Seasonal Variation in the Activity and Dietary Budgets of Cat Ba Langurs (*Trachypithecus poliocephalus*)

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Abstract Primate activity budgets are dictated by food availability and distribution; thus primates living in seasonal environments must adapt their behaviors to accommodate fluctuations in resources. Cat Ba langurs (*Trachypithecus poliocephalus*), a Critically Endangered Asian colobine and a member of the limestone langur group (*francoisi* superspecies group within genus *Trachypithecus*), live only in fragmented and disturbed habitats on Cat Ba Island, northeastern Vietnam. This study aimed to assess the behaviors and diet of Cat Ba langurs by group, age, sex, and season. We predicted they would have high rates of inactivity and foraging, low rates of social behaviors, with seasonal variation that reflects an energy-maximizing strategy. We conducted behavioral observations through scan sampling over an 11-month period and found that Cat Ba langurs spent a significant portion of their day inactive (57 %) followed by foraging (18 %), socializing (13 %), locomoting (10 %), and engaging in "other" behaviors (2 %). Their diet was made up primarily of leaves (83 %) followed by flowers (8 %), fruit (6 %), and stems (3 %). We found groups to differ in diet and activity, which is likely owing to differences in demographics and home range between groups. Seasonally, the animals ate more leaves and spent more time foraging in the dry season than the wet season, suggesting that they are energy maximizers. Cat Ba langurs have activity and dietary budgets similar to those of other limestone langurs, and respond to a presumed seasonal fluctuation in food availability similarly.

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Introduction

All animals have a finite amount of energy with which to fuel daily activities. This means they need to balance the energy exerted to find food with the costs of traveling to find that food. Thus, although physiology is undoubtedly a key factor in determining activity budgets, animals are also largely influenced by diet, making the two quite interdependent (Milton 1980, 1998). Animals that eat primarily leaves, such as colobines, must spend considerable time foraging, to process bulky leaves (Clutton-Brock and Harvey 1977; Decker 1994), and resting, to allow for the digestion of these high-fiber dietary items (Dasilva 1992; Edwards and Ullrey 1999; Kirkpatrick 2007). This also has consequences for social behavior; because leaves are nonmonopolizable and do not require cooperative defense, social behavior is rare for leaf eating primates (Newton and Dunbar 1994). For example, macaques (*Macaca* spp.), whose diet can include up to 87 % fruit (Thierry 2007), spend 15–32 % of their time inactive and up to a third of their day engaged in social behaviors (Alami *et al.* 2012; Hambali *et al.* 2012; Hanya 2004; Kumar *et al.* 2007), whereas colobines, whose diets can include up to 92 % leaves (Snaith and Chapman 2008), spend as much as 61 % of their time inactive and as little as 0 % of their day in social behaviors (Kirkpatrick 2007; McGraw 1998; Newton 1992; Phiapalath and Suwanwaree 2010; Rawson 2009).

In colobines, activity budgets are known to vary between groups, age classes, and sexes. Given the higher energetic and reproductive costs of adults compared to juveniles, adults often spend more time resting than individuals in younger age categories (Agmen 2014; Li 1992; Li and Rogers 2004; Newton 1992; Phiapalath and Suwanwaree 2010; Rawson 2009; Schneider *et al.* 2010). Owing to reproductive demands, females also spend significantly more time foraging than males (Clutton-Brock 1977; Dunbar and Dunbar 1988; Workman 2010a). They also spend significantly more time than males engaged in social behaviors (Clutton-Brock 1977; Fashing 2001; Fashing *et al.* 2007b; Newton 1992; Witte 2011; Workman 2010a), partially owing to the high rates of infant transfers (Jin *et al.* 2015; Kumar *et al.* 2005; Yao *et al.* 2012). Males, in contrast, spend more time being vigilant for predators and outside males (Agmen 2014; Fashing 2001; Workman Workman 2010a), resulting in high rates of inactivity among males (Clutton-Brock 1977; Fashing 2001; Fashing *et al.* 2007b).

Food availability plays a key role in determining the diet of a species, particularly on a seasonal basis. When food resources are seasonally limited, two typical responses allow animals to maintain energy budgets: conserving energy and being more sedentary, or exerting more energy for increased traveling and foraging than during times of year when food resources are abundant (Hemingway and Bynum 2005; Schoener 1971). The energy conservation, or time minimizing, strategy involves reducing foraging energy expenditure at times of low food availability, while energy maximizing strategies are those that increase time and energy spent trying to find sufficient resources (Schoener 1971). For example, king colobus (*Colobus polykomos*) spend more time resting and less time feeding when preferred seeds are not available (Dasilva 1992), suggesting that they are adopting an energy conservation strategy. Spectral tarsiers (*Tarsius* sp.: Gursky 2000) and Yunnan snub-nosed monkeys (*Rhinopithecus*

bieti: (Grueter *et al.* 2013) forage more in the resource-poor season, with tarsiers also traveling more at this time, suggesting an energy maximizing strategy. Similarly, François' (*Trachypithecus francoisi*) and white-headed (*T. leucocephalus*) langurs feed and travel more in the dry season (Huang *et al.* 2000, 2003; Yang *et al.* 2007; Zhou *et al.* 2007, 2010) when they consume more mature leaves (Hu 2007; Li and Rogers 2006; Zhou *et al.* 2009).

The limestone langur group (a superspecies group within the *Trachypithecus* genus) currently includes François', Delacour's (*T. delacouri*), Laotian (*T. laotum*), Hatinh (*T. hatinensis*), black (*T. ebenus*), white-headed, and Cat Ba (*T. poliocephalus*) langurs (Groves 2007). As with other colobines, limestone langurs have specialized digestive tracts, salivary glands, and dentition to handle the high amount of leaves in their largely folivorous diet (Bauchop 1975; Caton 1999; Kay and Hylander 1975; Oates and Davies 1994).

