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Research

Cold and hungry: combined effects of low temperature and resource scarcity on an edge-of-range temperate primate, the golden snub-nosed monkey

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Both biotic and abiotic factors play important roles in influencing ecological distributions and niche limits. Where biotic and abiotic stressors co-occur in space and time, homeostatic systems face a scenario in which stressors can compound to impose a challenge that is greater than the sum of the separate factors. We studied the homeostatic strategies of the golden snub-nosed monkey *Rhinopithecus roxellana*, a species living in temperate deciduous forests at the edge of the global distribution range for folivorous primates, to cope with the co-occurrence of cold temperatures and resource scarcity during winter. We discovered that in winter the monkeys experience a dietary energy deficit of $101\,kJ\,mbm^{-1}\,d^{-1}$ compared with calculated needs, despite increased feeding. This is partly offset by behavioral changes (reduced locomotion and increased resting) and reducing skin temperature by an average of 3.2°C through a cutaneous vasoconstriction to decrease heat loss. However, their major strategy is ingesting surplus energy and accumulating fat reserves when food was not limiting during summer and autumn. Their 14% of body mass lost over the winter represented an energy yield of $102\,kJ\,mbm^{-1}\,d^{-1}$, which closely matched the calculated winter energy deficit of $101\,kJ\,mbm^{-1}\,d^{-1}$. However, the latter value assumes that all the $75.41\,kJ\,mbm^{-1}\,d^{-1}$ of protein ingested in winter was available for energy metabolism. This is almost certainly an over-estimate, suggesting that the study population was in negative energy balance over the study period. Our study therefore suggests that despite its suit of integrated homeostatic responses, the confluence of low temperatures and resource limitation during winter places this edge-of-range primate close the threshold of what is energetically viable. It also provides a framework for quantitative models predicting the vulnerability of temperate primates to global change.

Keywords: cold stress, energy intake and expenditure, geographic distribution, niche limits, temperate-living primate, thermoregulation

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Introduction

Understanding the factors that influence geographic ranges is a central aim in ecology, and has become more urgent by the need to forecast responses to accelerating global change (Rosenzweig 1995, Humphries et al. 2002, Sexton et al. 2009). This information is needed to understand biotic and abiotic dimensions of niches, particularly at range edges where climate change will have the most impact (Waldvogel et al. 2020). While many studies have examined these issues, two critical factors remain surprisingly under researched. First, are the ways that biotic and abiotic factors interact to influence the persistence of populations at the edge of the species range (Sexton et al. 2009). Such interactions are important because they can synergistically amplify environmental constraints experienced by animals, for example the effects of temperature on susceptibility to parasites and pathogens (Briers 2003, Péron et al. 2016, Bruns et al. 2018). The second critical factor is the dynamic homeostatic responses that animals employ to deal with habitat constraints. These are fundamental because homeostatic limits determine the tolerance ranges (Raubenheimer et al. 2012) and niche breadth (Machovsky-Capuska et al. 2016) of animals.

Cold is a prominent limiting factor in the distribution of animals. Not only is it a pronounced and widespread abiotic challenge for many species (Franks et al. 1990, Williams et al. 2015), but it also profoundly affects the ecological communities within which species interact (Garcia et al. 2019). Ambient temperature change thus simultaneously presents direct thermoregulatory challenges for animals and imposes biotic stresses via, for example, its impact on food availability (Hou et al. 2018). In such cases, either thermoregulatory capacity or food availability can define a species niche limits, or the interaction of the two could be the critical factor. This would be the case, for example, if the species could tolerate ambient temperatures, and could tolerate the level of resource scarcity imposed by prolonged cold periods, but could not tolerate diminished resources when cold demanded increased energetic expenditure for maintaining normothermia.

The ability of species to occupy a specific niche is often determined by seasonal energetic bottlenecks (Root 1988, Weiner 1992), especially the energetic constraints of winter (Humphries et al. 2002). Several thermoregulatory strategies have been identified in cold-adapted homeotherms, including autonomic and behavioral responses (Stocks et al. 2004, Terrien 2011). These responses do not act in isolation, but are integrated into an overall thermoregulatory strategy – for example, balancing energy acquisition and expenditure within a specific thermal environment (Satinoff 1996, Terrien 2011). The energy demands to maintain thermal homeostasis is inevitably elevated when ambient temperature differs from the thermoneutral zone. When cold, animals typically need extra energy and increase energy intake to support an elevated heat production and/or decrease energy expenditure to reduce heat loss (Arnold et al. 2006, Wang et al. 2006, Davenport 2012). Animals often decrease energy expenditure by altering

their behavior (e.g. basking, sheltering, huddling, torpor or hibernation) (Dausmann et al. 2004, Hanya et al. 2007, Grueter et al. 2013, Brinkmann et al. 2014, McFarland et al. 2015, Sukhchuluun et al. 2018), or use autonomic response to reduce thermal loss via convection and radiation (e.g. secondary to a reduced skin temperature by triggering cutaneous vasoconstriction) (Schmid and Speakman 2000, Arnold et al. 2006) or burn stored fat for thermogenesis (Kurita et al. 2002).

The golden snub-nosed monkey *Rhinopithecus roxellana* is an ideal species for examining integrated homeostatic responses to cold and resource stresses. As a primate, this species belongs to a taxon in which over 94% of extant members are tropical and are unable to tolerate extreme cold (Wiederholt and Post 2009). Among the approximately 30 primate species (mainly macaques and colobines) that live in temperate regions (Estrada et al. 2017), golden snub-nosed monkeys face a particularly acute combination of thermal and resource stresses. It is the third most northerly-distributed primate. However, the other two species, *Macaca fuscata* and *Macaca mulatta*, are dietary generalists and have the advantage of switching between seasonally abundant resources, which is not the case for golden snub-nosed monkeys. The rhesus macaque *Macaca mullata*, for example, predominately eats abundant seeds in autumn and winter and leaves in spring and summer (Cui et al. 2019). In contrast, the largely folivorous golden snub-nosed monkey (Hou et al. 2018) faces more acute dietary challenges during seasons when leaves are not abundant, particularly in winter when energy demands for thermoregulation are high (Guo et al. 2018).

