

Black-and-white snub-nosed monkey (*Rhinopithecus bieti*) feeding behavior in a degraded forest fragment: clues to a stressed population

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Abstract Rapid global deforestation has forced many of the world's primates to live in fragmented habitats, making the understanding of their behavioral responses to degraded and fragmented habitats a key challenge for their future protection and management. The black-and-white snub-nosed monkey (*Rhinopithecus bieti*) is an endangered species endemic to southwest China. The forest habitat ranges from near-continuous to fragmented. In this study, we investigated the activity budget and diet of a *R. bieti* population that live in an isolated and degraded habitat patch at Mt. Lasha in Yunnan Province, near the current southern limit of the species. We used our data along with data from six other sites in more-continuous habitats across its range to model factors that predict stress, including feeding effort and time feeding on lichens against potential predictive parameters. Models showed feeding effort across all sites increased with increasing altitude and latitude, and with decreasing food species diversity. There was also a strong positive relationship between feeding effort

and time feeding lichens. The Mt. Lasha *R. bieti* population exploited a total of 36 food species, spending 80.2% of feeding time feeding on lichens, *Bryoria* spp. and *Usnea longissima*. These figures are more comparable to those living in the north than those living in the mid- and southern part of the species' range. Given the models for feeding effort and time feeding on lichens, the unexpectedly high time spend feeding on lichens and feeding effort relative to latitude and elevation are suggestive of a stressed population at Mt. Lasha.

Keywords Black-and-white snub-nosed monkey · Feeding effort · Fallback food · Habitat fragment

Introduction

Habitat loss, degradation, and fragmentation represent a pervasive threat to primate conservation worldwide (Cowlshaw 1999; Cowlshaw and Dunbar 2000; Li et al. 2002; Xiao et al. 2003; Estrada et al. 2017). Primates are particularly vulnerable to habitat transformations with most species depending on forest habitats, and half of the world's primate species are currently threatened with extinction (Mittermeier and Cheney 1987; IUCN 2010; Estrada et al. 2017). As well as reduced habitat area and increased geographic isolation, primates in forest fragments face potentially life-threatening reductions in food resources and food quality (Pride 2005; Arroyo Rodríguez and Mandujano 2006; Dunn et al. 2013; Balestri et al. 2014). Consequently, understanding behavioral indicators of stress in response to reductions and changes in habitat has become one of the key challenges for the conservation and management of primates.

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An important underpinning to the optimal foraging theory (MacArthur and Pianka 1966) is that as foods become limited, more less-preferred foods will be included in the diet. As food resources continue to decline, nutritional needs may become increasingly difficult to meet, and individuals may compensate by modifying behavior (Agetsuma and Nakagawa 1998). Populations may adapt their daily activity pattern, move into a different habitat patch where food resource abundance is higher, or increase their intake of fallback foods (for definition see Marshall et al. (2009)). Some primates faced with degraded and fragmented habitats must increase feeding effort, defined as time spent on feeding and moving divided by time spent resting, in comparison to groups living in continuous or larger habitat patches (e.g., *Alouatta palliata mexicana*: Asensio et al. 2007; Dunn et al. 2010, 2013). More critically, these groups may also suffer higher levels of physiological stress from persisting in small or fragment habitat (*Papio anubis*: Sapolsky 1986; *Colobus angolensis palliatus*: Dunham 2011; *Alouatta palliata*: Dunn et al. 2013; *Eulemur collaris*: Balestri et al. 2014). These results support feeding effort as a good predictor of stress or risk for primates in fragmented or degraded habitat.