Cat Ba langurs are endemic to Cat Ba Island, northeastern Vietnam. The Cat Ba langur is listed as Critically Endangered on the IUCN Red List of Threatened Species (Bleisch *et al.* 2008) and has been consistently listed on the global 25 most endangered primate list since 2000 (Leonard *et al.* 2016). In the 1960s, the langur population may have been as large as 2400–2700, declining to *ca.* 135 individuals by 1999 because of intense hunting pressure (Nadler and Ha Thang Long 2000). Estimates after this time placed the population at only *ca.* 60–70 individuals (Schrudde *et al.* 2010; Stenke and Chu Xuan Canh 2004), but more recent reanalysis of monitoring data from the period suggests that the population was much lower than this, and may have been not much more than 40 at its low point (Leonard 2014). Based on 2014 figures, the global wild population of the species consists of fewer than 70 individuals and includes two breeding subpopulations (one, containing *ca.* 31 individuals based in an area known as the sanctuary and the other, consisting of 17–24 individuals, is in the Cua Dong area) and one nonbreeding subpopulation (five adult females) on Cat Ba Island (Lees *et al.* 2014). There is also an *ex situ* breeding group of five individuals housed at the Endangered Primate Rescue Centre in Cuc Phuong National Park. The three *in situ* Cat Ba langur subpopulations are completely isolated from one another. Despite their vulnerability to extinction from extremely low population size (Lees *et al.* 2014), only one published, peer-reviewed study has been conducted on their behavior, which resulted from only 22 days of observations (Schneider *et al.* 2010).

This study aims to explore the activity and dietary budget of two groups of Cat Ba langurs over an 11-mo period to provide the first detailed description of their behavior that can be compared to closely related species. We first assess overall behavior and dietary differences across groups, ages, and sexes and then explore seasonal changes in activity and dietary budgets. Based on studies of other limestone langurs (Hu 2007; Huang *et al.* 2000, 2008; Li *et al.* 2003, 2009; Workman 2010a; Workman and Le Van Dung 2009; Yin *et al.* 2011; Zhou *et al.* 2010, 2011, 2013), we predict that leaves would make up most of the Cat Ba langur diet, and, as a result, we would see the majority of the langurs' day spent inactive and feeding to cope with this low-quality diet. We also predict that, as a result, social behavior will be minimal, as with most folivores. In addition, we assume that resource availability changes throughout the year, as it does in geographically similar habitats (Hu 2007; Li and Rogers 2006; Workman 2010a; Zhou *et al.* 2009), which leads us to predict that both activity and dietary budgets will change seasonally in accordance with the

changing food supply (Huang et al. 2003; Zhou et al. 2007). Based on studies of other limestone langurs (Huang et al. 2000, 2003; Yang et al. 2007; Zhou et al. 2007, 2010), we hypothesize that Cat Ba langurs will be energy maximizers, and predict that they increase energy expenditure through increased foraging and travel times at times of low resource availability to find enough food to meet energy demands.

Methods

Study Site

Cat Ba Island (20°42′–20°55′N; 106°54′–107°10′E) is the largest of the hundreds of limestone karst islands in the Cat Ba archipelago in Ha Long Bay, northeastern Vietnam. In this part of Vietnam, there is a distinct, hot, rainy season from May to October (when 80–90 % of the year's rain falls: 150–160 cm; Nguyen Quan Van et al. 2010), and a distinct, cool, dry season from November to April; we term these simply wet and dry seasons, respectively, in this study. Established in 1986, roughly half of the 285-km² island is designated as National Park, a subset of which is a langur sanctuary, a strictly protected core zone within the National Park created for langur protection (Schrudde et al. 2010). Because of the porous nature of limestone karst, there are no permanent freshwater pools on the island (Sterling et al. 2006). Cat Ba Island has tropical moist deciduous and karst forests (Nguyen Quan Van et al. 2010; Nisbett and Ciochon 1993); vegetative growth is stunted, shrubby, and discontinuous (Day and Chenoweth 2004; Liu et al. 2004; Nisbett and Ciochon 1993); and historical logging has left little primary forest remaining (Nadler and Ha Thang Long 2000).

Study Groups

This study focused on the Cua Dong breeding population, located on a peninsula in the southeast corner of Cat Ba and consisting of two social groups. The two groups (Table I) have neighboring home ranges with a slight overlap (Fig. 1). They live in auditory proximity to floating villages, and were habituated to fishing boats and people's presence at ground level. The larger group (group A, $N = 10$–13) has a home range that could possibly be expanded into mainland territory, whereas the smaller group's (group B, $N = 7$) home range is limited by ocean front and the home range of the larger group (Fig. 1).

Females are identifiable by white patches on their inner thighs and, if parous, pendulous nipples. We identified adults as being full size with species-specific pelage, and immature individuals (ranging from newborns to juveniles) by the state of their natal coat (with newborns being bright orange, and juveniles being mostly adult colored but with orange that extends further down their neck and shoulders than adults).

