



RESEARCH ARTICLE

The geometry of resource constraint: An empirical study of the golden snub-nosed monkey

Rong Hou^{1,2} | Colin A. Chapman^{1,2,3,4} | Jessica M. Rothman⁵ | He Zhang¹ | Kang Huang¹ | Songtao Guo¹ | Baoguo Li^{1,6} | David Raubenheimer⁷

¹Shaanxi Key Laboratory for Animal Conservation, College of Life Sciences, Northwest University, Xi'an, China; ²Department of Anthropology, McGill University, Montreal, QC, Canada; ³Department of Anthropology, Center for the Advanced Study of Human Paleobiology, The George Washington University, Washington, DC, USA; ⁴School of Life Sciences, University of KwaZulu-Natal, Pietermaritzburg, South Africa; ⁵Department of Anthropology, Hunter College of the City University of New York, New York, NY, USA; ⁶CAS Center for Excellence in Animal Evolution and Genetics, Chinese Academy of Sciences, Kunming, China and ⁷Charles Perkins Centre and School of Life and Environmental Sciences, The University of Sydney, Sydney, NSW, Australia

Correspondence

Baoguo Li
Email: baoguoli@nwu.edu.cn

Songtao Guo
Email: songtaoguo@nwu.edu.cn

Funding information

Strategic Priority Research Program of the Chinese Academy of Sciences, Grant/Award Number: XDB31020302; National Key Programme of Research and Development; Ministry of Science and Technology, Grant/Award Number: 2016YFC0503200; National Nature Science Foundation of China, Grant/Award Number: 31870396, 31672301 and 31872247; Natural Science Foundation of Shaanxi Province in China, Grant/Award Number: 2018JC-022

Handling Editor: Audrey Dussutour

Abstract

1. Apposite conceptualization and measurement of resource variation is critical for understanding many issues in ecology, including ecological niches, persistence and distribution of populations, the structure of communities and population resilience to perturbations.
2. We apply the nutritional geometry framework to conceptualize and quantify the responses of a temperate-living primate, the golden snub-nosed monkey *Rhinopithecus roxellana* to variation in resource quality and quantity and in nutrient requirements associated with seasonal environments.
3. We present a geometric model distinguishing qualitative constraint, quantitative constraint and 'pseudo-constraint' whereby nutrient intakes resemble response to qualitative resource constraint but are in fact driven by variation in nutrient requirements. The model is applied to analyse nutrient intakes recorded in 164 full-day observations of monkeys from two populations, one wild and the other captive, across seasons. Additionally, we recorded the diet of a single animal over 32 consecutive days in the wild.
4. Despite considerable differences in available resources, the captive and wild populations showed marked similarities in nutrient intakes, including indistinguishable amounts and ratios of ingested macronutrients during summer and autumn and strong year-round maintenance of protein compared to seasonally variable fat and carbohydrate intakes. These similarities suggest homeostatically regulated nutritional targets and provide reference points to identify factors driving population differences in macronutrient intake in winter and spring.
5. Our framework enabled us to distinguish examples of quantitative, qualitative and 'pseudo-constraint'. We suggest that this approach can increase the resolution at which resource constraint is conceptualized and measured in ecological studies.

KEYWORDS

nutritional geometry, protein prioritization, pseudo-constraint, quantity and quality, resource constraint

1 | INTRODUCTION

How organisms respond to resource variability is central to many aspects of ecology (Owen-Smith, 2008; Prins & van Langevelde, 2008), including the breadth and nature of niches (Machovsky-Capuska et al., 2016), persistence and distribution of populations and the structure (Raubenheimer et al., 2009) and robustness of communities to perturbations (Parepa et al., 2013). Core to understanding these relationships is the way that resource variation is conceptualized, defined and measured. A substantial body of research has demonstrated that this is a complex issue. In particular, many consumer traits, including behaviour, physiology, life history and demography are best understood and predicted using approaches that distinguish quantitative from qualitative resource variation, that measure resource quality in a multi-nutrient context, and that distinguish resource variation from variation in animals' nutrient requirements (Raubenheimer et al., 2015; Simpson & Raubenheimer, 2012).

A tool that implements this approach to understand the strategies animals use to respond to resource variability is nutritional geometry (Raubenheimer et al., 2009). By conceptualizing these interactions in a multi-dimensional nutritional context and using measures of the animal's homeostatic responses to identify how these responses weight different nutritional dimensions, nutritional geometry provides a framework for categorizing and measuring resource constraints (Raubenheimer et al., 2016; Figure 1). Much of the work applying nutritional geometry is tightly controlled laboratory studies that factor out confounds and enable causal analysis of the responses of animals to systematic variation in resources, often using chemically defined foods (reviewed in Simpson & Raubenheimer, 2012). Such studies have provided fresh insights into many basic and applied challenges, including the links between diet, ageing and reproduction (Jang & Lee, 2018; Solon-Biet et al., 2015), host-gut microbiome interactions (Holmes et al., 2017), mechanisms of appetite regulation (Gosby et al., 2016), dietary causes of human obesity (Gosby et al., 2014, 2016) and the optimization of animal feeds (Hewson-Hughes et al., 2011; Ruohonen et al., 2007).

Several studies have attempted to incorporate nutritional geometry into ecological theory and its application. These include examinations of constraints on food webs (Raubenheimer et al., 2009; Wilder et al., 2013), trait-based models of community structure (Simpson et al., 2010), niche theory (Behmer & Joern, 2008; Kearney et al., 2010; Machovsky-Capuska, Senior, et al., 2016), conservation ecology (Birnie-Gauvin et al., 2017; Raubenheimer & Simpson, 2006; Raubenheimer et al., 2012), invasion ecology (Krabbe et al., 2019; Shik & Dussutour, 2020), foraging theory (Bressendorff & Toft, 2011; Raubenheimer & Simpson, 2018), urban ecology (Coogan et al., 2018) and models predicting human-wildlife conflict (Coogan & Raubenheimer, 2016). A recent modelling study demonstrated that explicitly distinguishing resource quantity and quality in a multi-dimensional context can yield counter-intuitive insights. For example, the impact on consumers of food quality can be reversed by changes in food quantity (Burian et al., 2020). Critical for advancing ecological theory