The black-and-white snub-nosed monkey (*Rhinopithecus bieti*) is a large-bodied colobine endemic to mixed broadleaved-conifer and conifer forests of the Hengduan mountains in southwestern China (Long et al. 1994; Xiao et al. 2003). A combination of historic and recent land transformations have significantly restricted the total population to a string of forest remnants in less-populated areas between 2600 and 4600 m a.s.l. (Li et al. 2002). Between 1958 and 1997, more than 30% “useable” forest habitat was lost in Yunnan province (Xiao et al. 2003). Numerous studies have detailed activity patterns and diet of *R. bieti* populations over the latitudinal range of the species (Kirkpatrick 1996; Ding and Zhao 2004; Liu et al. 2004; Huo 2005; Xiang et al. 2007; Grueter et al. 2009; Xiang et al. 2010; Grueter et al. 2013). These studies indicate feeding generally forms the greatest part of the daily routine, and that a fallback food lichens, mainly arboreal fruticose *Bryoria* and *Usnea* spp., form an important part of the species diet, particularly in winter when preferred foods are unavailable (Kirkpatrick 1996; Ding and Zhao 2004; Liu et al. 2004; Xiang et al. 2007; Grueter et al. 2009). Lichen consumption was influenced by latitude and altitude, and environmental factors (e.g., temperature and rainfall) could be an indicator of forestry productivity as well as feeding strategies for Asian colobine including *R. bieti* (Tsuji et al. 2013). For the present study, we recorded the activity budget and diet of a *R. bieti* population (ca. 100 individuals) at Mt Lasha. The Mt Lasha population is distinctive from previously studied populations in that it exists in a small (ca 10 km²), and ecologically isolated

forest fragment. Its home range includes the entire forest fragment, which is also an important forest for local people that collect food, medicine, timber and fuel wood from the forest fragment. In this study, we aimed to (1) quantify the feeding behavior of the Mt Lasha population in a degraded forest fragment habitat, and (2) evaluate predictors of stress (feeding effort and percentage of time eating fallback food) for primates in all habitats, and discuss its implication for primate conservation.

Methods

Study site

We studied a single group of black-and-white snub-nosed monkeys from Jan. 2008 to Sept. 2010 at Mt. Lasha (26°20'N, 99°15'E) in Yunling Nature Reserve, Yunnan, China. The study site is a forest patch ranging from 2900–3600 m a.s.l. and situated in a 1400 ha catchment. Forest vegetation transitions from deciduous broad-leaved forest at lower elevations, through a belt of mixed deciduous-conifer forest to dark conifer forest (*Abies georgei*, *A. fabri*, *Tsuga dumosa*) at the highest elevations. Two patches (<25 ha) of evergreen oak (*Quercus semecarpifolia*) occur at an elevation of approximately 3100 m a.s.l. The forest undergrowth primarily comprises *Rhododendron* spp. and bamboo (*Fargesia strigosa*, *F. edulis*, *F. solida*) (Huang et al. 2012). The upper ridgeline of the catchment has been cleared to be used as summer pastures by local pastoralists. Grazing land, human settlements, farm land, and secondary scrub/forest dominated by Yunnan pine (*Pinus yunnanensis*) occupy all the regions outside and below the primary forest patch (Fig. 1).

Annual precipitation as recorded near the lower forest boundary averaged 910 mm, with 85% of rainfall occurring from May to October (Huang et al. 2012). During the study period, mean monthly temperatures ranged from 4.4 °C in February to 17.4 °C in July. The mean annual temperature was 11.7 °C. The lowest temperature recorded was –5.6 °C in February 2008, though temperatures <0 °C were regularly recorded between December and March (Huang et al. 2012).

The study group at Mt. Lasha represents one of three *R. bieti* groups located at the southern extent of the species range. Of these groups, the southernmost group occurs at Mt. Longma (26°14'N, 99°15'E) and contains less than 50 individuals. The northern group occurs at Mt. Fuhe (26°20'N, 99°25'E) contains less than 100 individuals, and our study group was located between these two groups (Fig. 1; also see Long et al 1994). The study group consisted of approximately 100 individuals in 11 one-male multi-female units (OMU) and two all-male units (AMU);