Data Collection

We collected data from February 2014 to January 2015, with time spent in visual contact ranging from 12.5 to 72.3 h/mo (Table II). As it is very difficult to traverse

Table I Group composition of Cua Dong Cat Ba langur (*Trachypithecus poliocephalus*) breeding groups (located in southeastern Cat Ba Island, northeastern Vietnam) as of January 2015 with notes on births throughout the study period (February 2014–January 2015)

Age-Sex Class	Number of individuals	
	Group A	Group B
Adult male	1	1
Adult female	5	2
Subadult male	0	1
Subadult female	0	1
Young male	4 (1 born August 2014, 1 born October/November 2014)	1
Young female	2	1
Young unsexed	1 (born December 2014/January 2015)	0
Total	13 (10 at the start)	7

limestone karst terrain, our observations were made from a boat, following the protocol of previous studies in similar environments (Agmen 2014; Schneider *et al.* 2010; Workman 2010a). We used stabilizing binoculars to identify the group and age–sex class of individuals from a distance of 30–250 m. We used instantaneous scan sampling to record behaviors at 10-min intervals (Altmann 1974; Martin and Bateson 2009); a total of 245–1655 individual scans were collected each month, with a monthly range of 2.8–4.0 individuals scanned per 10-min interval (Table II). As individual identification was not possible, we were able to note only the age–sex class of each individual. To avoid repeat sampling of the same individual in the same scan, we started at the center of the group and then spiraled out from that point. To ensure the scans were instantaneous, we recorded all information within roughly 30–40 s.

We recorded activities using an ethogram adapted from closely related species (Agmen 2014; Li and Rogers 2004; Workman and Schmitt 2012), and then recoded all behaviors into bigger categories for analysis. Categories of behaviors included inactivity (sunbathing, resting, scanning/vigilance, and autogrooming), foraging (manipulating, searching for, and ingesting food), social behavior (grooming, social play, vocalizing, same- and opposite-sex mounting, embracing, young transferring, presenting, harassing a mounting pair, submission, displacement, and aggression), locomotion (quadrupedal walking or running, climbing, leaping, dropping, and arm swinging), and "other" behaviors (nonsocial play, exploring, struggle against being held, maternal rejection, and masturbation). We classified dietary items as leaves (both young and mature leaves as it was difficult to differentiate between the two), flowers (blossoms), fruits (both immature and ripe fruit; may include unseen seed consumption), or stems (herbaceous stems connecting leaves to branches or nonleafy parts of vines).

We were often not able to observe langurs because of dense foliage, which is a common problem for primate researchers, particularly in this habitat type (Agmen 2014; Huang *et al.* 2003; Li and Rogers 2004, 2006; Li *et al.* 2009; Rawson 2009; Workman and Schmitt 2012). This may have created a bias in our data against rare or subtle behaviors being recorded, but we obtained the best conservative estimate of behavior, making this study comparable to other limestone langur studies.
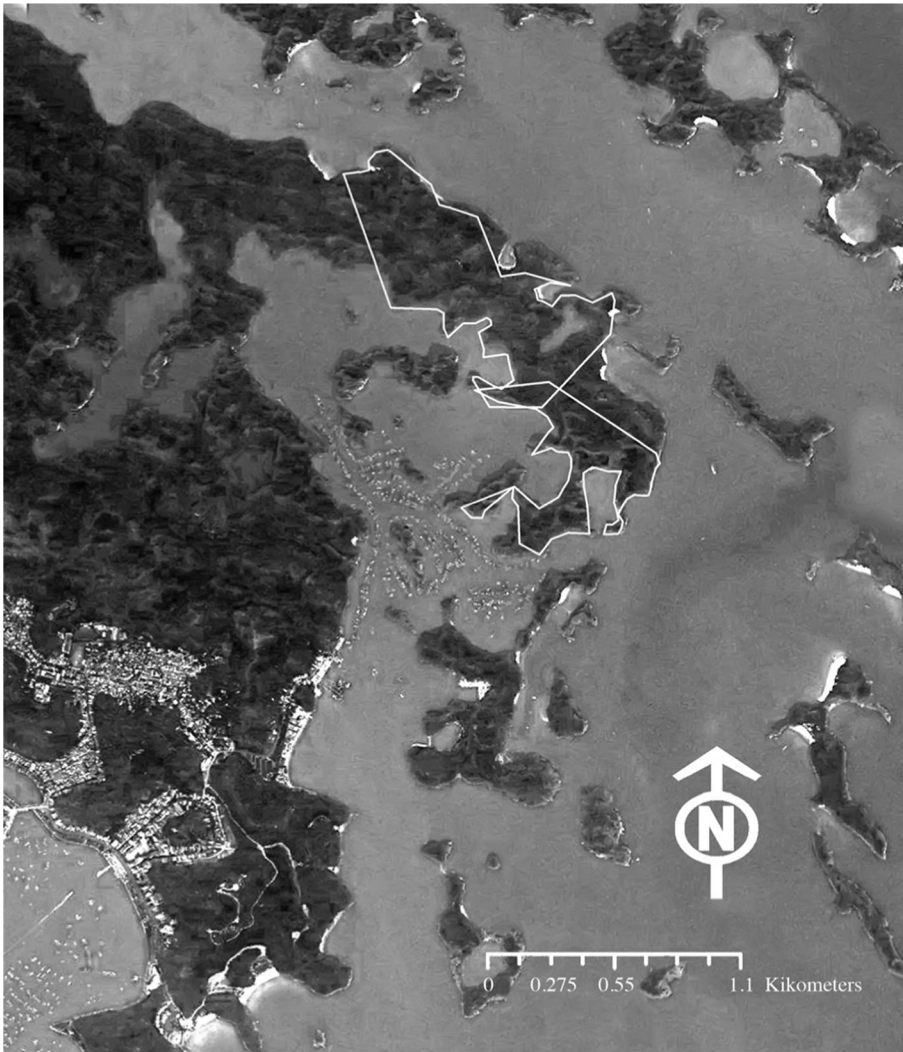
Fig. 1 Map of home ranges (outlined in white) for Cat Ba langurs (*Trachypithecus poliocephalus*) living in Cua Dong (southeastern Cat Ba Island, northeastern Vietnam) February 2014–January 2015; group A (10–13 individuals) occupies the northern range and group B (7 individuals) the southern range. Map source: ArcGIS.