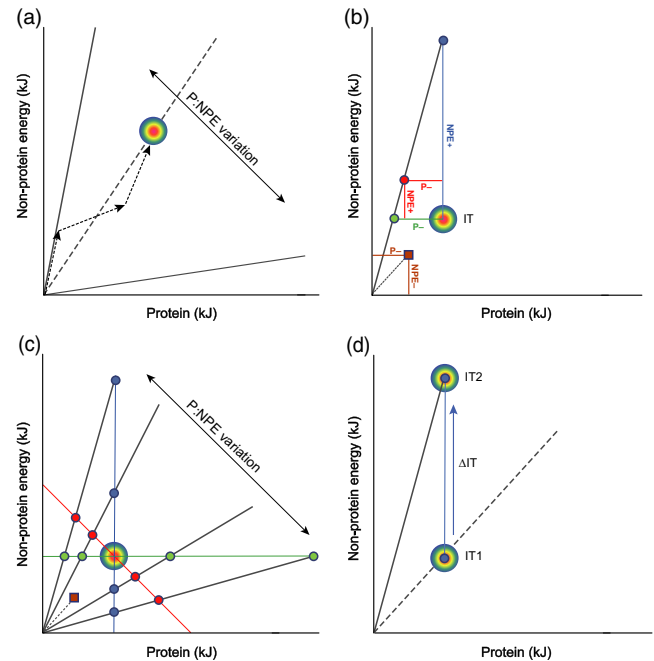


FIGURE 1 Geometric model of homeostatic responses to variation in the protein:non-protein energy ratios of resources. The large circle represents the nutrient intake selected by the animal when unconstrained ('intake target, IT'). Foods are represented as lines projecting from the origin at an angle determined by the balance of the nutrients they contain ('nutritional rails'). (a) The animal can achieve its intake target by eating a balanced food (dashed rail) or combining its intake from two or more imbalanced but nutritionally complementary foods (dashed arrows). (b) Qualitative and quantitative resource constraint. In qualitative constraint, the animal is restricted to a diet that is imbalanced with respect to the intake target (circles) and is thus forced into a trade-off between over-ingesting one nutrient (e.g. NPE+ represents surplus ingested non-protein energy) and under-ingesting another (e.g. P- represents a protein shortage). Green, red and blue circles show different patterns of response to the same qualitative constraint. All three patterns have been observed in primates in the wild. Blue: protein intake is kept constant [P prioritization (e.g. spider monkeys *Ateles chamek*, Felton, Felton, Raubenheimer, et al., 2009)]; green: NPE is prioritized (e.g. mountain gorillas *Gorilla beringei*, Rothman et al., 2011); red: the deficit of one nutrient matches the excess of the other (P- = NPE+) so total energy intake is kept constant (e.g. rhesus macaques *Macaca mulatta* (Cui et al., 2018)). The square is an example of quantitative constraint, in which intake is limited by the amount of the food that can be acquired and processed and thus suffers a shortage of both nutrients (as indicated by the truncated nutritional rail). (c) Patterns of intake diagnostic of the responses in (b). (d) Example where changes in the position of the intake target (ΔIT) resemble a pattern generated by qualitative constraint (i.e. pseudo constraint), in this case protein prioritization (blue circles in c)

and its applications, are empirical studies that quantify how animal homeostatic systems interact with multi-dimensional resource variability in realistic ecological settings.

Many detailed field studies of feeding regulation have involved primates, partly because they habituate easily, making them amenable to prolonged and detailed feeding observations. Encouragingly,

several field studies of primates have recorded responses to multi-dimensional resource variation like those observed in laboratory experiments of other taxa. These include intake patterns that suggest regulation to a specific amount and balance of macronutrients, termed an 'intake target' (Cui et al., 2018; Felton, Felton, Raubenheimer, et al., 2009; Irwin et al., 2015; Johnson et al., 2013; Rothman et al., 2011; Figure 1a). Intake targets provide a homeostasis-defined metric of nutrient requirements, and thus an objective reference point for identifying resource constraint and measuring how animals respond to it (Raubenheimer & Simpson, 1997). Several such responses to variation in macronutrient availability have been reported for wild primates (Figure 1), but considerable challenges remain for interpreting the drivers of these responses and their implications for ecology.

The challenges arise from the complexity of ecological environments and the difficulties of establishing causality from field observation. A fundamental issue is distinguishing variation in feeding that is due to ecological constraints that prevent animals from achieving their intake target from variation in what the animal is targeting in its feeding, driven by specific changes in nutrient requirements. The latter is not a constraint at all but in field studies can easily be misinterpreted as such and can thus be considered a form of 'pseudo-constraint' (Figure 1). For example, an increase in the proportion of protein-rich foods such as young leaves or insects in the diets of primates might either be enforced by a shortage of fat- and carbohydrate-rich foods (Cui et al., 2018), or reflect increased protein requirements, e.g. due to lactation (Tirado Herrera & Heymann, 2004).

Another challenge of field studies is to partition the roles of qualitative and quantitative constraint to understand the ways that animals respond to each category. Qualitative, quantitative and pseudo constraints can readily be distinguished in laboratory-based studies using nutritional geometry (Raubenheimer et al., 2016), but as yet have not been partitioned in the wild for any species. Achieving this would be an important step in understanding how animals respond to resource variation in the wild and integrating the findings of geometric laboratory studies into theoretical and applied ecology.

In this study, we capitalized on the variation in resource quality and quantity and in nutrient requirements associated with seasonal environments to examine these relationships, using a temperate primate, the golden snub-nosed monkey *Rhinopithecus roxellana*. We used nutritional geometry to analyse 164 full-day focal animal feeding observations and compare nutritional regulatory responses of a minimally provisioned wild population subject to natural variation in resources with a captive population provided continuous access to a wide variety of wild-sourced and domesticated foods. Both populations were studied year-round, enabling us to compare regulatory responses across four seasons, which in the temperate habitat generated substantial variation in resource availability as well as nutritional demands for thermoregulation (Guo et al., 2018; Hou, Chapman, Jay, et al., 2020). At a finer scale, replicate animals were studied within each population and season, enabling us to examine variability between animals, while

controlling for season and population. At the finest scale, we followed one individual for 32 consecutive days to quantify within-animal responses to dietary variation over time. These multi-scale data enable us to disentangle qualitative quantitative and pseudo resource constraint in the natural context and elucidate how *R. roxellana* responds to each.

2 | MATERIALS AND METHODS

2.1 | Field data collection

This study was conducted in Zhouzhi National Nature Reserve (107°45'–108°18'E, 33°42'–33°54'N, 56.39 km²) on the northern slope of the Qinling Mountains, China, which is the northernmost edge of *R. roxellana*'s range (Hou et al., 2018). The area is 90.5% forest, primarily deciduous broadleaf, mixed deciduous broadleaf and conifer forests (Li & He, 2007). A meteorological monitoring system (CR200X) was used to record the air temperature in the group's core home range, and the standard classification recommended by the China Meteorological Administration (C.M.A., 2012) was used to define seasons. The average annual precipitation during past 8 years (2011–2018) was 605.9 ± 26.0 mm ($M \pm SD$) and temperature was 10.8 ± 0.4 °C, the lowest monthly temperature was -4.2 ± 1.3 °C in January and the highest monthly temperature was 27.5 ± 0.9 °C in July. All deciduous plants in this temperate forest lose their leaves by the middle of November and young leaves do not come out until middle April. Hence, the monkeys experience 5 months of extreme cold, combined with food shortage (Hou et al., 2018).

Our study group has been continuously studied since 2001. It uses 2,250 ha that covers an elevational gradient from 1,380 to 2,974 m (Li et al., 2000). During our study, the group had 146–159 individuals, including 12–14 one male with multi-female units (OMUs, comprise 48–56 adult females, nine sub-adult females, 38–43 Juveniles and 20–24 Infants) and an all-male band (24–36 individuals). All the monkeys are habituated to the presence of researchers and adults and juveniles are individually recognizable.

We collected feeding data from September 2014 to August 2015 and categorized it into four seasons: spring (April to June), summer (July to August), autumn (September to October) and winter (November to March). Each day one individual was followed from dawn to dusk. We collected 80 full-day follows (10.14 ± 0.04 hr/day, $M \pm SE$) of 66 monkeys, which included 20 days per season, and 5 days for each of the four age-sex classes (adult male, lactating female, non-lactating female and juvenile). During the full-day follow, we recorded the amount of time feeding and the plant species and part consumed (e.g. leaf with petiole or not, bark with periderm or not) using predefined food units (e.g. a fruit, seed, bud, leaf or 1 cm of bark and twig) that were appropriate for how the monkeys usually ate that food item (Hou et al., 2018). Simultaneously, we counted the number of leaves, flowers, fruits, seeds or buds ingested during each feeding bout. We also recorded the length and circumference of the

branch the monkey was eating from. We calibrated predefined units (e.g. 500 leaf, seeds, buds and ten branches 10 cm long) every month. Within the food trees, we collected sample foods from the branches with the same characteristics. To estimate grams of food intake, we weighed the predefined units three times after oven drying at 45°C.

Food availability was determined by sampling 32 plots (50 m × 50 m) in the group's core area and quantifying the composition of the available vegetation. Subsequently, for the 25 most frequently eaten food species [determined in a previous study to comprise 88.7% of the overall diet (Hou et al., 2018)], we selected 10 individual trees and each month recorded the abundance of four main plant parts (leaves, fruits, seeds and buds) on a scale of 0–4. The food availability index (FAI) was then calculated each month by multiplying the phenology score by the density of tree species (number of stem/ha).

