterbalance any thermoregulatory stress incurred from staying at high altitude. Fan and Jiang [16] found for another montane subtropical-temperate primate population that it was not temperature but food distribution that was the driving force behind the altitudinal ranging patterns of the group. While the sunshine hypothesis of Quan et al. [6] may explain microhabitat use within the winter range of snub-nosed monkeys (but see [17]), it does not determine use of high altitudes in the first place.

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