Guo et al. (2018) documented that golden snub-nosed monkeys can compensate quantitatively for the extra energy costs of winter thermoregulation, by specifically increasing the intake of non-protein calories by a magnitude that closely matched the seasonal difference in energy requirements for thermoregulation. However, in that study the ecological context was manipulated by providing a surplus of provisioned foods to control for nutrient availability across seasons. That manipulation enabled the authors to demonstrate a remarkable, nutrient-specific, regulatory capacity, but it did not establish how that trait interacts with nutritional stresses encountered in an ecological context where the winter cost of thermoregulation cannot be offset using supplementary foods, which are the conditions to which the animals must typically respond. Measuring such interactions, while challenging to achieve, provides valuable information linking physiology and behavior to population processes such as the geographic distributions of species (Goldstein and Pinshow 2006).

The present study was designed to examine the combined responses to cold and seasonal food resource scarcity in a population of golden snub-nosed monkeys at the northernmost edge of the species range. For standardization with Guo et al. (2018), we studied a population that was supplemented, but minimally so, to an extent we calculated would leave a significant resource deficit in winter. We used a nutritionally

explicit, quantitative approach, in which resource income was partitioned into its different macronutritional components (Raubenheimer et al. 2009) and matched this with estimates of seasonal energy expenditure using year-round focal observation in a free-ranging population. In this way, we could construct quantitative energy budgets and examine the strategies used by golden snub-nosed monkeys to persist at the edge of their range in conditions combining extreme cold with energy shortages. Our hope is that this study will not only help to understand the factors that limit the geographical range for an endangered species, and for the primates, but more generally illustrate the importance of ecological synergies for understanding and predicting species distributions.

Material and methods

Study site

Our study was conducted in Zhouzhi National Nature Reserve on the northern slope of the Qinling Mountains, which is the northernmost edge of *R. roxellana*'s range (107°45′–108°18′E, 33°42′–33°54′N, 56.39 km²). The area is 90.5% forest, primarily deciduous broadleaf, mixed deciduous broadleaf and conifer forests (Li and He 2007). Our focal group (GNG group) has been studied since the 1999 and uses 2250 ha that covers an elevational gradient from 1380 to 2974 m (Li et al. 2000). There were 12–14 one male with multi-female units and an all-male band (24–36 individuals), totaling 146–159 individuals.

Even though our aim was to examine the nutritional budget of *R. roxellana* in a situation where resource scarcity coincided with high energy demand, we nonetheless provided a low level of supplementary foods (30 g freshly sliced radish and 60 g dry corn per individual per day) in April and May and between October and December (Hou et al. 2018). This maintained a provisioning cycle they had experienced since 2001, albeit at a reduced level, avoiding a situation where an abrupt change affected the behavior and observability of the monkeys. So doing helped ensure that our results are comparable to the earlier study Guo et al. (2018), which were similarly provisioned but to a higher level.

We used a meteorological monitoring system (CR200X, USA) located at 1600 m to record the temperature in the group's core area. The China Meteorological Administration (C.M.A. 2012) views the winter as starting when the daily average temperature (DAT) is below 10°C for 5 d and ends on the first day the DAT exceed or equal 10°C for 5 d. Similarly, the summer is defined as starting when the DAT exceeds 22°C for 5 d and ends on the first day the DAT is equal to or less 22°C for 5 d. The in between periods are spring and autumn. Over the last seven years (May 2011–April 2018) winter lasted 163.8 ± 6.8 d (M ± SD, mainly from middle October to March). The average daily temperature in winter was 2.4 ± 0.6°C (range from −15.8 to 13.6°C). The monthly average minimum temperature was below 0°C from late November to early March (totally 113 d, Fig. 1).
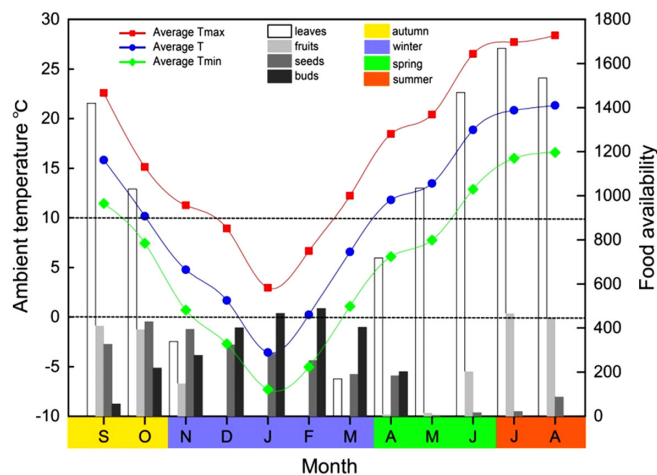

Figure 1. Food availability and ambient temperature across seasons. Lines indicate average maximum, average minimum and average temperature in Zhouzhi National Nature Reserve, China. The bars indicate the monthly availability of food items for *Rhinopithecus roxellana*.

We selected 25 food species that previous research indicated were frequently eaten (constituting 88.7% of the overall diet (Hou et al. 2018)) and recorded the abundance of leaves, fruits, seeds and buds on a scale of 0–4. We calculated a seasonal food availability index (FAI) by multiplying this phenology score (mean score of three months) by the density of each species (number of stem ha⁻¹; Fig. 1) and summed this score across species.