To quantify within-animal responses to dietary variation over time, we collected all day (10.40 ± 0.12 hr/day) feeding data on a 9.2 kg non-lactating female (named Chanel) for 32 consecutive days from 21 April to 22 May 2016. For each plant part eaten samples were collected from at least 10 different plants within 2 days of the observed feeding bout (Rothman et al., 2012), to account for intra-specific variability (Chapman et al., 2003). Because of the high dietary diversity, we did not sample rarely eaten foods that were in low density (<0.5% of feeding time). We weighed food samples within 3 hr of collection and dried to a constant weight (45°C), packed and sealed the samples for chemical analysis in Northwest University, Xi'an, China.

2.2 | Data collection from captive animals

From October 2017 to September 2018 we collected feeding data from *R. roxellana* at the Shaanxi Wild Animal Rescue and Research Center, China (108°32'E, 32°06'N). The centre is located in the northern slope of Qinling Mountains and is approximately 35 km northwest of the field station. We observed eight adults (four males and four females) consuming captive diets; all four females gave birth in April 2018. The captive animal's diet included two natural evergreen plants (including leaves, twigs and bark), and supplementary foods, including apple, carrot, cucumber, eggplant, soy bean, sunflower seeds, corn, peanut, milk powder, boiled egg and bread. We collected 84 full-day follows (10.42 ± 0.06 hr/day) in the spring ($N = 20$ days), summer ($N = 23$), autumn ($N = 21$) and winter ($N = 20$).

2.3 | Laboratory methods

We milled the collected samples sieved through a 1-mm screen using a Baijie mill (BJ-750A). We used Kjeldahl method (BUCHI, K-360) to estimate nitrogen content; crude protein was calculated by multiplying nitrogen content by 6.25 (AOAC, 1990). Fat was analysed using a ST-310 Extraction Unit, FOSS, Sweden, using petroleum ether as extract (Rothman et al., 2012). All fibre fractions [neutral detergent

fibre (NDF), acid detergent fibre, acid detergent lignin] were measured and sequentially analysed via an automatic fibre analyser (A2000i, ANKOM; van Soest et al., 1991). The plant samples were burned in a muffle furnace for 3.5 hr at 550°C to obtain ash content (Rothman et al., 2012). All nutrients were expressed as proportions of dry mass.

Total non-structural carbohydrates (TNC) was calculated by subtracting crude protein, fat, NDF and ash from total dry mass (Rothman et al., 2012). We estimated the metabolizable energy of food using the summation of the calories in crude protein, fat, total non-structural carbohydrate and NDF with conversion factors of 17 kJ/g for CP, 37 kJ/g for fat and 16 kJ/g for TNC (Conklin-Brittain et al., 2006). The energy value of NDF were estimated using a previously published NDF digestibility coefficient of 74.3% (Huang, 2014). We used a conversion factor of 9 kJ/g [(16–4) × 0.743 kJ/g] for NDF (Hou et al., 2018). Non-protein energy (NPE) was calculated using the summation of the energetic contributions from TNC, NDF and fat. To compare macronutrients and energy intake among four 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. Specifically, we weighed animals with a platform scale (EM-60KAL, A&D) and lured the monkeys onto the platform with a small amount of corn (Hou, Chapman, Jay, et al., 2020). We do not have the body mass data of captive monkeys, so we used the weight per size class from data collected for the wild monkeys.

2.4 | Data analysis

Except where otherwise stated, all analyses were performed using R, version 4.0.0 (The R Foundation for Statistical Computing: <http://www.r-project.org>). We reported parametric data as $M \pm SE$ unless otherwise stated. We used linear mixed models (LMMs) to test the effects of environment (wild, captive), season and their interaction (coded as fixed factors) on protein, NPE, total energy intake and ratio of fat to TNC. LMM was also used to make comparisons of seasonal and overall proportions of protein, carbohydrate (the combination of TNC and NDF) and fat between wild and captive populations. In both cases, population was set as fixed factor, and individual as random factor. Proportion data were logit transformed, and count data were square-root-transformed. LMMs were performed with 'lmer' function in the package `LMERTEST`. The statistical significance ($p \leq 0.05$) of fixed factors was assessed with 'ANOVA' function (Pinheiro & Bates, 2000).

Power regression (IBM SPSS Statistics v. 25) was used to test for protein prioritization (Hall, 2019; Raubenheimer & Simpson, 2019). This approach is based on the fact that to maintain a constant absolute intake of protein (P) when the P:NPE ratio of the diet (p) varies, Pp^L calories of energy must be eaten.

If the exponent (L) takes a value of -1 , this indicates complete protein prioritization (absolute protein intake remains constant and energy intake increases with decreasing P:NPE ratio). Where $-1 < L < 0$, there is partial protein prioritization (i.e. absolute P intake decreases with decreasing P:NPE, but to a lesser extent than energy intake increases) and $L = 0$ indicates no relationship. L values smaller than -1 indicate an influence of factors other than P:NPE ratio on the variance in energy intake, for example a scarcity of high protein foods in the environment. Positive values of L indicate that energy intake is positively associated with dietary P:NPE ratio (Raubenheimer & Simpson, 2019).

3 | RESULTS

3.1 | Temperature and food availability

Zhouzhi National Nature Reserve has a distinctly seasonal climate, with a shorter summer and autumn (about 60 days each) and a prolonged winter (153 days). The highest temperature recorded during the study was 33.5°C, the monthly average minimum temperature was below 0°C from November to March, and the average daily temperature in winter was 2.0°C (range from -15.1 to 12.4°C; Figure 2a). The location of the captive monkeys was warmer than the field station, with the summer temperature reaching 36.1°C and the winter being shorter (118 days) and warmer (average 3.2°C, range -10.1 to 21.5°C) than the field site (Figure 2b).

The foods available to the monkeys in the Qinling Mountains varied markedly across seasons (Figure 2a), and so too did the diets. In spring, the main foods were young leaves, mature buds and fruits; in summer, mature leaves, and high-fat fruits; and in autumn, mature leaves, seeds (predominantly of *Quercus*), fruits and buds. By mid-November (early winter) the deciduous plants had shed their leaves, but *Quercus* seeds were still available on the ground although

the quantity and quality decreased with time and snowfall. Hence, bark and dormant buds were the main foods in the diet in winter, when leaves were scarce.

3.2 | Macronutrient compositions of foods and diets

There was appreciable seasonal variation in the regions of macronutrient space (i.e. the range of food compositions) accessible to the wild population, whereas that for the captive population varied little across seasons (Figure 3a-d). When aggregated across all seasons, the region of macronutrient space available to the wild population was wider than that available to the captive population (Figure 3e-f). Consequently, the region of macronutrient space that was accessible to wild monkeys throughout the year (pink region in Figure 3e) was appreciably smaller than that accessible to captive monkeys (yellow region in Figure 3f).

There were no significant difference in the proportions of protein, carbohydrate or fat in the annual diets of wild and captive monkeys (Table 1). There were, however, seasonal differences between them in the dietary proportions of all three macronutrients. The proportion of dietary energy contributed by protein was slightly higher in the wild ($17.55 \pm 0.71\%$) than the captive ($15.04 \pm 0.55\%$) population, whereas the opposite was true in winter (wild: $10.06 \pm 0.21\%$; captive: $11.48 \pm 0.36\%$). Dietary carbohydrate was higher for the captive population in summer (captive: $70.55 \pm 2.02\%$; wild: $47.59 \pm 2.16\%$), but in winter was higher in the wild ($82.43 \pm 0.27\%$) than in captivity ($77.74 \pm 1.51\%$). Fat showed the opposite trend to carbohydrate in summer, being higher for the wild ($38.87 \pm 2.30\%$) than the captive ($15.41 \pm 1.80\%$) population. There was also a suggestion that fat showed the opposite pattern to carbohydrate in winter, being higher for the captive ($10.79 \pm 1.45\%$) than the wild ($7.51 \pm 0.26\%$) population, but this narrowly missed statistical significance ($p = 0.051$, Table 1).