Statistical Analysis

We calculated activity and dietary budgets based on 541 contact hours, across 180 days of observation spanning 11 mo in the field (Table II). Activity and dietary budgets are presented as the proportion of scans that included each specific behavior category or the proportion of feeding records that included a specific dietary item. Owing to the irregular distribution of behaviors and consumed food items, we first assessed group, age, sex, and seasonal differences with a Fisher's Exact test (FET). If we found significant differences with contingency tables ($P < 0.05$), we carried out *post hoc* analyses by creating binomials for behavior and food items, then by running each

Table II The number of scans, contact hours, and number of Cat Ba langur (*Trachypithecus poliocephalus*) individuals included in scans within each 10-min interval for each month of observations (February 2014–January 2015) in Cua Dong (southeastern Cat Ba Island, northeastern Vietnam)

Season	Month	Scans	Hours	Scans/interval
Dry	February 2014	245	12.5	3.3
	March 2014	1335	70.3	3.2
	April 2014	1368	72.3	3.2
Wet	May 2014	1333	60.7	3.7
	June 2014	335	20.5	2.7
	July 2014	815	39.8	3.4
	August 2014	1655	68.8	4.0
	September 2014	883	45.3	3.2
	October 2014	406	23.8	2.8
Dry	November 2014	817	48.3	2.8
	December 2014	1400	62.7	3.7
	January 2015	376	15.8	4.0
	Total	10,968	541.0	3.4

behavior or food item separately within a generalized linear model (GLM). For seasonal analyses, as all categories tested (group, age, and sex) show a similar behavioral and dietary pattern across seasons (Hendershott *unpubl. data*), they are grouped together. We removed newborns from all analyses because their behaviors are nonindependent. While the foraging category includes water drinking ($N = 26$), this was not analyzed as part of the dietary budget. We used SPSS 23 for Windows® for all analyses, with significance set to $P < 0.05$ for two-tailed tests.

Ethical Note

We obtained ethics approval from the Australian National University Animal Experimentation Ethics Committee (Animal Ethics Protocol Number: A2013/18) for July 1, 2013–June 30, 2016. We received research permissions from Cat Ba National Park and the Hai Phong People's Committee and designed all data collection so as to minimize the impact on the langurs.

Results

Overall Activity and Dietary Budget

Out of a total of 10,879 scans in which behavior could be identified (excluding newborns), inactivity was the most common behavior, occupying 57 % of the overall activity budget. Foraging was the next most common activity, at 18 %, followed by social behaviors (13 %), locomotion (10 %), and "other" behaviors (2 %). Out of a total

of 746 scans in which feeding was observed and consumed items identified, the majority were leaves (83 %), followed by flowers (8 %), fruit (6 %), and finally stems (3 %). The langurs were seen to drink ocean water, lick rocks, and lick cavities of rock pools, spending 0.3 % of scans engaged in these drinking/licking behaviors.

Group Differences

The two groups differed in their activity (FET: $P < 0.001$, $N = 10,809$; Fig. 2) and dietary (FET: $P < 0.001$, $N = 743$; Fig. 3) budgets. The larger group, A, spent significantly more time inactive (GLM: $\chi^2 = 23.771$, df = 1, $P < 0.001$, $N = 6111$), engaging in social (GLM: $\chi^2 = 5.615$, df = 1, $P = 0.018$, $N = 1409$) and "other" (GLM: $\chi^2 = 49.650$, df = 1, $P < 0.001$, $N = 245$) behaviors. Their diet included significantly more leaves (GLM: $\chi^2 = 5.695$, df = 1, $P = 0.017$, $N = 615$) and almost three times the fruit (GLM: $\chi^2 = 8.213$, df = 1, $P = 0.004$, $N = 46$) of group B. The smaller group, B, spent significantly more time foraging (GLM: $\chi^2 = 86.440$, df = 1, $P < 0.001$, $N = 2000$) and locomoting (GLM: $\chi^2 = 6.278$, df = 1, $P = 0.012$, $N = 1044$), and their diet included significantly more flowers (GLM: $\chi^2 = 21.838$, df = 1, $P < 0.001$, $N = 60$) than that of group A. Groups did not differ in their consumption of stems (GLM: $\chi^2 = 2.374$, df = 1, $P = 0.123$, $N = 22$).