Behavioural data

We collected feeding data for one year (September 2014–August 2015) for adult males, lactating females, non-lactating females and juveniles. Golden snub-nosed monkeys are strictly seasonal breeders that reproduce every second year. Females conceive in autumn (1–2 months after the peak of food availability), gestating during winter and giving birth from mid-March to May (2–4 months before the peak of the food availability) (Xiang et al. 2017). Each day one individual was followed from dawn to dark. We collected 80 full-day follows (10.14 ± 0.04 h d⁻¹, M ± SE), including 20 d per season, and 5 d for each of the four categories of individuals per season. For each feeding bout, we recorded plant species, part (e.g. leaf with petiole or not, bark with periderm or not), and start–stop time. In general, we defined a feeding patch as a single tree or liana (woody vines that twine the trees); however, when animals fed on fallen oak seeds, an important food items from late autumn to early spring, the area below the canopy was regarded as a food patch.

We used Shannon–Wiener diversity index (H') to characterize the diversity of food items eaten each season (Krebs 1989) using the top 20 food species each season, based on the proportion of consumption time. We quantified the time allocation of individuals to different activities to determine activity budgets. The activities considered were feeding,

moving, resting and other activities. We determine daily path length (DPL) only of adults, as juveniles were not identified individually. We are able to be within 3–10 m of focal adults when they were feeding, resting and moving, which facilitated individual recognition and permitted accurate estimation of location with the GPS (Garmin, GPSMAP 63SC, Garmin, USA).

Body mass and temperature

All the monkeys are fully habituated, which enabled us to take thermal images from a distance of 3 to 5 m. To determine if animals lost body mass over the winter, we weighed individually recognizable animals with a platform scale (accuracy, 0.02 kg; EM-60KAL, A&D, Japan, Fig. 2a) over two weeks shortly after the start of winter (early December; Fig. 1) and in two weeks shortly after the start of spring (in early April). We lured the monkeys onto the platform of the scale using a small amount of corn, enabling us to record their body mass. We were unable to individually recognize juveniles, so the same juvenile may have been weighed more than once. We collected 188 body weights (adult males, n = 40; adult females, n = 80; juveniles, n = 68) with the two sampling periods having equal sample sizes. We estimated the energy value of decreased fatty tissues by multiplying the body mass loss by 37 kJ g^{-1} (energetic conversion factor for fat). It is difficult to measure animal's internal temperature in the wild, so we used a thermal infrared imager (FLIR T640, USA) to assess monkeys' facial skin temperature (T_{fs}) (Fig. 2b). We measured T_{fs} from recognizable adults from a distance of about 2 m in mid-December (winter) and mid-April (spring), respectively. To avoid any potential bias of T_{fs} due to the time of day and differences in activity levels, we measured the monkeys' T_{fs} from 10:00 am to 12:00 pm when monkeys were resting and inactive. Samples were taken once a day for a two-week period per season. Temperature data were assessed using FLIR R&D analysis software using only high-quality images (front view and near-distance).

Diet

We used the standard techniques to collect the food samples (Rothman et al. 2012), and analyze the foods nutrients and calculate the energy values (van Soest 1994), as used in our previous studies (Guo et al. 2018, Hou et al. 2018).

Total non-structural carbohydrates (TNC) was calculated by subtracting protein, lipids, NDF and ash from total dry mass (Rothman et al. 2012). Non-protein energy (NPE) was calculated using the summation of TNC, NDF and lipids. Daily energy intake (DEI) was calculated through summation of all foods eaten during a day. To standardise the difference among different age–sex classes, we divided our calculated results by the individual's metabolic body mass (mbm = M$^{0.762}$, where M is body mass in kg (Nagy 1994)). Body mass for age/sex classes was based on average measurement for adult individuals and juveniles in winter and spring and we used the averaged body mass in spring and winter to represent the body mass in summer and autumn.

Energy expenditure

We evaluated energy budgets using two different indices: average daily metabolic need (ADMN) and daily energy expenditure (DEE). ADMN had been used by DaSilva (1992) to estimate the energy budget of *Colobus polykomos* (see also Wasserman and Chapman 2003). DEE was evaluated following the regression equation recommended by Pontzer et al. (2014), who formulated the relationship between DEE (using the doubly labelled water technique) and body mass for 17 primate species and derived the following equation:

$$y = 0.69x + 2.09, \; r^2 = 0.97$$

where y indicates $\log_{10}$DEE (kcal d^{-1}), x indicates $\log_{10}$ body mass (kg). We did not distinguish body weight difference between lactating and non-lactating female.

The primates used by Pontzer et al. (2014) occupy tropical and subtropical regions, so we calculated the DEE only for warm seasons (spring, summer and autumn). For temperature-living primates, the DEE in winter (DEEW) should take into account the additional daily energetic costs of thermoregulation (ADECT) and baseline DEE (calculated from the above equation). The difference value of the ADECT between winter and spring was measured as 329 kJ mbm^{-1} (Guo et al. 2018).
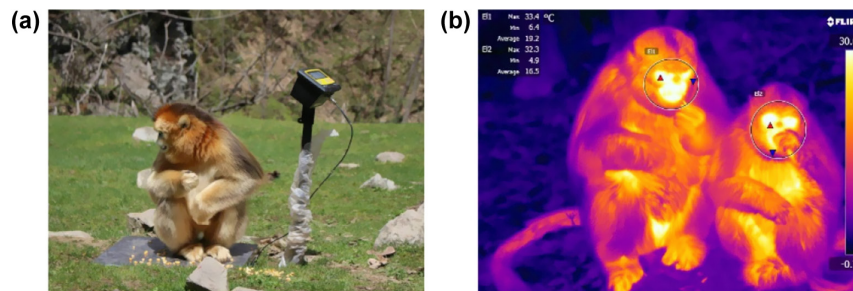

Figure 2. The measuring methods of body mass (a) and facial skin temperature (b) in site for *R. roxellana* in Zhouzhi National Nature Reserve, China. In (b), the red triangle and blue inverted triangle indicate the maximum temperature and minimum temperature of the circle area, respectively; in addition, we would also measure the average temperature of the circle area.