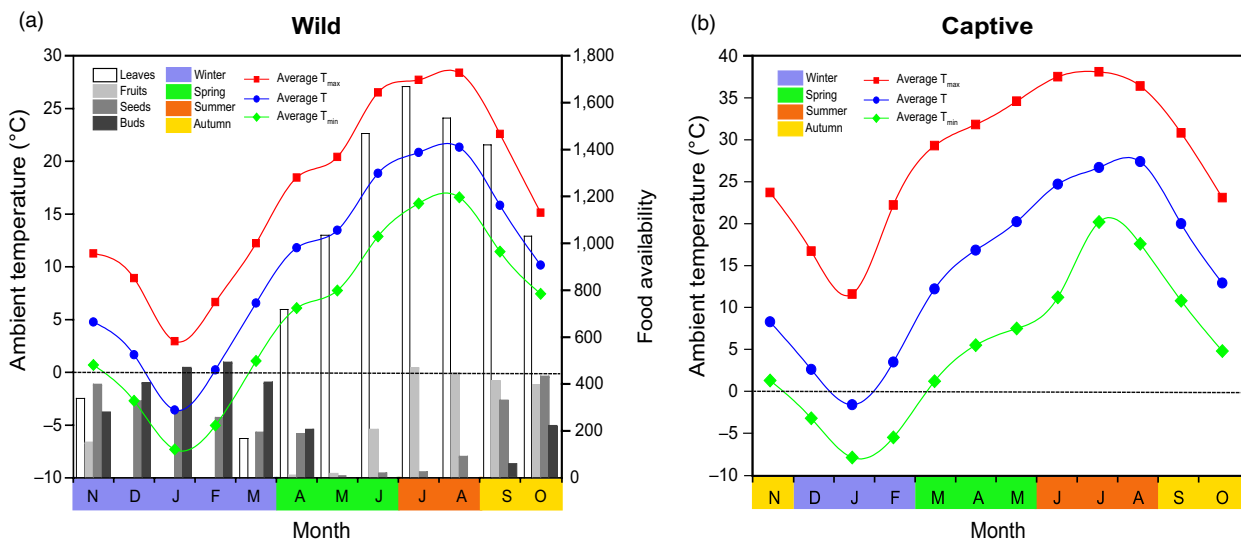


FIGURE 2 Monthly temperature and Food Availability Index for different types of foods for the wild population (a) and temperature at the centre that houses the captive population (b)

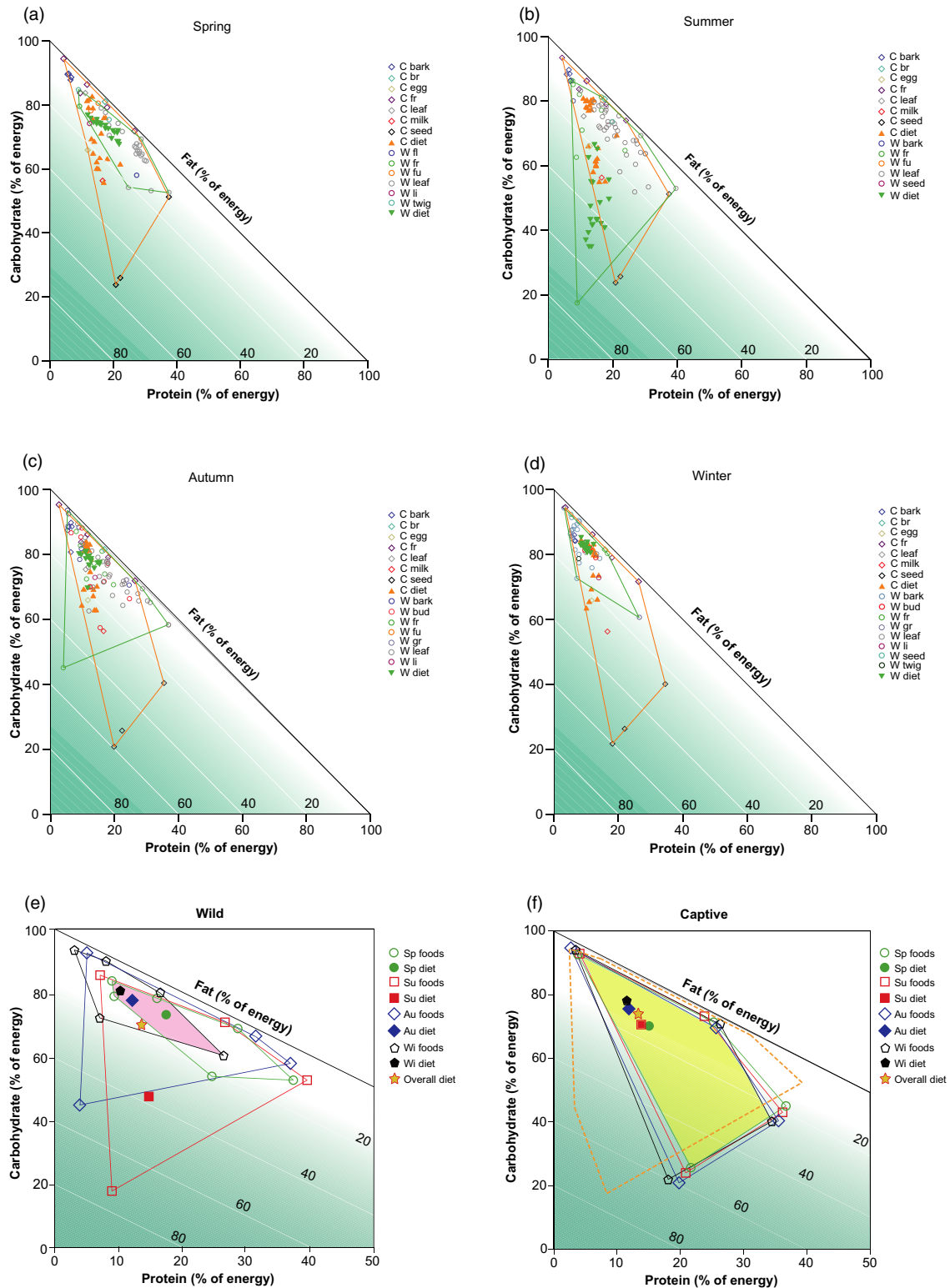


FIGURE 3 Right-angled mixture triangles (Raubenheimer, 2011) showing the region of macronutrient space (% protein, fat and carbohydrate by energy) accessible to different season [(a) spring, (b) summer, (c) autumn, (d) winter; C = captive, W = wild; br = bread, fl = flower, fr = fruit, fu = fungi, gr = grass, li = lichen] for the wild (a) and captive (b) populations (Sp = spring, Su = summer, Au = autumn, Wi = winter, open symbols = foods, closed symbols = diets). Since the three macronutrients sum to 100%, fat concentration increases across the negative diagonals (fat isolines) from light to dark blue. Accessible regions are delineated by the polygon connecting the available foods for each season. The regions delineated by green and orange lines in (a), (b), (c) and (d) represent the macronutrient space for wild and captive populations respectively. For direct comparison, the overall region of macronutrient space accessible to wild monkeys (e) is also shown in (f) as the dashed polygon. The pink (e) and yellow (f) regions show the area that was accessible to the wild and captive populations, respectively, year-round (i.e. the region of macronutrient space that is common among the seasons)

TABLE 1 Linear mixed models for the comparison of proportional compositions of seasonal and annual diets of wild and captive populations of *Rhinopithecus roxellana*