Age Differences

Behaviors were significantly different between age classes ($N = 10186$; $P < 0.001$, FET; Fig. 4), and *post hoc* analyses indicate that this is true for each individual behavior (inactivity GLM: $\chi^2 = 89.276$, df = 1, $P < 0.001$, $N = 5722$; foraging GLM: $\chi^2 = 38.605$, df = 1, $P < 0.001$, $N = 1875$; social GLM: $\chi^2 = 28.724$, df = 1, $P < 0.001$, $N = 1358$; locomotion GLM: $\chi^2 = 64.647$, df = 1, $P < 0.001$, $N = 985$; "other" GLM: $\chi^2 = 106.283$, df = 1, $N = 246$). There was no significant effect of age on dietary budgets
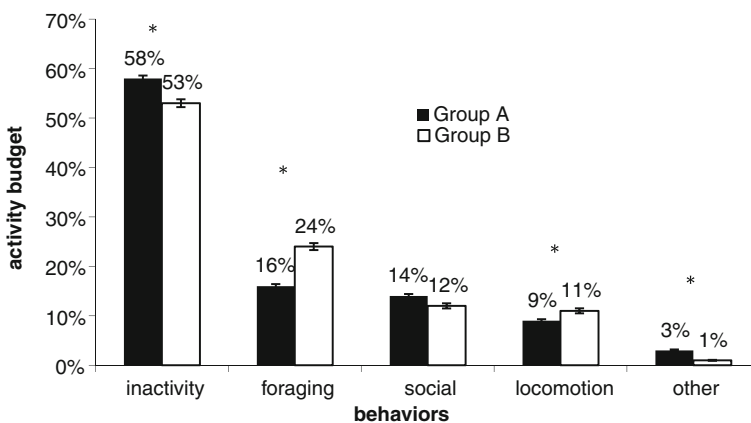
Fig. 2 Percentage of activity budget ($\pm$ SE) for each behavior by two groups (group A, $N = 10–13$; group B, $N = 7$) of Cat Ba langurs (*Trachypithecus poliocephalus*) living in Cua Dong (southeastern Cat Ba Island, northeastern Vietnam). An asterisk indicates significant group differences for that activity category as demonstrated through *post hoc* analyses, which were conducted following an initial analysis for activity budgets that indicated significant group variation.
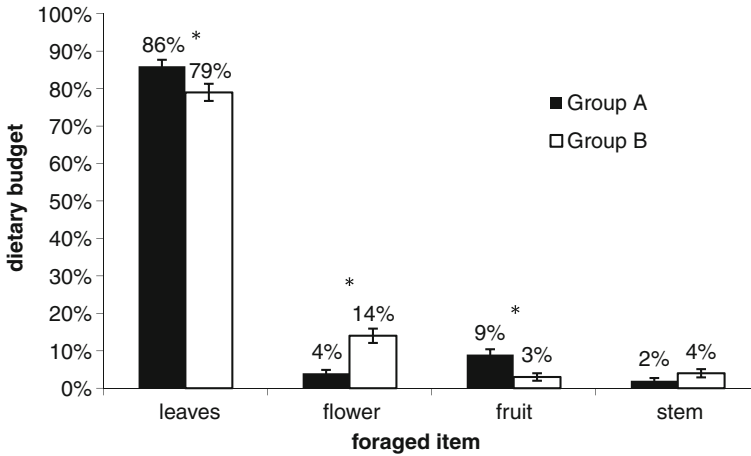
Fig. 3 Percentage of dietary budget (± SE) for each item consumed by two groups (group A, $N = 10$–13; group B, $N = 7$) of Cat Ba langurs (*Trachypithecus poliocephalus*) living in Cua Dong (southeastern Cat Ba Island, northeastern Vietnam). An asterisk indicates significant group differences for that dietary category as demonstrated through *post hoc* analyses, which were conducted following an initial analysis for dietary budgets that indicated significant group variation.

(FET: $P = 0.750$, $N = 716$). The general pattern is for social behaviors to increase with age, while locomotion and "other" behaviors decrease with age. Adults spend the most time inactive and subadults forage most often.

Sex Differences

Behaviors were significantly different between sex classes (FET: $P < 0.001$, $N = 7289$; Fig. 5): *post hoc* analyses indicate that this pattern holds for inactivity (GLM: $\chi^2 = 10.994$, df = 1, $P = 0.001$, $N = 4164$), foraging (GLM: $\chi^2 = 6.051$, df = 1, $P = 0.014$, N
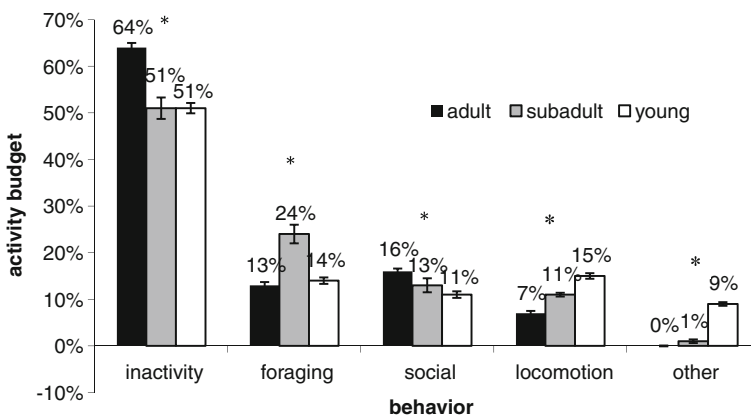
Fig. 4 Percentage of activity budget (± SE) across ages (adult, subadult, young) for each behavior of Cat Ba langurs (*Trachypithecus poliocephalus*) living in Cua Dong (southeastern Cat Ba Island, northeastern Vietnam) February 2014–January 2015. An asterisk indicates significant age differences for that activity category as demonstrated through *post hoc* analyses, which were conducted following an initial analysis for activity budgets that indicated significant age variation.
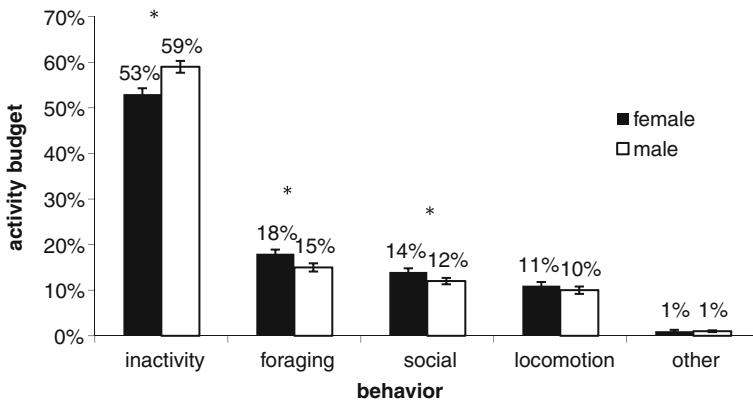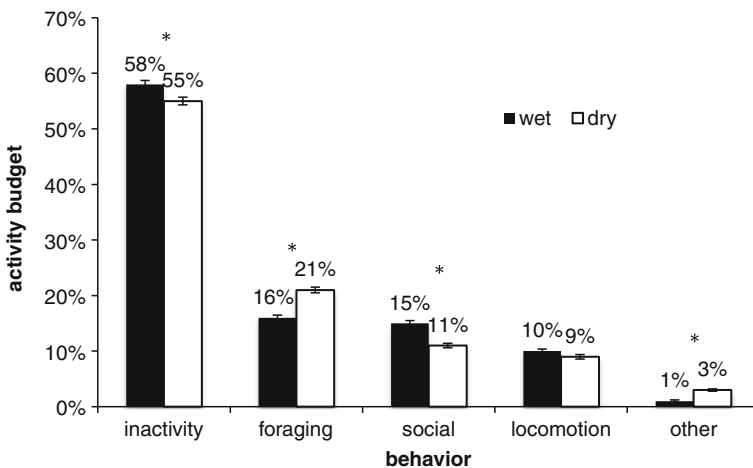
Fig. 5 Percentage of activity budget (± SE) across sexes for each behavior of Cat Ba langurs (*Trachypithecus poliocephalus*) living in Cua Dong (southeastern Cat Ba Island, northeastern Vietnam) February 2014–January 2015. An asterisk indicates significant sex differences for that activity category as demonstrated through *post hoc* analyses, which were conducted following an initial analysis for activity budgets that indicated significant sex variation.