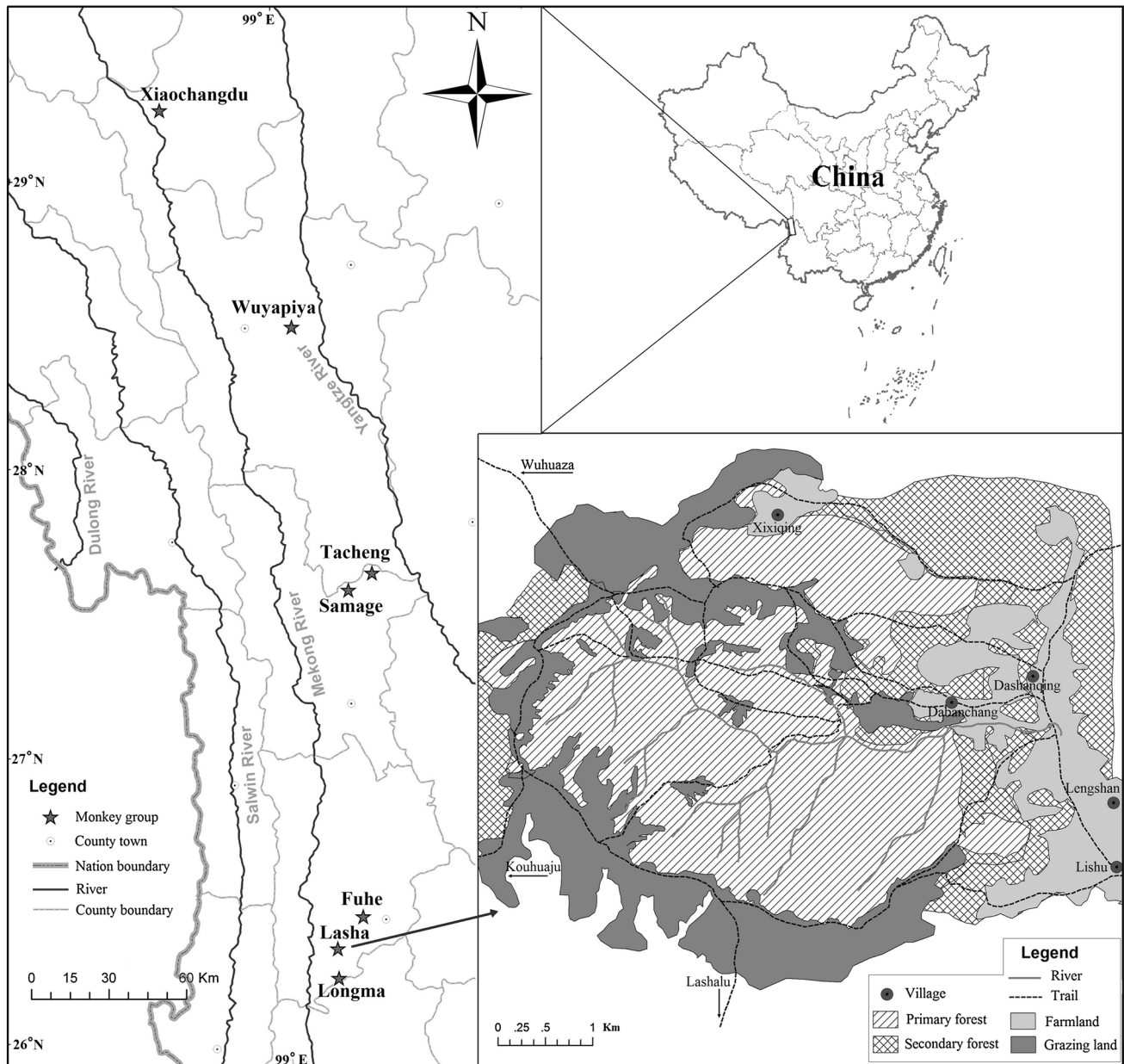


Fig. 1 Locations of previous studies and isolated forest fragment habitat of *Rhinopithecus bieti* in Mt. Lasha, Yunnan, China

for full description of *R. bieti* social units, see Kirkpatrick and Grueter (2010)). The Mt. Lasha study group was ecologically isolated from other groups by extensive areas of cattle grazing, villages, farmland, roads, and secondary scrub/forest (Fig. 1).

Data collection

We recorded behavior data using instantaneous and scan sampling at 10-min intervals (Altmann 1974) using a Leica 77 (Solms, Germany) field scope. We observed each individual for at least 5 s to determine its behavior, and

recorded that individual's behavior once for each scan. We defined four categories of activities: (1) feeding, including ingestion, manipulation, inspection or chewing of a food item; (2) moving, including walking, running, or climbing; (3) resting, including periods of inactivity and self-grooming; and (4) social (grooming and playing). When an animal was feeding, the species and plant parts consumed were noted. We categorized food items as follows: (1) lichens (primarily *Bryoria* spp. and *Usnea longissima*), (2) dicot bud and young leaves, (3) mature leaves including deciduous leaves and bamboo leaves, (4) flower, (5) fruits and seeds, (6) insect, and (7) unidentified/other, when an

animal was feeding but the plant item could not be identified, or the food item was different from those defined above.