	Season	Wild versus Captive %	Sum Sq.	Mean Sq.	Num df	Den df	F-value	p-value
Protein %	Spring	17.55 ± 0.71 versus 15.04 ± 0.55	0.029	0.029	1	16.674	6.819	0.019
	Summer	14.54 ± 0.46 versus 14.04 ± 0.47	0.002	0.002	1	19.713	0.628	0.438
	Autumn	12.23 ± 0.37 versus 11.94 ± 0.28	0.0009	0.0009	1	39	0.310	0.581
	Winter	10.06 ± 0.21 versus 11.48 ± 0.36	0.007	0.007	1	22.84	5.58	0.027
	Overall	13.60 ± 0.39 versus 13.14 ± 0.26	0.001	0.001	1	86.71	0.363	0.549
Carbohydrate%	Spring	72.86 ± 0.57 versus 70.26 ± 1.90	0.004	0.004	1	38	2.407	0.129
	Summer	47.59 ± 2.16 versus 70.55 ± 2.02	0.161	0.161	1	14.947	44.81	<0.0001
	Autumn	78.27 ± 0.54 versus 75.75 ± 1.68	0.003	0.003	1	39	2.322	0.136
	Winter	82.43 ± 0.27 versus 77.74 ± 1.51	0.007	0.007	1	38	9.104	0.005
	Overall	70.29 ± 1.62 versus 73.47 ± 0.96	0.007	0.007	1	70.179	2.236	0.139
Fat%	Spring	9.58 ± 0.30 versus 14.80 ± 1.67	0.173	0.173	1	38	5.262	0.027
	Summer	38.87 ± 2.30 versus 15.41 ± 1.80	1.565	1.565	1	24.404	42.506	<0.0001
	Autumn	9.50 ± 0.55 versus 12.31 ± 1.56	0.030	0.030	1	39	0.825	0.369
	Winter	7.51 ± 0.26 versus 10.79 ± 1.45	0.109	0.109	1	38	4.096	0.051
	Overall	16.11 ± 1.53 versus 13.39 ± 0.83	0.036	0.036	1	68.135	0.546	0.463

TABLE 2 Linear mixed models for the comparison of protein, non-protein energy and total energy intake of wild and captive populations of *Rhinopithecus roxellana*

Response variable	Fixed factor	Sum Sq.	Mean Sq.	Num df	Den df	F-value	p-value
Non-protein energy	Population	23.613	23.613	1	91.352	9.195	0.003
	Season	148.289	49.430	3	91.346	19.247	<0.001
	Population × Season	30.872	10.291	3	91.346	4.007	0.001
Protein	Population	0.724	0.724	1	76.803	4.346	0.108
	Season	0.695	0.2315	3	79.778	0.405	0.750
	Population × Season	9.744	3.248	3	79.778	5.685	0.016
Total energy	Population	24.487	24.487	1	90.956	8.862	0.004
	Season	126.896	42.299	3	90.950	15.308	<0.0001
	Population × Season	35.248	11.749	3	90.950	4.2521	0.007

3.3 | Population and seasonal macronutrient and energy intakes

Over the year, the wild population had a significantly lower absolute intake of non-protein energy (NPE) than the captive population (wild:

595.50 ± 18.19 kJ/mbm vs. captive: 669.53 ± 22.35 kJ/mbm; population main effect in Table 2, Hou, Chapman, Rothman, et al., 2020). Season and season × population terms were also a significant, showing that NPE intake was higher in the captive population in winter and spring, but did not differ between the populations in summer and autumn (Table 2, Figure 4).

In contrast with NPE, neither population nor season were significant for protein intake (Table 2). There was, however, a significant population \times season interaction, demonstrating that protein intake was lower in the wild than in captivity during winter, but similar

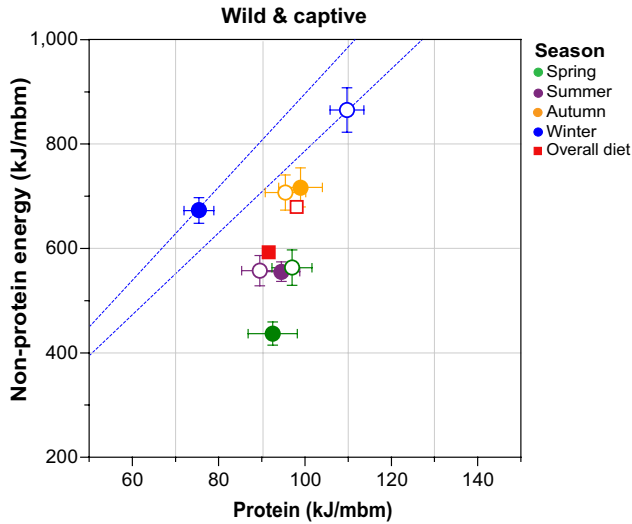


FIGURE 4 Seasonal patterns of macronutrient intake ($M \pm SE$) by the wild (filled circles) and captive (hollow circles) populations of golden snub-nosed monkeys. The red squares represent annual intakes of wild (filled) and captive (hollow) monkeys. The dashed blue lines show the dietary P:NPE ratios for the two populations in winter

between the populations in the spring, summer and autumn (Table 2, Figure 4).

For total energy intake, there were significant effects of population, season and a population \times season interaction. Since protein intake varied little between seasons and populations, the differences in total energy were driven largely by NPE intake.

3.4 | Within-season macronutrient and energy intakes

As was true for the comparison of populations and seasons, protein intakes were relatively invariant among observation days within seasons, whereas NPE intakes varied widely (Figure 5). This was the case for both the wild and captive populations, although the variance in protein intakes was larger for the wild (CV, 25.25%) than the captive (CV, 21.95%) animals. In contrast, the variance in NPE intakes was larger for captive (CV, 30.41%) than the wild (CV, 27.14%) monkeys.

For both the wild and captive populations, daily energy intakes across the year (in both cases $p < 0.0001$) fitted the model for protein prioritization (i.e. a power function of dietary percentage protein), with the exponent more strongly representing the theoretical value for complete protein prioritization ($L = -1$) in the captive population ($L = -1.038$) than the wild population ($L = -0.528$; Table 3). However, within individual seasons results for the wild and

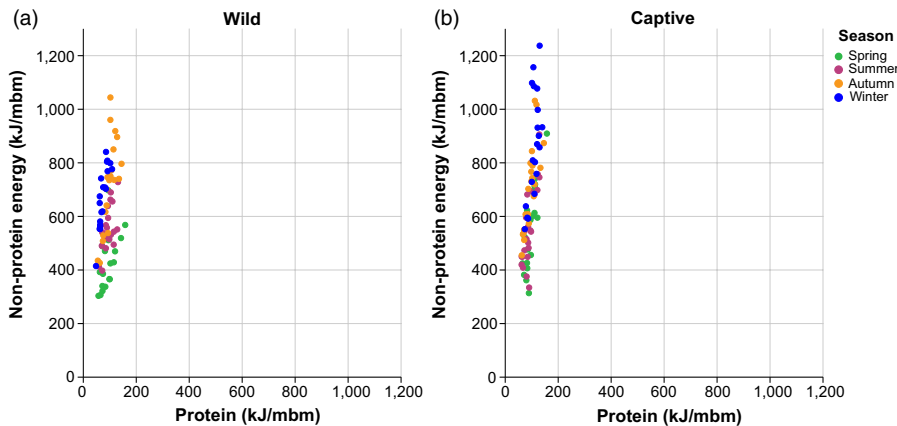


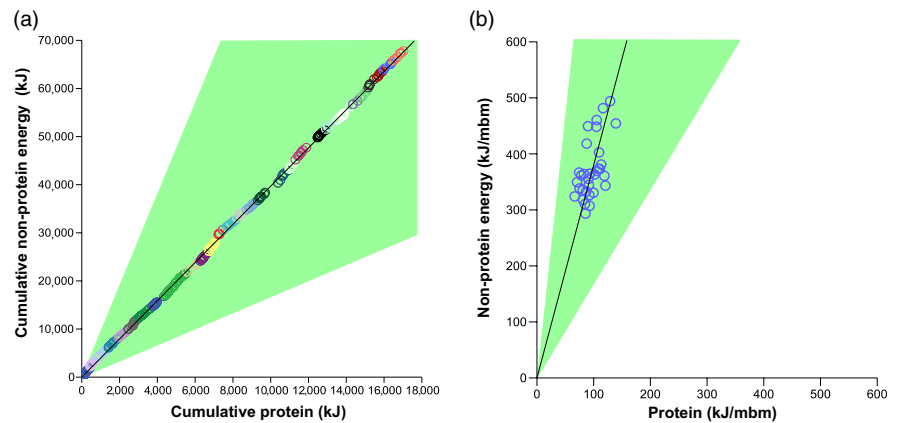
FIGURE 5 Patterns of macronutrient intakes by wild (a) and captive (b) golden snub-nosed monkeys. Each point represents the daily macronutrient intake of an individual monkey