= 1122), and social behaviors (GLM: $\chi^2 = 3.892$, df = 1, $P = 0.049$, $N = 1056$). There was no significant effect of sex on locomotion (GLM: $\chi^2 = 1.628$, df = 1, $P = 0.202$, $N = 726$), "other" behaviors (GLM: $\chi^2 = 3.155$, df = 1, $P = 0.076$, $N = 221$) or dietary budgets ($N = 466$, $P = 0.483$, FET). Males were inactive significantly more than females, while females forage and socialize more than males.

Seasonal Differences

Activity (FET: $P < 0.0001$, $N = 10879$; Fig. 6) and dietary (FET: $P < 0.0001$, $N = 746$; Fig. 7) budgets varied significantly by season. In the wet season (May–October), the

Fig. 6 Percentage of activity budget (± SE) for each behavior of Cat Ba langurs (*Trachypithecus poliocephalus*) living in Cua Dong (southeastern Cat Ba Island, northeastern Vietnam) in the wet (May–October) and dry (November–April) seasons February 2014–January 2015. An asterisk indicates significant seasonal differences for that activity category as demonstrated through *post hoc* analyses, which were conducted following an initial analysis for activity budgets that indicated significant seasonal variation.
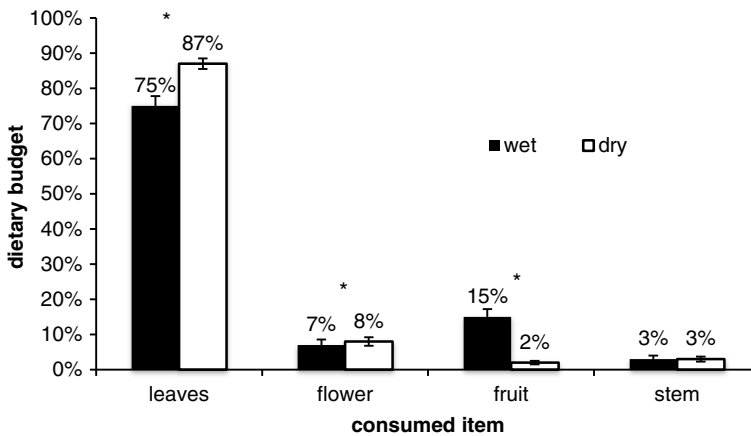
Fig. 7 Percentage of dietary budget (± SE) for each item consumed by Cat Ba langurs (*Trachypithecus poliocephalus*) living in Cua Dong (southeastern Cat Ba Island, northeastern Vietnam) in the wet (May–October) and dry (November–April) seasons of February 2014–January 2015. An asterisk indicates significant differences between seasons for that consumed item as demonstrated through *post hoc* analyses, which were conducted following an initial analysis for dietary budgets that indicated significant seasonal variation.

langurs were less active (GLM: $\chi^2 = 12.847$, df = 1, $P < 0.001$, $N = 6163$) and spent more time engaged in social behaviors (GLM: $\chi^2 = 23.358$, df = 1, $P < 0.001$, $N = 1413$) than in the dry season; at this time they also consumed significantly more fruit (GLM: $\chi^2 = 36.797$, df = 1, $P < 0.001$, $N = 46$). In the dry season (November–April), Cat Ba langurs spent significantly more time foraging (GLM: $\chi^2 = 55.130$, df = 1, $P < 0.001$, $N = 2007$), engaging in "other" behaviors (GLM: $\chi^2 = 31.187$, df = 1, $P < 0.001$, $N = 246$), and consuming leaves (GLM: $\chi^2 = 17.532$, df = 1, $P < 0.001$, $N = 618$) than in the wet season. Locomotion rates (GLM: $\chi^2 = 1.282$, df = 1, $P = 0.257$, $N = 1050$) and flower (GLM: $\chi^2 = 0.284$, df = 1, $P = 0.594$, $N = 60$) and stem (GLM: $\chi^2 = 0.017$, df = 1, $P = 0.896$, $N = 22$) consumption did not differ significantly between seasons.