We followed the study group from sleeping site to sleeping site whenever possible, and attempted to collect 5 full days or 50 h of behavioral data each month. In total, we followed the group for 15 months compiling 839 h of quantitative data. Severe weather in July 2008, June 2009 and August 2009 meant that observations in those months were less than 30 h per month, thus we excluded those data from our analysis (Table 1). We observed the monkeys on average for 11 days (range 6–18 days) and 66 h (39–121) per month for a total of 4552 scans of an average of 9 individuals resulting in 42,132 records.

Sampling data were nearly evenly distributed over hours of the day except for the first 2 h in the early morning and the last 2 h in the late afternoon. We combined those of the two earlier and two later hours when it was unevenly distributed. We calculated percent of each activity every hour and then calculated activity budget by month, by season, and by year. We also calculated feeding time devoted to different food types on these same time scales. Because the infants were not independent of their mothers, we did not include data of infants in our analysis.

For comparison, we obtained behavior activity (i.e., time spent feeding, moving, and resting), time feeding on lichens, as well as number of food species, home range, group size, forest fragment area, group density, mean altitude range of the group, annual rainfall, mean annual temperature, mean monthly minimum temperature, and

mean monthly maximum temperature for six other sites from previous publications (Table 2). We calculated group density and mean altitude based on the area of home range. We calculated mean altitude using a 250 m × 250 m grid over the home range of Mt. Lasha, and grid size basing on previous studies of each population (Kirkpatrick et al. 1998; Liu et al. 2004; Huo 2005; Grueter et al. 2008; Xiang et al. 2013), from which to produce a series of spot heights at each intersection using measuring tools in the GIS software ArcGIS version 10.2.2 (ESRI, Redlands, CA). We calculated feeding effort for each study group as the sum of time spent feeding and moving divided by the time spent resting (Cavigelli 1999; Dunn et al. 2010; Dunham 2011; Dunn et al. 2013).

Statistical analysis

Statistical analyses were performed with the software R, version 3.2.5 (R Core Team 2016). To model the relationship between feeding effort and each of the variables, we tested both linear and non-linear regressions. We also made comparisons with time feeding on lichens and each of the variables. We selected best-fit models using Akaike Information Criterion (AIC), where the highest-ranked (lowest AIC) model was considered to have the majority of support, given the data, if it was >2 AIC values lower than the next lowest AIC model (Burnham and Anderson 2002). If one or more models were within two AIC values of the highest ranked model, we considered there to be equivalent support given the data, and we selected the model with the highest R^2 value for presentation.

Table 1 Monthly time spent on core activities and dietary proportion of *R. bieti* at Mt. Lasha between May 2008 and Sept. 2009

Year	Month	Number of scan	Sampling individual	Relative time budget (%)				Dietary proportion (%)				
				Feeding	Moving	Resting	Social	Lichens	BY	ML	FF	Insect
2008	May	200	1941	31.38	29.91	28.84	9.90	64.98	1.81	22.59	8.95	1.67
	Jun	117	1071	31.95	32.44	29.74	5.87	70.80	0.45	9.83	14.28	4.64
	Aug	299	2573	38.79	28.65	21.38	11.14	77.20	0.00	0.46	16.96	5.38
	Oct	237	1880	37.19	31.62	22.07	9.12	81.91	1.68	0.20	15.86	0.35
	Nov	734	6301	41.29	23.14	28.21	7.37	88.99	0.16	1.97	8.68	0.20
	Dec	409	3448	45.95	17.33	29.27	7.44	96.17	0.36	3.17	0.00	0.30
2009	Jan	386	3543	51.94	15.39	26.78	5.92	93.45	0.07	6.31	0.00	0.20
	Feb	368	3495	48.40	11.64	30.75	9.20	89.99	1.14	7.56	1.26	0.05
	Mar	721	7020	45.28	16.85	31.36	6.54	77.47	14.55	5.51	2.42	0.05
	Apr	364	3499	43.14	22.48	27.62	6.78	63.96	27.46	0.98	7.53	0.07
	Jul	384	4152	46.25	19.40	24.25	10.08	85.17	0.19	1.65	4.76	8.22
	Sep	333	3209	38.66	21.65	28.57	11.12	72.09	0.00	0.60	25.18	2.13
	Mean ± SD		379 ± 184	3511 ± 1720	41.68 ± 6.35	22.54 ± 6.83	27.40 ± 3.23	8.37 ± 1.95	80.18 ± 10.86	3.99 ± 8.43	5.07 ± 6.35	8.82 ± 7.89