Average daily metabolic need (ADMN) was estimated using the follow equation:

$$ADMN = \left[\frac{130 \times W^{0.762}}{24} \times S + \frac{BMR \times 0.238846}{24} \times (24 - S) + T \times d \times W \right] \times 4.1868$$

where W = body mass (kg), S = number of active hours each day, T = travel costs $(kcal\,kg^{-1}\,km^{-1}) = 0.1(10)^{1.67 \times W^{-0.126}}$, d = daily path length, DPL (km), we used seasonal average DPL to represent d, Basal Metabolic Rate (BMR) was estimated by the following equation: $BMR = 70 \times 4.1868\,kJ\,kcal \times body\,mass^{0.762}$. The ADMN values calculated through the above equation are used in warm seasons (spring, summer and autumn), while the ADMN in winter (ADMNW) should take the additional daily energetic costs of thermoregulation ($329\,kJ\,mbm^{-1}$) and baseline ADMN in winter (calculated from above equation) into account.

We considered the energetic costs of pregnancy and lactation for females when calculating ADMN and DEE. The costs of pregnancy and lactation individuals have been considered to increase energy expenditure, so, we multiply 1.25 and 1.5 in calculating the ADMN and DEE, respectively (Vogel et al. 2017).

Statistical analyses

Kruskal–Wallis H tests with Steel–Dwass post-hoc comparisons were used to test for seasonal differences in activity budgets, daily path length, number of feeding patches visited by focal animals per day, daily energy expenditure (DEE), daily metabolic need (ADMN) among different categories of individuals, and daily macronutrients and energy intake. One-way ANOVA with Bonferroni correction for multiple post-hoc pairwise comparison was used to compare different categories of individuals with respect to seasonal difference in DEE, ADMN, and the intake of dry matter, macronutrient and energy. Differences in body mass loss and facial skin temperature between winter and spring were evaluated with t-tests. We used one-sample Kolmogorov–Smirnov test to evaluate normality of all data sets. Steel–Dwass test was run in R ver. 3.6.1, while other tests were performed in SPSS V21.0. The significance level was set at $\alpha = 0.05$.

Results

Macronutrient and energy intake

As we anticipated, in this study supplementary foods contributed substantially less to the daily diet than in the study of Guo et al. (2018). In winter, they provided $89.8\,kJ\,mbm^{-1}\,d^{-1}$ (versus $505.4\,kJ\,mbm^{-1}\,d^{-1}$ in the previous study) and in spring $36.2\,kJ\,mbm^{-1}\,d^{-1}$ (versus $160.4\,kJ\,mbm^{-1}\,d^{-1}$). Across the whole study period, this averaged out at 10.6% of energy intake, compared with 56.2% in the previous study.

There were seasonal differences in daily intakes of dry matter ($H = 12.672$, df = 3, p = 0.005), daily energy intake (DEI) ($H = 10.319$, p = 0.016), and all measured dietary constituents, except protein (Table 1). More dry matter was consumed in autumn ($58.6\,g\,mbm^{-1}$) and winter ($54.1\,g\,mbm^{-1}$), than spring and summer (38.2 and $43.3\,g\,mbm^{-1}$ (p < 0.05). DEI in spring was significantly lower than the other three seasons (p < 0.01, Table 1). Non-protein energy intake was lower in the spring compared to other seasons (p < 0.01), being highest in autumn. Monkeys consumed two-fold more TNC in autumn and winter than spring and summer (p < 0.01), but there was no difference between autumn and winter (p = 0.823). Carbohydrates contribution to dietary energy exceeded 70% in spring, autumn and winter. Fat contribution was lower than 10% in these seasons, while in summer, carbohydrates contributed 48% of daily energy and fat provided 38% of the energy in daily diet (Fig. 3). In addition,

Table 1. Seasonal comparisons of dry matters ($g\,mbm^{-1}$) and macronutrients intakes ($kJ\,mbm^{-1}$) for *Rhinopithecus roxellana* inhabiting in Zhouzhi National Nature Reserve, China. The overall comparison was tested with Kruskal–Wallis H test, Steel–Dwass test were used to compare the difference among four seasons. p-value less than 0.05 were highlighted in bold.

		DM	CP	Lipids	NDF	TNC	NPE	DEI
Overall	Statistic	12.672	4.161	40.454	14.150	34.377	12.922	10.319
	p-value	**0.005**	0.245	**0.000**	**0.003**	**0.000**	**0.005**	**0.016**
Sp versus Su	Statistic	1.447	1.163	5.383	1.731	3.246	3.489	3.165
	p-value	0.470	0.650	**0.000**	0.307	**0.006**	**0.003**	**0.008**
Sp versus Au	Statistic	3.895	1.568	2.911	3.489	4.409	4.166	3.896
	p-value	**0.000**	0.396	**0.018**	**0.003**	**0.000**	**0.000**	**0.000**
Sp versus Wi	Statistic	3.976	1.407	1.000	3.922	4.382	4.274	3.868
	p-value	**0.000**	0.495	0.749	**0.000**	**0.000**	**0.000**	**0.000**
Su versus Au	Statistic	3.327	0.568	5.194	1.866	5.302	2.083	1.866
	p-value	**0.005**	0.396	**0.000**	0.243	**0.000**	0.159	0.243
Su versus Wi	Statistic	3.057	3.030	5.410	2.407	5.329	1.948	1.055
	p-value	**0.012**	**0.013**	**0.000**	0.076	**0.000**	0.208	0.717
Au versus Wi	Statistic	1.055	3.300	2.921	0.839	0.866	0.771	1.163
	p-value	0.717	**0.005**	**0.018**	0.836	0.823	0.868	0.650