Discussion

We found the activity budgets for Cat Ba langurs to be similar to those of other, closely related limestone langurs, with rates of inactivity, foraging, and locomotion fitting well within the range for the group (Table III). The high percentage of time inactive supported our prediction, and is likely due to the langurs' emphasis on leaf-eating (Clutton-Brock and Harvey 1977; Dasilva 1992; Kirkpatrick 2007; Newton 1992; Oates 1977), as high rates of inactivity are expected given the processing time required for breaking down fibrous cell walls into usable energy (Edwards and Ullrey 1999). Feeding is also expected to dominate folivore activity budgets, given that leaf eating requires more processing time compared to other food sources (Clutton-Brock and Harvey 1977; Decker 1994). Our findings support this as leaves were the most common food item ingested and inactivity was the most common behavior, followed by feeding.

As we predicted, time spent in social behaviors is low for Cat Ba langurs compared to fruit-eating species such as macaques. We found that social behavior occupied a similar portion of the activity budget as those reported for white-headed langurs, but

Table III Annual activity budgets for limestone langurs (*francoisi* superspecies group in genus *Trachypithecus*) living in Vietnam and China in percentage (%) of observations

Species	Inactive	Forage/Feed	Locomote	Social	Other	Source
T. poliocephalus	57	18	10	13	2	This study
T. leucocephalus	52	13	15	14[a]	7[c]	Li and Rogers 2004
	46	20	29		4[d]	Zhou *et al*. 2010
T. delacouri	61	29	4	6		Workman 2010a
	75	21	2	2	<1	Agmen 2014
T. francoisi	50[b]	27[b]	13[b]	<1[a]	10[b,c]	Yang *et al*. 2007
	41	25	17	5[a]	12[c]	Hu 2007
	52	23	17	2[a]	6[c]	Zhou *et al*. 2007

Totals may not be exactly 100 % due to rounding

[a] Grooming only.

[b] Averaging of two groups.

[c] Includes play and/or huddling, which could also be social.

[d] Combination of social and "other" behaviors.

much higher than seen in Delacour's or François' langurs (Table III). Often social interactions of Asian colobine females are centered on newborns, as they are known to interact because of their attraction to young, and high rates of young transfer (Jin *et al*. 2015; Kumar *et al*. 2005; Yao *et al*. 2012). Accordingly, the high social budget of Cat Ba langurs in our study may be a result of the high number of young present in the study groups. This may have also resulted in higher levels of social play than in other studies, as we also included social play in the social behavior category.

As with activity, the dietary budgets of Cat Ba langurs fell within the range of other limestone langurs (Table IV). Leaves, especially young leaves, are an important source of protein for folivores (Hladik 1978), especially as colobines select leaves with a high protein-to-fibre ratio (Fashing *et al*. 2007a; Milton 1979; Workman 2010b; Workman and Le Van Dung 2009). The combination of a specialized digestive tract (Caton 1999; Oates and Davies 1994), and the nutritional value, and availability, of leaves explains the extremely high proportion of leaf eating by Cat Ba langurs. However, despite their moniker, leaf-eating colobines consume a wide range of plant parts, e.g., fruit, flowers, seeds, bark, gum and sap, stems and pith, and roots; fungi, e.g., lichen and mushrooms; and animal matter, e.g., insect galls (Kirkpatrick 2007), which we saw in this study, with langurs eating fruits/seeds, flowers, and stems.

Compared to other limestone langurs, we found that Cat Ba Langurs include a high amount of flowers in their dietary budget. Flowers generally have a higher percentage of water (Oftedal 1991) and nitrogen (Waterman and Kool 1994) than mature leaves, and are also relatively high in copper (Behie and Pavelka 2012). The high amount of flower eating may therefore be a method of meeting macronutrient or mineral needs or to serve as a way to increase water consumption.

Fruits are an energy-rich resource, but they contain less protein than leaves (Oftedal 1991; Waterman and Kool 1994). In our study Cat Ba langurs primarily ate green, unripened fruits, which is common among colobines because their gut flora cannot

Table IV Annual dietary budgets for limestone langurs (*francoisi* superspecies group in genus *Trachypithecus*) living in Vietnam and China in percentage (%) of observations. Percentages may not add up to 100 % due to rounding

Species	Leaves	Flowers	Fruits	Other	Source
T. poliocephalus	83	8	6	3	This study
T. leucocephalus	88	2	7	3	Li *et al.* 2003
	87	2	8	3	Zhou *et al.* 2011[a]
	88	3	9		Yin *et al.* 2011
	91			6–9[b]	Zhou *et al.* 2010
	63–95	0–6	5–35		Huang *et al.* 2000
	92	<1	4	4	Zhou *et al.* 2013
T. delacouri	80	5		15[b]	Workman 2010a
T. francoisi	64	4	26	7	Hu 2007
	95	1	3	2	Huang *et al.* 2008
	87	1	9	3	Li *et al.* 2009
	53–71	*ca.* 7–8	*ca.* 9–17	*ca.* 8–22	Zhou *et al.* 2009

[a] Mean between two groups reported.

[b] Combination of fruit and all other food items.

handle the large amount of sugar present in mature fruits (Davies *et al.* 1999; Waterman and Kool 1994; Workman 2010a; Workman and Le Van Dung 2009). We also found that Cat Ba langurs ate more fruit in the wet season than in the dry season. Similarly, white-headed (Li and Rogers 2006) and Delacour's (Workman 2010a) langurs eat more fruit at this time of year, when it is more available in karst habitats (Workman 2010a; Zhou *et al* 2009), compared to times when food is scarce. This suggests that, as with closely related species, Cat Ba langurs are eating fruit in accordance with its availability.