BY bud and young leaves, ML mature leaves, FF flower and fruit

Table 2 Activity budget, feeding effort and population density in *Rhinopithecus bieti* at different sites

Sites	Lat	Ele	GS	HR	F	M	R	S	FE	TFL	FS	T _{mean}	T _{min}	T _{max}	Rain	OT (year#month#hrs.)	Reference
Xiaochangdu	29.25 N	3800	210	21.2	49.1	20.4	17.8	12.7	3.90	82.1	25	4.7	-0.01	13.8	740	Jun 2003–Mar 2005/12/549	Xiang et al. 2010
Wuyapiya*	28.50 N	4250	175	16.3	32	36	22	10	3.09	85	27	0.9	-	-	-	Jul 1993–Jun 1999/8/394	Kirkpatrick 1996
Tacheng	27.60 N	3038	360	-	35	15	33	13	1.52	60	59	9.8	2.2	16.2	1371	Mar 1999–Dec 2000/13/n. a.	Ding & Zhao 2004
Samage	27.57 N	2448	410	32	38.5	19.1	28.5	13.9	2.02	67	94	14.3	-	-	1004	Sep 2005–Jul 2007/12/456	Grueter et al. 2013
Fuhe	26.42 N	2600	80	10.7	30	15	41	16	1.10	63	-	11.1	6.2	23.8	906	Nov 2000–Jan 2002/>12/384	Liu et al. 2004
Lasha	26.33 N	2720	100	8.2	41.7	22.6	27.5	8.4	2.34	80.2	36	11.8	4.7	19.2	971	May 2008–Sep 2009/>12/839	This study
Longma	26.23 N	2930	80	9.6	-	-	-	-	-	-	98	8.8	5.2	13.5	1306	Dec 2003–Jan 2005/14/n. a.	Huo 2005

Lat latitude, Ele elevation (m a.s.l.), GS group size, HR home range (km²), F feeding (%), M moving (%), R resting (%), S social (%), FE feeding effort, TFL time feeding lichens (%), FS food species, T_{mean} annual mean temperature (°C), T_{min} mean monthly minimum temperature (°C), T_{max} mean monthly maximum temperature (°C), Rain annual rainfall (mm), OT observation time

* The annual activity budget for Wuyapiya may have been influenced by a less underrepresentation of data collected in winter

Results

Activity budget and diet at Mt. Lasha

Rhinopithecus bieti at Mt. Lasha spent 41.7% of their time feeding, 27.4% resting, 22.5% moving, and 8.4% engaged in social interactions (5.9% grooming and 2.2% playing, Table 1). The monkeys consumed 36 food species during the study period, including three lichen species, three bamboo species, one fungus species, and 29 tree species.

On average, 80.2% of feeding time was spent consuming lichens, of which 81.0% was on *Bryoria* spp. and 19.0% was *Usnea longissima*. The remaining feeding time was divided at 4.0% on bud and young leaves, 5.1% on mature leaves, 7.3% on fruits, 1.5% on flowers, 1.9% on insects (invertebrates), and 1.3% unidentified/other (Table 1).