Sp, spring; Su, summer; Au, autumn; Wi, winter; DM, dry matter; CP, crude protein; NDF, neutral detergent fiber; TNC, total non-structural carbohydrates; NPE, non-protein energy; DEI, daily energy intake.
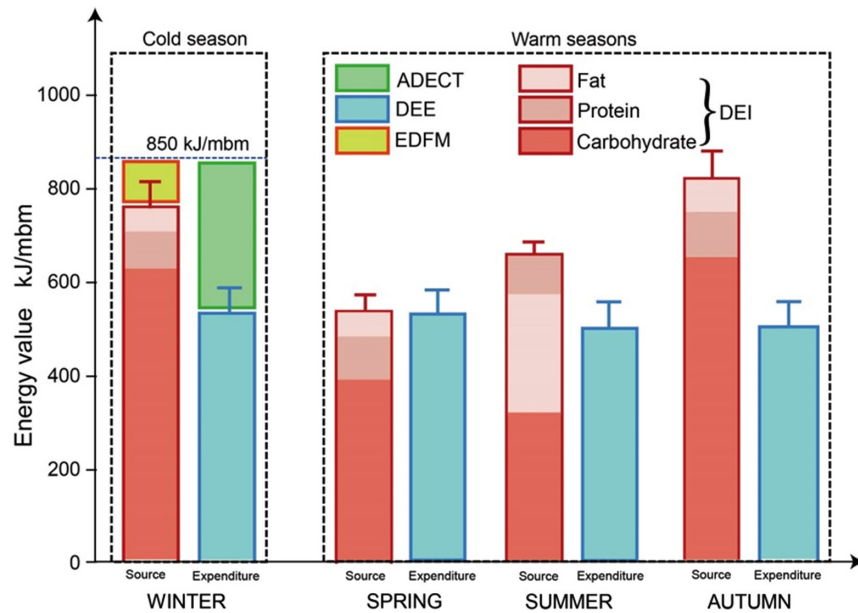
Figure 3. Energy budgets of *Rhinopithecus roxellana* in cold (winter) and warm (spring, summer and autumn) seasons at Zhouzhi National Nature Reserve. In cold season, the source energy [daily energy intake (DEI, M ± SE) + energy drawn from fat metabolism (EDFM), 850 kJ mbm^{-1}] is almost identical to the expenditure energy [baseline daily energy expenditure (DEE) + additional daily energetic costs of thermoregulation (ADECT), 849 kJ mbm^{-1}]. In the warm season, the ADECT and EDFM are substantially lower and negligible, but the animals increase DEI to deposit the surplus energy as fatty tissue to fund thermoregulation in winter. DEI was divided into carbohydrate, protein and fat to compare the contribution among three main macronutrients.

there were no significant difference (p > 0.05) in energy intake (kJ mbm^{-1}) among different age–sex classes.

Energy expenditure

There were no differences among the warm seasons (spring, summer and autumn) in either average daily metabolic need (ADMN, 427 kJ mbm^{-1}, one-way ANOVA, $F_{(2,57)}$ = 0.555, p = 0.577), or daily energy expenditure (DEE, 506 kJ mbm^{-1}, one-way ANOVA, $F_{(2,57)}$ = 0.610, p = 0.547). However, the energy expenditure in winter was appreciably higher (ADMNW, 757 kJ mbm^{-1} and DEEW, 849 kJ mbm^{-1}) than in warm seasons once the baseline ADMN and DEE value in winter (428 kJ mbm^{-1} and 520 kJ mbm^{-1}, respectively) were combined with additional daily energetic costs of thermoregulation (329 kJ mbm^{-1}, Fig. 3). There was no difference (p > 0.05) in energy expenditure among adult males, non-lactating females and juveniles. However, energy expenditure of lactating females was significantly higher (p < 0.05) than the other three age/sex classes.

The overall ADMN and DEE accounted for 75.21 ± 5.39% and 87.23 ± 6.11% of DEI (M ± SE). The surplus energy (difference value between DEI and ADMN or between DEI and DEE) were much higher in autumn (399 kJ mbm^{-1} and 326 kJ mbm^{-1}, respectively, Fig. 3) and summer (229 kJ mbm^{-1} and 154 kJ mbm^{-1}, respectively), compared to the spring (87 kJ mbm^{-1} (DEI–ADMN) and 4 kJ mbm^{-1} (DEI–DEE)). Whereas, the difference value between DEI and ADMN, and between DEI and DEE were lowest (−9 kJ mbm^{-1} and −101 kJ mbm^{-1}, respectively) in

winter. These comparisons suggest that the monkeys accumulated surplus energy in summer and autumn and faced an energy deficit in winter.

Body mass and temperature

The body mass of adults was higher shortly after winter started compared to shortly after the start of the spring (2.46 kg loss in adult males and 1.31 kg loss in adult females; t = 2.432, df = 118, p = 0.017; Fig. 4a). Males and females showed similar declines (14%), of which pregnant and lactating females lost 12% and 15% of body mass, respectively. In contrast, juvenile's body mass did not differ between seasons (t = 0.737, df = 66, p = 0.464).

Facial skin temperature (T_{fs}) in winter was lower (32.01 ± 0.21°C, M ± SE) than in the spring (t = −12.362, df = 114, p < 0.001; 35.17 ± 0.14°C, Fig. 4b). There was no difference in facial skin temperature between males and females in the winter (t = 1.863, df = 67, p = 0.067) or spring (t = 1.486, df = 67, p = 0.142).