TABLE 3 Exponent (L) and probabilities (p) from power regressions testing for protein prioritization in the wild, captive and long-follow monkeys at annual and seasonal time-scales. Complete protein prioritization (i.e. absolute protein intake remains constant and fat and carbohydrate vary with percentage protein in the diet) is indicated by an exponent of -1

Subjects	Year-round		Spring		Summer		Autumn		Winter	
	L	p	L	p	L	p	L	p	L	p
Wild	-0.528	<0.001	-0.178	0.527	0.046	0.865	-0.502	0.243	0.142	0.757
Captive	-1.038	<0.001	-1.037	0.004	-0.642	0.059	-0.322	0.502	-0.931	0.004
Individual			0.047	0.767						

Note: There were significant effects of population ($F = 7.77$, $p = 0.006$), season ($F = 56.32$, $p < 0.001$) and the interaction ($F = 32.13$, $p < 0.001$) on the dietary fat: TNC ratio of the monkeys in our study (Table 4). The ratio was higher for the captive population in all seasons except summer, when the ratio for the wild population (1.39 ± 0.13) was the highest observed in the entire study.

FIGURE 6 Cumulative (a) and daily (b) macronutrient intakes in the long-follow individual observed during spring in the wild. The green-shaded area shows the range of food compositions comprising the diet over 32 days. In (a), days are distinguished by colour and separate data points within days represent cumulative meals. The solid black line shows the P:NPE ratio of the cumulative diet over 32 days



captive populations differed. For the captive population, seasonal non-protein energy intakes significantly fitted the model in winter ($p < 0.004$, $L = -1.037$) and spring ($p < 0.004$, $L = -0.931$), but not in summer and autumn (Table 3). In the wild, the pattern of non-protein energy intake did not fit the protein prioritization model in any season, either in the population studies or across days in the long-follow individual (Table 3).

3.5 | Daily intakes and cumulative diet in the long-follow individual in the wild

The cumulative intake of the long-follow individual was tightly linear, aggregating over the 32-days to a dietary NPE:P ratio of 4.0:1 (19.5% energy from protein; Figure 6).

4 | DISCUSSION

As we anticipated, our study system encompassed substantial resource variation, across scales from gross differences in the food environments of the wild and captive monkeys, through seasonal differences in temperature and, for the wild population, resource quality and quantity, to daily variation in individual foraging. Nutritional geometry revealed interesting similarities and differences in macronutritional outcomes for the monkeys across this range of ecological situations. Given the markedly contrasting food environments of the two populations, the similarities between the populations attest to the strength of nutrient-specific regulatory biology in this species (Raubenheimer et al., 2015). The differences illuminate how this regulatory biology interacts with resource variability.

4.1 | Diet selection

Strikingly, the proportional macronutrient compositions of the annual diets of captive and wild monkeys did not differ, despite the very different foods from which these were compiled. Such situations, where diet compositions are maintained constant despite differences in

available food combinations, strongly suggest nutrient-specific homeostatic regulation to an intake target (Raubenheimer et al., 2015). While several studies, principally of insects, have demonstrated this in tightly controlled laboratory studies (reviewed in Simpson & Raubenheimer, 2012), few have documented it in the wild.

To establish target regulation, it is necessary to demonstrate that animals maintain constant nutrient balance when feeding on different food combinations, or else alter their nutrient intake to track specific changes in nutrient requirements (Simpson & Raubenheimer, 2012). Considering constant nutrient balance, Felton, Felton, Wood, et al. (2009) demonstrated that spider monkeys *Ateles chamek* target *Ficus boliviana* figs and when these are not available, they combine other foods in proportions that provide the same balance of macronutrients in the diet. Rothman et al. (2007) reported similar proportional macronutrient intakes for mountain gorillas *Gorilla beringei* inhabiting different forests and feeding on different food combinations in Bwindi and Virunga (see also (Raubenheimer et al., 2015)). Johnson et al. (2013) found that over 30 consecutive days a single baboon composed daily diets with similar macronutrient balance from different food combinations. Dunham and Rodriguez-Saona (2018) showed that female *Colobus angolensis* ingested a consistent ratio of macronutrients despite intergroup differences in the foods consumed.

It has seldom been demonstrated that diet selection in the wild specifically tracks changes in requirements for particular macronutrients. Many studies have shown that mammals increase energy intake during lactation (Cui et al., 2018; Douhard et al., 2016; Droscher et al., 2016; Speakman, 2008), and that they change their diet compositions with a shift to higher protein foods (Dias et al., 2011; Ruivo et al., 2017; Rydell, 1989; Tirado Herrera & Heymann, 2004); few, however, have demonstrated that they specifically select a diet with different macronutrient ratios than when not lactating. Guo et al. (2018) found for a different wild population of *R. roxellana* than this study that intake of fat and carbohydrate, which in primates are the principle macronutrients used in energy metabolism, increased during the cold winter compared with spring, by an amount that closely matched the seasonal difference in energetic requirements for thermoregulation, whereas protein intake remained unchanged. Taken together with this study, *R. roxellana* is thus the only species of which we are

aware for which target selection has been demonstrated both in the context of constant dietary balance across different environments (i.e. captive and wild), and shifts in intake that track specific changes in nutrient requirements.

4.2 | Response to constraint

Measures of intake targets provide a powerful reference point for interpreting how the nutrient-specific regulatory systems of animals respond to dietary constraints (Figure 1). Our data demonstrate that *R. roxellana* maintain protein intake within tight limits, while allowing non-protein energy to vary widely. This pattern, called 'protein prioritization' (Figure 1), has previously been recorded in several species in the wild, all of which are primates. Felton, Felton, Raubenheimer, et al. (2009) found that spider monkeys *Ateles chamek* observed across different phenological periods (seasons) in Bolivia maintained protein intake constant, while allowing NPE to vary with variation in the P:NPE ratio of the diet. The same pattern was observed in blue monkeys *Cercopithecus mitis* in Kenya (Takahashi et al., 2019), small-bodied lemurs *Lepilemur leucopus* in Madagascar (Droscher et al., 2016) and chimpanzees in Uganda (Uwimbimbazi et al., accepted).

Such measures of how absolute nutrient intakes vary with variation in dietary balance are important because they provide a measure of the breadth of specific dimensions of the nutritional niche of animals (Machovsky-Capuska, Senior, et al., 2016). The protein prioritization pattern, for example, indicates *R. roxellana* (and other species that show it) are protein specialists (adapted to a narrow range of protein intakes) and NPE generalists (consume a wider range of NPE intakes). An important goal of nutritional ecology, however, is to take such studies further and disentangle the ecological and organismal biological drivers of the patterns of nutrient intake. In laboratory studies, this is achieved by emulating a vastly simplified ecology in which animals, standardized in their nutritional state, are restricted over a defined period to one of a range of diets that differ systematically in the balance of nutrients from the target balance (Simpson & Raubenheimer, 2012). The pattern of intakes is then analysed to determine the relative priorities the animals assign to each nutrient in the face of constrained nutrient imbalance. Such patterns are called 'rules of compromise', to reflect the fact that they represent a balance of strategic weightings of nutrient-specific appetites employed to cope with variable resource quality (Raubenheimer & Simpson, 1997).