We found group differences in activity and dietary budgets to be likely the result of differences in group size, demographics, and variation between home range size and quality between the two groups. Group A had a higher ratio of adults than group B (46–60 % vs. 43 %), which may explain the higher rate of inactivity and social behaviors. Higher rates of social behavior in group A may also be due to the higher number of females in this group compared to group B (58–70 % vs. 57 %). Whereas other studies of Asian colobines show higher rates of social behaviors in young individuals (Agmen 2014; Li and Rogers 2004; Newton 1992; Phiapalath and Suwanwaree 2010; Schneider *et al.* 2010), our results found higher social behaviors among older individuals and females. As adult females interact socially in attempts to hold or groom newborns and infants (Jin *et al.* 2015; Kumar *et al.* 2005; Yao *et al.* 2012), it stands to reason that group A's larger proportion of adult females and newborns may explain the higher degree of social interaction in that group.

We found group B to forage more than group A, which may be due to the fact that only group B had subadults, the group found to forage for the highest proportion of scans. This could, however, also represent differences in food tree density between the ranges of the two groups; for example, white-headed langur groups in poor quality habitat fed more and engaged in less social behavior (Li and Rogers 2004). Group B's

higher population density (0.227 ind/ha) compared to group A's (0.120 ind/ha) may necessitate group B to travel farther to find adequate food resources, as in other taxa (Fashing *et al.* 2007b; van Schaik *et al.* 1983; van Schaik and van Noordwijk 1988).

In other limestone langur habitats, fewer preferred foods and fruits are available in the dry than in the wet season (Li and Rogers 2006; Workman 2010a; Zhou *et al.* 2009). Primates have several approaches to dealing with decreased resource abundance. One approach is to reduce energy expended in search of food, and the other is to put more time into increasing energy intake compared to when food is abundant (Hemingway and Bynum 2005; Schoener 1971). Supporting our prediction, our results suggest that more effort may be needed for foraging in a resource poor environment, as foraging increases, and social behaviors and inactivity decrease, in the dry season compared to during the wet season. This has been documented for other limestone langurs (Huang *et al.* 2000, 2003; Yang *et al.* 2007; Zhou *et al.* 2007, 2010). For example, François' langurs spend significantly more time feeding in the dry season than in the wet season (26 % vs. 19 %) (Zhou *et al.* 2007), and white-headed langurs spend significantly more time inactive in the wet season compared to the dry season (84 % vs. 67 %) (Huang *et al.* 2003). This is most likely due to the poorer quality foods available in the dry season (more nutritious young leaves are more common in the wet season than the dry season: Workman 2010a), when langurs use fallback foods such as mature leaves (Hu 2007; Li and Rogers 2006; Workman 2010a; Zhou *et al.* 2009). Conversely, in the wet summer season, when more preferred foods are available than in the dry season, François' and white-headed langurs rest more (53–84 % wet season vs. 40–67 % dry season), with François' langurs also grooming more at this time (3 % wet season vs. 2 % dry season) (Huang *et al.* 2003; Yang *et al.* 2007; Zhou *et al.* 2007, 2010).

Cat Ba langurs eat more leaves in the dry season than in the wet season, suggesting that they are falling back on the use of leaves when other items are less available. The pattern of increasing activity levels (including foraging and traveling) in the dry season, and reducing resting time (including inactivity and socializing), is considered an energy-maximizing strategy. Cat Ba langurs, and several other limestone langurs (Huang *et al.* 2000, 2003; Yang *et al.* 2007; Zhou *et al.* 2007, 2010), can therefore be considered energy maximizers.

Conclusion

Cat Ba langurs had activity and dietary budgets similar to closely related species living on limestone karst throughout Southeast Asia and southern China. As we predicted, the majority of their day was spent inactive and foraging, with relatively little social time. Cat Ba langurs had a high rate of social behavior compared to other limestone langurs, possibly due to the high percentage of immature individuals in one of the groups (which serve as an attractant for transfers of young and interactions among adult females). Alternatively, this may be due to the variable definitions of "social" behavior across studies. Their diet was predominantly leaves, but other foods played an important role throughout the year, including relatively high rates of flower consumption. Groups showed significant differences in activity patterns due to differences in demographic makeup, and in diet, likely due to differences in home range quality. To accommodate the presumed drop in preferred, valuable resources in the dry season,

activity and dietary budgets change for Cat Ba langurs, as we had predicted. The monkeys fall back on a higher rate of leaf eating and foraging in general in the dry season than the wet season, at the expense of inactivity and social time. This qualifies this species as energy maximizers.

Obtaining information on the activity and dietary budgets of species affected by habitat change can allow us to better determine how these threats are impacting behavior and ecology, with implications for long-term survival. This information can, in turn, be used to improve conservation planning. As Cat Ba langurs have activity budgets similar to those of other limestone langurs, this suggests that, although they may be negatively affected by anthropogenically altered habitats, their behaviors are not drastically different from those of animals living in similar circumstances, i.e., they are not putting excessive energy into traveling or feeding compared to other animals in similar habitats. Similarly, Cat Ba langurs respond to seasonal reductions in preferred food availability like other limestone langurs, by exerting more energy, i.e., increasing foraging and activity and decreasing socializing, into finding less preferred foods, i.e., leaves, in the dry season compared to the wet season. Thus, the Cat Ba langur activity and dietary budgets are similar to those of other limestone langurs living in highly fragmented habitats, suggesting they are not more energetically stressed than these other Endangered and Critically Endangered species.

However, there are no limestone langurs living in pristine habitat, so a comparison to their "natural" state is not possible. Nonetheless, monitoring of activity and dietary budgets helps to document the effects of humans on nonhuman primates, and we hope that this study can serve as a baseline for future assessment of how human disturbance affects this Critically Endangered species.

Compliance with Ethical Standards

Conflict of Interest   The authors declare they have no conflicts of interest.

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