Integrated energy budget

Adults lost 14% of body mass over the winter, most likely principally from fatty tissue (Garcia et al. 2011). The lost energy was 90 872 and 48 498 kJ, for males and females respectively. The interval between when body mass was evaluated was 92 d (from 15 December to 17 March), thus the monkeys lost on average 988 kJ (males) and 527 kJ (females) per day. If these results are weighted by the average adult metabolic body mass
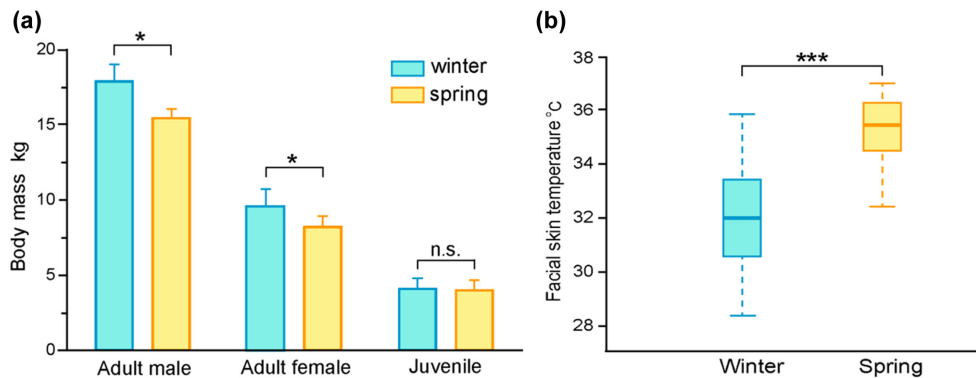
Figure 4. (a) Body mass (kg, M ± SD) of individuals from different age–sex classes of *Rhinopithecus roxellana* inhabiting in Zhouzhi National Nature Reserve, China between winter and spring. AM, adult male; AF, adult female; J, juvenile. Juvenile's body mass was not significantly different between these two periods; (b). Facial skin temperature (T_{fs}) of *Rhinopithecus roxellana* in Zhouzhi between winter and spring. Animals' T_{fs} in winter is 3°C lower than it in spring. The resulting p values are indicated as follows: n.s., p > 0.05; * p < 0.05; *** p < 0.001.

in winter (9.03 of males and 5.60 of females), then the energy drawn from fat metabolism (EDFM) is $102 \, kJ \, mbm^{-1} \, d^{-1}$ during the 92 d. This value was almost identical to the difference ($101 \, kJ \, mbm^{-1}$) between daily energy expenditure (DEEW) and daily energy intake (DEI) in winter (please see the equation in Fig. 3).

Behavioural responses

Besides using energetic and physiological strategies to cope with a cold resource–scarce environment, the golden snub-nosed monkeys implemented various behavioral strategies. The time spent feeding, moving and resting differed among the seasons (feeding, $H = 28.26$, df = 3, p < 0.001; moving, $H = 34.48$, p < 0.001; resting, $H = 12.66$, df = 3, p = 0.005), but other behaviours did not ($H = 1.914$, df = 3, p = 0.590). The animals spent more time feeding ($25.49 \pm 1.07\%$) in winter and autumn ($21.16 \pm 0.41\%$) compared to the other seasons (p < 0.05). Time spent moving in spring ($17.86 \pm 0.86\%$) and summer ($17.05 \pm 0.63\%$) was higher than the other seasons (p < 0.01), with winter being lowest ($9.32 \pm 0.72\%$; Fig. 5a). Monkeys on average spent $56.46 \pm 0.01\%$ resting, but it was lowest in the spring ($53.09 \pm 0.81\%$) and highest in winter ($58.17 \pm 1.06\%$). Daily path length varied seasonally ($H = 11.069$, df = 3, p = 0.011, 20 samples, 5 adults in 5 d per season, Fig. 5b) and was shortest in the winter ($1.70 \pm 0.12 \, km$) and longest in summer ($2.73 \pm 0.14 \, km$; Fig. 5b).

The number of feeding patches visited by focal animals per day varied among seasons (Kruskal–Wallis H test, $H = 39.703$, p < 0.001; Fig. 5c). The number of feeding patches visited in the autumn and winter was higher than the other seasons (p < 0.01) and was highest in autumn (23.10 ± 1.22, M ± SE) and lowest in summer (14.95 ± 0.52), but there was no significant difference between autumn and winter (t = 1.473, p = 0.454).

Leaves dominated (56.3%) the diet in the spring, summer and autumn. The food diversity was higher in the winter ($H' = 2.74$) when the animals mainly ate buds (31.04% of

diet) and bark (50.40% of diet). The dietary diversity was less in the summer ($H' = 2.33$), when monkeys consumed mostly fruits (37.91%) and leaves (59.51%). In autumn, the animals ate oak acorns (*Quercus*; 16.36% of diet), while leaf consumption decreased to 50.90%. At this time the dietary diversity (H') was 2.50. In spring the group's diet was dominated by young leaves (62.8% of diet) and the H' value was 2.67.

Discussion

Our study has quantified how the regulatory systems of a cold-adapted primate at the edge of its range are integrated to cope with the simultaneous challenges of extreme cold and resource scarcity. Such integration is key to understanding how species cope with the congruence of biotic and abiotic challenges that shape their niche space and geographic distributions at broad and fine scales (Sexton et al. 2009, Lewis et al. 2017). This will be important to understand and predict how species ranges will shift in the face of climate change and where the species will not be able to survive.

As we anticipated, our data demonstrate that during the cold winter *R. roxellana* required more energy than could be obtained from foraging. The monkeys showed several behavioral changes that could help compensate for this winter energy deficit. They increased feeding time, albeit on nutrient poor foods such as bark, moved less and rested more than in warmer seasons. Decreased movement and increased resting would both save energy and increase the effectiveness of thermoregulation through huddling and adopting postures that minimize convective and radiant heat loss (Terrien 2011, Parsons 2015). Additionally, reduced skin temperature of approximately 3°C can be partly attributed to a strong cold-induced cutaneous vasoconstriction to decrease dry heat loss.