Feeding effort and time feeding on lichens

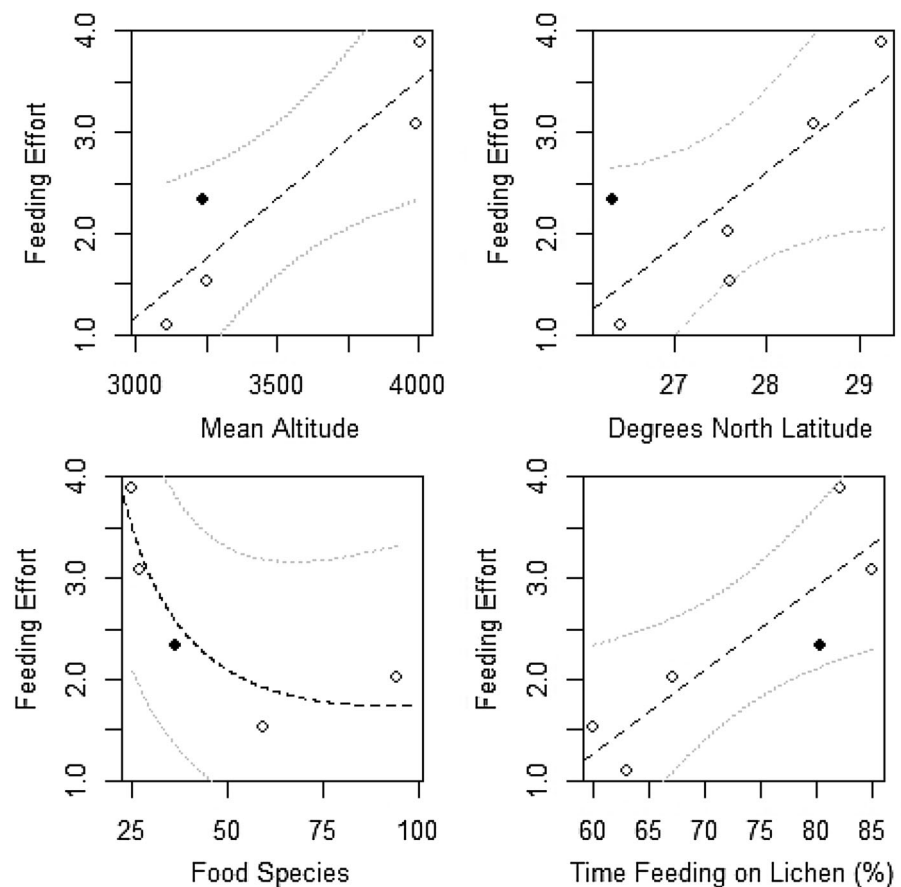
The relationships between feeding effort and variables latitude ($\hat{y}_i = -17.15 + 0.71x_i + \varepsilon_i$, where $\varepsilon = 0.69$, $R^2_{adj} = 0.55$, $F_{1,4} = 7.11$, $p = 0.056$) and altitude ($\hat{y}_i = -5.91 + 0.0024x_i + \varepsilon_i$, where $\varepsilon = 0.53$, $R^2_{adj} = 0.78$, $F_{1,4} = 15.44$, $p = 0.03$), were best described by linearity (Fig. 2). The relationship between feeding effort and food species was better described by the nonlinear equation ($\hat{y}_i = (1/x_i \times 81.15) + 0.0093x_i + \varepsilon_i$, where $\varepsilon = 0.41$) than linearity. Forest fragmentation area, group size, density, rainfall and temperature had poor linear and nonlinear relationships with feeding effort.

Time feeding on lichens was not significantly related to altitude, latitude, forest area, home range, group size, density, food species, rainfall or temperature. However, time feeding on lichens and feeding effort had a positive linear relation ($\hat{y}_i = -3.69 + 0.083x_i + \varepsilon_i$, where $\varepsilon = 0.58$, $R^2_{adj} = 0.69$, $F_{1,4} = 11.94$, $p = 0.025$).

Discussion

Across its geographic range, *R. bieti* exhibits a wide range in feeding effort. We found that the diversity of food species and proxies of climate (altitude, latitude) were more meaningful indicators of feeding effort than forest area, home range, group size or animal density. Unsurprisingly, we found that feeding effort in *R. bieti* increased with increasing altitude, latitude, and time feeding on lichens, and with decreasing food species diversity. In regions where conditions are more severe, and less food species to choose from, monkeys spent relatively more time feeding and moving relative to resting. However, we found that the Mt. Lasha population, a population near to the southern extent of the species, exhibited feeding behaviors more similar to