Our data demonstrate, however, that in free-ranging primates the situation is considerably more complex, with patterns of intake being driven by a combination of several factors, including regulatory responses to qualitative resource constraint, quantitative resource constraints and shifts in the position of intake targets (pseudo constraint).

4.3 | Ecology of protein prioritization

The year-round data for both the captive and wild populations tightly fitted the power equation used to test for protein

prioritization (in both cases $p < 0.001$, Table 3). In laboratory studies, the mechanism that has been associated with protein prioritization is termed 'protein leverage', where a strong appetite for protein causes the animal to over-eat NPE relative to the intake target on low P:NPE diets and under-eat NPE on high P:NPE diets (Raubenheimer & Simpson, 2019). Protein leverage has been demonstrated in several species, including humans (Gosby et al., 2011, 2014), mice (Sorensen et al., 2008), grasshoppers *Melanoplus differentialis* (Le Gall & Behmer, 2014) and flies (Almeida de Carvalho & Mirth, 2017). However, protein leverage cannot on its own explain protein prioritization in *R. roxellana* because, as discussed above, high NPE intakes in winter were not driven by qualitative constraint forcing the animals to over-eat NPE, but by an increased requirement for NPE to meet the energetic requirements for thermoregulation in winter (Guo et al., 2018; Hou, Chapman, Jay, et al., 2020). It is likely that the variance in NPE intake across other seasons is likewise driven, at least in part, by seasonal variation in nutrient requirements, rather than by qualitative constraint. This is suggested, firstly, by the fact that NPE intakes varied between spring, summer and autumn in the captive monkeys, which were able to freely select a diet from a uniformly wide range of foods year-round (Figure 3f). Secondly, Hou, Chapman, Rothman, et al. (2020) demonstrated that the wild population in this study relies on increased NPE intake in summer and autumn to build fat stores that compensate for restricted energy intake during the cold winter.

There is, however, also evidence of constraint-driven variation in intake in our data. In contrast with the captive population, and the heavily supplemented wild monkeys in Guo et al., (2018), the wild monkeys in this study showed only a modest increase in NPE intake in winter, and were energy deficient during that season (Hou, Chapman, Jay, et al., 2020). This suggests that, when possible, macronutrient selection by *R. roxellana* tracks winter increases in NPE requirements for thermoregulation, but in the wild their capacity to meet those requirements during winter is ecologically constrained. Furthermore, our results suggest that the constraint in question is quantitative constraint rather than qualitative constraint—i.e. a limit to the amount of food available during winter, rather than the balance of macronutrients available from those foods. This is indicated by the fact that the P:NPE ratio of the winter diets was lower for the wild than the captive population (as demonstrated by the steeper nutritional rail in Figure 4), whereas qualitative constraint would be due to a higher P:NPE ratio. However, the wild population ate less macronutrients overall (moved a shorter distance along the rail), including protein (Figure 4). That protein intakes were tightly conserved both across the other seasons and the populations, and the same was observed by Guo et al. (2018) in a wild provisioned population, suggests their limitation was on the quantity of food available in winter, not the composition relative to their macronutrient requirements.

Interestingly, the only other significant deviation in protein intake is that during winter the captive monkeys ate more of this macronutrient than any other season-population combination (Figure 4). The likely reason is that the relative amounts of the different foods available in captivity constrained them to a diet with higher P:NPE

balance than the winter intake target, forcing them to overeat protein to meet their winter thermoregulatory requirements for NPE. Indeed, given the angle of their diet rail, had they not overeaten protein their winter NPE intake would have been scarcely higher than that observed for the wild population, and equivalent to autumn intakes of both populations (Figure 4). This is an example of qualitative constraint, in which there is no restriction on the overall quantity of food available, but the relative quantities of different foods force the animals into trade-offs between overeating some nutrients and/or undereating others (Figure 1). The response, in this case, is NPE leverage (Raubenheimer & Simpson, 2019), in which animals restricted to diets with higher P:NPE ratio than the target ratio over ingest P to compensate, as previously demonstrated for mountain gorillas (Rothman et al., 2011). Humans, too, show this response when confined to excess-protein diets, even though the extent to which they overeat protein diets is small relative to the extent to which they over-eat NPE on low protein diets—i.e. they show protein prioritization (Raubenheimer & Simpson, 2019).

The patterns of intake within seasons revealed further nuances in the regulatory responses of *R. roxellana* to ecological variation. As was true for seasonal means (Figure 4), daily protein intakes were maintained more tightly than NPE—i.e. protein prioritization (Figure 5). However, statistical analysis of the within-season patterns revealed that this was true only for captive monkeys, and only in spring and winter (as evidenced using power regressions, Table 3). For the wild monkeys, in contrast, the power regression was not significant within any season, raising the question of what it is about the natural versus captive habitats that account for this difference. One possible explanation is that the accuracy of observations in the wild was lower than in captivity due to the larger numbers of foods available and more complex terrain, and the added noise decreased statistical power to detect protein prioritization. However, this is unlikely because there is no reason to suspect that the accuracy of observations of captive monkeys differed seasonally, and they had significant coefficients only in spring and winter. Furthermore, the intake data for the wild animals did not lack a pattern altogether, but for all seasons the linear regression excluding constant (i.e. forced through the origin) was highly significant, suggesting adherence to a particular nutritional rail. This was clearly illustrated by the long-follow individual, for which cumulative intakes over 32 consecutive days tightly adhered to a specific ratio of NPE:P (Figure 6a), as did the scatter of individual day data (Figure 6b).

Overall, the above analysis suggests that, at least in part, the strong pattern of protein prioritization observed in *R. roxellana* (Figures 4 and 5) reflects homeostatic tracking of seasonal nutrient requirements, with NPE demand varying more than protein

demand. Of all the within-season data, however, only winter and spring intakes of the captive population adhered to the protein prioritization model (Table 3), raising the question of what it is about these season-population combinations that differed from the others. Interestingly, winter and spring were also the two seasons in which NPE and total energy intake were higher in captivity than in the wild, suggesting the possibility that protein prioritization is linked with increased energy intake. A likely explanation for winter is that increased energy requirements for thermoregulation resulted in competition for high NPE (low P:NPE) foods among the captive monkeys, and consequently variation in daily access to these foods. Consistent with this, is the relatively high P:NPE ratio of the winter diet of the captive monkeys (compared with wild monkeys) and high consumption of protein energy (Figure 4). The same would not be observed in the wild population, because qualitative limitation on food availability (discussed above) would prevent wide variation in energy intakes. In spring, however, the same does not apply. First, our analysis suggests that the wild monkeys were neither qualitatively nor quantitatively constrained in the spring, but followed a target diet. The same was suggested in the analysis of Guo et al., (2018), which showed that despite the relatively high P:NPE diet and low energy intakes in spring, a large proportion of high-carbohydrate supplementary foods was left uneaten by the monkeys in this season, in contrast with winter when those foods were heavily targeted. This is suggested also in this study by the fact that intakes adhered to a linear P:NPE trajectory, which applied both for the population analysis and the long-follow individual (Figure 6). Why, then, did the captive monkeys show protein prioritization and increased energy intake in spring?

A fascinating possibility comes from analysis of the proportional composition of fat:carbohydrate in the spring diets of the two populations. In the wild, non-protein energy in the spring diet comprised largely non-structural carbohydrates (fat:TNC ratio = 0.17 ± 0.01 , Table 4); in contrast, the contribution of fat in the captive spring diet was almost double that value (0.31 ± 0.04). In many animals, primates included, fat and carbohydrate interact synergistically to increase palatability (DiFeliceantonio et al., 2018; Drewnowski & Greenwood, 1983), a factor that has been implicated in the human obesity epidemic (Moss, 2014). Intriguingly, in summer the fat:TNC ratio of the wild monkeys increased substantially (1.39 ± 0.13) and concomitantly energy intake increased to levels comparable with the spring and summer diets in captivity. This suggests that year-round access to highly palatable foods in captivity might drive an unseasonal increase in energy intake, resulting in higher annual energy intakes compared with the natural ecology.