However, the major strategy to offset the winter energy deficit was through ingesting excess fats and carbohydrates when sufficient food was available and storing the energy as fat for later use. The 14% winter decrease in body mass
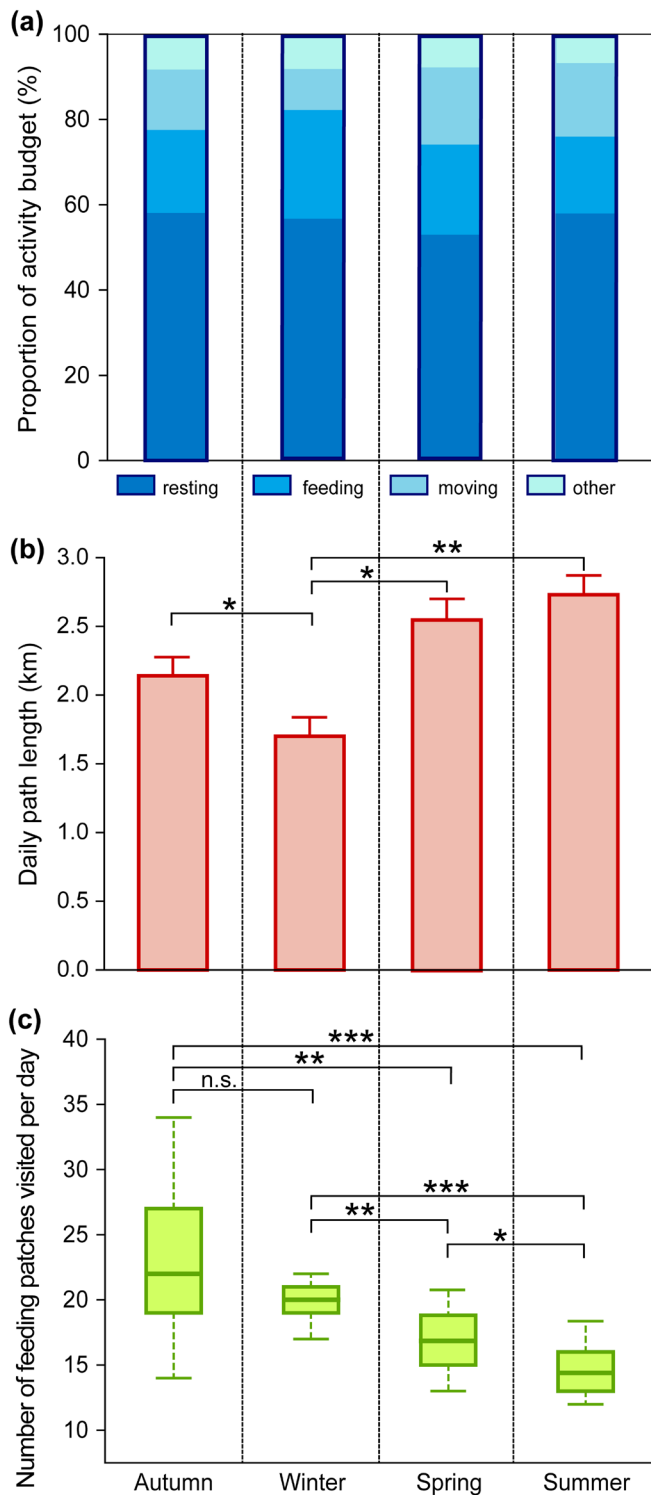
Figure 5. Seasonally behavioural strategies implemented by *Rhinopithecus roxellana* inhabiting in Zhouzhi National Nature Reserve, China, based on day long focal individual follows, including (a) Activity budget (time proportion). (b) Daily path length. (c) Number of feeding patches visited per day. The resulting p values are indicated as follows: n.s., $p > 0.05$; * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$.

we recorded is very likely from the loss of adipose tissues, as the average daily caloric value of losing fat ($102\,\text{kJ\,mbm}^{-1}$) matched the difference between daily energy expenditure and daily energy intake in winter ($101\,\text{kJ\,mbm}^{-1}$). This close match between the energy that could be obtained by burning stored fat and winter energy deficiency, suggests that adipose tissues play a critical role in regulating the seasonal energy budget of our study population. In contrast, the body mass of juveniles did not change during winter and their energy intake was higher than expenditure even with the additional daily energetic costs of thermoregulation in the winter. Equivalent use of fat stores has seldom been demonstrated for primates, even though it is widespread among temperate and polar birds and mammals (Witter and Cuthill 1993, Gosler 1996, Garcia et al. 2010).

Among the few cases documented for primates, *Macaca fuscata*, the northern-most non-human primate, consume high quality foods (fruits/seeds) to deposit fat (Hanya et al. 2006), increasing energy intake two to five times in autumn to survive the severe conditions of winter (Nakayama et al. 1999, Kurita et al. 2002). For *R. roxellana*, we found the daily energy intake (DEI) was higher than expenditure (including ADMN and DEE) through both summer and autumn, suggesting that this end of range population accumulated fat much earlier (5–6 months) than other primates (3–4 months).

Only a very few tropical primates have been documented to be adapted to prolonged energy shortages with fat stores accumulated previously. Fat-tailed dwarf lemur *Cheirogaleus medius* eat high-sugar fruits and deposit fat and double their mass before the dry-cold season, and then they hibernate for seven months to reduce energy expenditure (Fietz and Ganzhorn 1999, Dausmann et al. 2004). Orangutans increase daily caloric intake by entering positive energy balance when carbohydrate-rich fruits are abundantly available and subsist on stored energy and fallback foods when fruit is scarce (Knott 1998).