Fig. 2 Linear regressions between feeding effort (the ratio of time spent feeding and moving divided by time spent at rest) and mean altitude, degrees north latitude, food species (non-linear) and time feeding on lichen in different sites. *Solid circle* is Mt. Lasha site; *black dash* is regression, *grey dash* is 95% confidence interval



populations at higher latitudes and elevations (Table 2, Fig. 2). Feeding effort is a measure of behavior and used as a predictor of stress in primates suffering food scarcity (Cavigelli 1999). Relatively small increases in stress (fecal glucocorticoid) have been shown to predict individual survival in wild primates (Pride 2005), and increases in feeding effort negatively affect fitness as it is related to higher levels of stress in *Papio anubis* (Sapolsky 1986) and *Lemur catta* (Cavigelli 1999). Furthermore some primates (e.g., howler monkeys, *Alouatta palliata mexicana*) respond to living in degraded or fragmented habitats with increased feeding effort (Asensio et al. 2007; Dunn et al. 2010). Given the unexpectedly high feeding effort relative to latitude and elevation for population at Mt. Lasha, suggested that this population of *R. bieti* suffer stress under a degraded fragment habitat.

The fallback food lichens comprise the most important component of *R. bieti* diet (Grueter et al. 2009). These lichens are generally widespread in primary forest habitat in the region and available year-round, making them a readily available food source. For the Mt. Lasha population, over 80% of the feeding time was spent feeding on lichens, much higher than groups at similar latitudes, and more comparable to populations living at higher elevations near the northern range limit (Table 2; Fig. 2). *R. bieti*

seasonally adjust their intake of plant food items according to phenological changes in the environment (Grueter et al. 2009). Lichens are nutritionally inferior, but serve as a key strategy to survival, functioning as staple fallback food that facilitate seasonal shortages in preferred plant food items (Marshall and Wrangham 2007; Xiang et al. 2007; Grueter et al. 2009). As time feeding on lichens is a direct measure of the primates visiting a fallback food, we argue the anomalously greater reliance by the Mt. Lasha group on lichens and increased feeding effort are behavioral responses to existing in a degraded forest fragment and indicative of a stressed population. Indeed, other primates, such as black-and-white ruffed lemur (*Varecia variegata*) and Diademed Sifakas (*Propithecus diadema*) respond to habitat disturbance by integrating fallback foods (Ratsimbazafy et al. 2002; Fontanillas et al. 2004; Marshall et al. 2009; Stumpf 2011).

Implication for conservation

The ability to use lichens as a fallback food has enabled *R. bieti* to occupy a harsh environment, as well as to support large group sizes (Kirkpatrick and Grueter 2010). However, this reliance on lichens puts *R. bieti* groups in degraded habitat fragments at a greater risk of survival

(Jernvall and Wright 1998; Wright 2007). First, lichens *Bryoria* and *Usnea* are low in protein (Kirkpatrick 1996; Zhang et al. 2012) and contain usnic acids as well as other compounds that are toxic to mammals, causing malnutrition and possibly affecting reproduction (Perry et al. 1999; Marante et al. 2003; Dailey et al. 2008). Second, lichens in forest fragments in Yunnan are particularly susceptible to depletion. Lichens have relatively slow growth rates and are slow to re-establish, making them uncommon outside old-growth forests. *Bryoria* and *Usnea* are collected by local residents for food and medicine, and harvested along with the felling of old-growth trees (Kirkpatrick 1996; Wang et al. 2001). For example, lichens at Mt. Lasha have been depleted in the core habitat area requiring more time spent feeding and foraging by the monkeys (HZP, personal observation). Monkey populations near the southern extent of the range face the greatest human interfaces, where more people live in close proximity to the monkey populations and use the forests for resources. Consequently, more habitat has been lost and the *R. bieti* range has been greatly reduced in the south (Li et al. 2002). With particular regard to these southern populations, we suggest that establishing habitat corridors and expanding habitat area will benefit *R. bieti* in small habitat fragments and safe-guard against effects of localized deforestation and food scarcities. We also suggest that monitoring feeding effort change can be a good predictor of stress in a wild population of primates, if elevation and latitude are controlled. The significant correlation between feeding effort and time spent eating fallback food lichen indicates time spent on eating fallback food may be a predictor of stress in *R. bieti*, suitable for rapid assessment of the survival status of a population, particularly where funds are limiting.

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