There are, however, important differences in the fat storage strategies of temperate and tropical primates. Rather than the predictable seasonal changes characteristic of temperate habitats, orangutans experience marked fluctuations in energy availability due to their reliance on masting species that intermittently produce abundant fruit crops. Furthermore, the strategy of temperate primates is demand-driven, in the sense that an abiotically-induced stress, cold temperatures, places additional energy demands on the animals that need to be subsided from energy abundant seasons. In orangutans, entering positive energy balance during mast periods is an opportunistic strategy for insuring against subsequent periods of resource shortage, not specifically to meet environmentally induced increases in energy demand (Knott 1998, Vogel et al. 2017). Indeed, for orangutans the reverse is true. High fruit abundance increases the likelihood of reproduction (Vogel et al. 2017), and in this sense increased food availability drives increased demand rather than increased demand for thermoregulation driving an increased energy requirement.

Those differences aside, the fat storage capabilities of tropical primates suggest that their employment and elaboration for use in temperate habitats was not a large evolutionary step.

Implications of our findings for understanding and predicting the ecological distribution of primates in temperate regions are significant. In general, the primary winter foods (lichens, acorns, buds and bark) of temperate-living primates contain high concentrations of carbohydrate (Hanya et al. 2011, Cui et al. 2018, Hou et al. 2018). The fact that *R. roxellana* specifically targets carbohydrates and fats to fuel energy metabolism (Guo et al. 2018), suggests that availability of carbohydrate- and fat-rich foods during winter plays an important role in determining the distributions of primates in temperate climates. However, as we show for *R. roxellana*, necessary as they may be, winter sources of carbohydrates and fat are not sufficient to meet the energetic requirements of at least some temperate primates. *Macaca fuscata* relies on abundant energy-rich foods during autumn to accumulate fat (Hanya et al. 2006), and the *R. roxellana* population in our study required the same to be true in both summer and autumn. The same appears to be true also of the population of *R. bieti* living on the Tibetan Plateau (northern-most range of that species) (Xiang et al. 2007). At altitude > 3500 m, and temperatures as low as −15°C, climatologically this is the harshest environment inhabited by any non-human primate. For this population carbohydrate-rich lichens are a major component of the diet throughout the year, and in winter these are supplemented with energy-rich acorns (Xiang et al. 2007).

The second northernmost primate species, the rhesus macaque *Macaca mulatta*, has an interesting capacity that eases the requirement for carbohydrate and fat-rich foods. Cui et al. (2018) showed that this species can subsist at high latitudes despite substantial variation in the availability of their primary source of dietary carbohydrates and fats, acorns. Their pattern of macronutrient regulation combined with their reproductive performance (Cui et al. 2020) suggests that they do this through a well-developed capacity to use protein as a source of energy (gluconeogenesis) when non-protein energy is scarce. That such metabolic flexibility (Smith et al. 2018) is predicted to be associated with ecological generalism (Simpson et al. 2002, Raubenheimer and Simpson 2003) is interesting, because *M. mulatta* is not a specialized temperate species, as is *R. roxellana*, but is an ecological generalist with a range spanning temperate and subtropical latitudes (Fooden 2000).

An important question concerns the extent to which *R. roxellana* can use protein as an energy substrate. Our measurements suggest that across the year the energy ingested by the study population equals energy expenditure. This, however, concerns total energy, including fats, carbohydrates and protein, and the conclusion that the energy budget balances rests on the assumption that all three macronutrients are used to fuel energy metabolism. Given that gluconeogenesis is likely a universal capability (Miyamoto and Amrein 2017) that has evolved to buffer animals during periods of energy restriction (Zhang et al. 2019), it is almost certain that *R. roxellana* does

use protein in energy metabolism. However, the fact that, unlike *M. mullata*, our study population did not increase the intake of protein during periods when fats and carbohydrates are scarce, suggests that *R. roxellana* has a lower capacity than *M. mullata* for gluconeogenesis (Cui et al. 2018).

It is most likely, therefore, that *R. roxellana* can use ingested protein (75.41 kJ mbm^{-1} d^{-1} in winter) in energy metabolism, but to a limited extent, suggesting that our study population was in negative energy balance during the period we studied them. This might have been partly offset by energetic savings due to behavioral changes discussed above, which our measurements did not have the resolution to capture. However, considering that 10.6% of the energy ingested during the study period derived from supplementary foods, these calculations suggest that our study population exists right at the edge of what is possible calorically, and energy constraint is likely an important factor limiting their distribution.

Our results have exposed many important questions around the role of diet and energetics as a range-limiting factor in *R. roxellana* and primates more generally. Studies on the capacity of this species to use protein as a source of energy would help to reveal the metabolic flexibility this species has to buffer against inter-annual variation in resource availability and ambient temperatures. Relatedly, ecological research examining the actual extent and projected future changes in annual variation in temperature and resources will enable predictions to be made of future range changes and local extinctions of *R. roxellana*. More broadly, similar studies of other species would help to explain the factors that enabled a small number of primates to become established in cold temperate habitats, when the majority is restricted to warm tropical habitats.

With climate change altering many aspects of seasonal variability, there is an urgent need to understand the factors that limit the distributions of species and their capacities to adapt to change (Zelazowski et al. 2011, IPCC 2014, Chapman et al. 2019). The mechanism of adaptation to environment change, especially for the organisms living at the edge of the species range, will determine the ability of species to persist in the face of global climate change (Williams et al. 2015, 2017). When climate change forces animals into new harsh environments, animals must use new integrated strategies. They may have to forage on resources they are unaccustomed to, but that have the nutrients to meet their physiological need, or develop new behaviours, while reducing or abandoning others. The adaptive plasticity allowing edge-of-range animals to survive in their native habitats must be understood if informed conservation actions are to be taken. This is because populations often cannot move to more suitable habitats as these habitats have either been destroyed through human actions or are inaccessible (Burrows et al. 2014). The approach we have taken here modeling the combined impacts of biotic and abiotic stressors in a context that is nutritionally explicit, can provide novel insights to evaluate and predict species geographic distribution and niche evolution in the light of climate change.

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