Finally, it is interesting to consider why *R. roxellana* has evolved a macronutrient regulatory strategy where NPE intake varies widely

TABLE 4 The ratio of fat to TNC (fat:TNC, $M \pm SE$) in the diets of wild and captive populations of *Rhinopithecus roxellana*

	Spring	Summer	Autumn	Winter	Overall
Wild	0.17 ± 0.01	1.39 ± 0.13	0.16 ± 0.01	0.12 ± 0.01	0.46 ± 0.05
Captive	0.31 ± 0.04	0.32 ± 0.05	0.22 ± 0.03	0.19 ± 0.03	0.25 ± 0.03

across the year whereas protein remains more constant. A likely contributor is that both protein demand and protein supply are relatively constant in time, whereas NPE availability fluctuates with energy-rich foods, such as acorns, and demand fluctuates with, for example, reproduction (e.g. lactation) and thermoregulation. Additionally, primates have a limited capacity to store protein, consequently, there is a greater urgency to ingest the required levels on a daily basis. Adipose tissues, in contrast, provide storage for excess ingested NPE, and these stores provide a buffer that enables the monkeys to cope with periods of energy shortage such as winter (Hou, Chapman, Rothman, et al., 2020).

5 | CONCLUSIONS

Our study provides further evidence that macronutrient balancing is a primary driver of food selection and dietary regulation in the wild (Felton et al., 2009). Although the most detailed studies have been performed on primates, there is increasing evidence that the same applies for other taxa, spanning herbivores, omnivores and carnivores (Kohl et al., 2015; Machovsky-Capuska & Raubenheimer, 2020; Remonti et al., 2016; Robbins et al., 2007; Toft et al., 2019). This study has integrated this view of foraging into a geometric model of resource constraint, at the centre of which are the homeostatic responses of animals to resource variation. There are several potential benefits to this homeostasis-centred view of resource constraint. First, as demonstrated in our study, it provides a framework for interpreting in detail the patterns of food selection observed by animals in the wild. Second, the teleonomic nature of homeostasis provides strong predictability (Kearney et al., 2013), which is a priority in ecology (Houlahan et al., 2017). Third, the homeostatic framework expands the definition and evaluation of ecological constraint beyond situations in which resource variation has detectable negative impacts on individuals or populations, to encompass also the compensatory responses of animals that mitigate such impacts. Finally, as demonstrated in our analysis, the geometric view of constraint can link a wealth of laboratory-based studies of nutritional regulation in animals to patterns of resource variation in a realistic ecological context. For many taxa it will, however, be challenging to collect field data at the resolution possible for primates. On the other hand, recent advances in modelling approaches (Raubenheimer, 2011; Raubenheimer et al., 2015) and technology (Machovsky-Capuska, Priddel, et al., 2016) make this increasingly possible.

ACKNOWLEDGEMENTS

This work was supported by the Strategic Priority Research Program of the Chinese Academy of Sciences: XDB31020302; the National Key Programme of Research and Development, Ministry of Science and Technology: 2016YFC0503200; the National Nature Science Foundation of China: 31870396, 31672301, 31872247; the Natural Science Foundation of Shaanxi Province in China: 2018JC-022). We thank Zhouzhi National Nature Reserve and Shaanxi Wild Animal Rescue and Research Center for permitting and supporting this study.

We thank all the local field assistants for their logistical assistance, we also thank Li Min, Wang Jiajia, Zhang Shuqing for their assistance with nutritional analysis. Rong Hou wishes to thank his wife, Yanyan Cao, for her contribution to the family and selfless support for the wildlife research.

AUTHORS' CONTRIBUTIONS

B.L., R.H. and S.G., conceived the ideas; R.H., H.Z. and K.H. collected the field data and plant samples; R.H. and D.R. analysed the data; R.H., D.R., C.A.C. and J.M.R. wrote and edited the manuscript. All authors contributed critically to the drafts and gave final approval for publication. The co-authors do not have any conflict of interest to declare.

DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository <https://doi.org/10.5061/dryad.wstqjq2jx> (Hou, Chapman, Rothman, et al., 2020).

ORCID

Rong Hou  <https://orcid.org/0000-0002-8236-6318>

Colin A. Chapman  <https://orcid.org/0000-0002-8827-8140>

He Zhang  <https://orcid.org/0000-0002-1832-8480>

Kang Huang  <https://orcid.org/0000-0002-8357-117X>

Songtao Guo  <https://orcid.org/0000-0002-8291-5487>

Baoguo Li  <https://orcid.org/0000-0001-7430-3889>

David Raubenheimer  <https://orcid.org/0000-0001-9050-1447>

REFERENCES

- Almeida de Carvalho, M. J., & Mirth, C. K. (2017). Food intake and food choice are altered by the developmental transition at critical weight in *Drosophila melanogaster*. *Animal Behaviour*, 126, 195–208. <https://doi.org/10.1016/j.anbehav.2017.02.005>
- AOAC. (1990). *Official methods of analysis* (15th ed.). Association of Official Analytical Chemists.
- Behmer, S. T., & Joern, A. (2008). Coexisting generalist herbivores occupy unique nutritional feeding niches. *Proceedings of the National Academy of Sciences of the United States of America*, 105, 1977–1982. <https://doi.org/10.1073/pnas.0711870105>
- Birnie-Gauvin, K., Peiman, K. S., Raubenheimer, D., & Cooke, S. J. (2017). Nutritional physiology and ecology of wildlife in a changing world. *Conservation Physiology*, 5. <https://doi.org/10.1093/conphys/cox030>
- Bressendorff, B. B., & Toft, S. (2011). Dome-shaped functional response induced by nutrient imbalance of the prey. *Biology Letters*, 7, 517–520. <https://doi.org/10.1098/rsbl.2011.0103>
- Burian, A., Nielsen, J. M., & Winder, M. (2020). Food quantity-quality interactions and their impact on consumer behavior and trophic transfer. *Ecological Monographs*, 90, e01395. <https://doi.org/10.1002/ecm.1395>
- C.M.A. (2012). Meteorological standards of the People's Republic of China: *Division of climatic season*. China Meteorological Press.
- Chapman, C. A., Chapman, L. J., Rode, K. D., Hauck, E. M., & McDowell, L. R. (2003). Variation in the nutritional value of primate foods: Among trees, time periods, and areas. *International Journal of Primatology*, 24, 317–333. <https://doi.org/10.1023/A:1023049200150>
- Conklin-Brittain, N. L., Knott, C. D., & Wrangham, R. W. (2006). Energy intake by wild chimpanzees and orangutans: Methodological

- considerations and a preliminary comparison. In G. Hohmann, M. M. Robbins, & C. Boesch (Eds.), *Feeding ecology in apes and other primates. Ecological, physical and behavior aspects* (pp. 445–471). Cambridge University Press.
- Coogan, S. C., & Raubenheimer, D. (2016). Might macronutrient requirements influence grizzly bear-human conflict? Insights from nutritional geometry. *Ecosphere*, *7*, e01204. <https://doi.org/10.1002/ecs2.1204>
- Coogan, S. C. P., Raubenheimer, D., Zantis, S. P., & Machovsky-Capuska, G. E. (2018). Multidimensional nutritional ecology and urban birds. *Ecosphere*, *9*, e02177. <https://doi.org/10.1002/ecs2.2177>
- Cui, Z., Wang, Z., Shao, Q., Raubenheimer, D., & Lu, J. (2018). Macronutrient signature of dietary generalism in an ecologically diverse primate in the wild. *Behavioral Ecology*, *29*, 804–813. <https://doi.org/10.1093/beheco/ary003>
- Dias, P. A. D., Rangel-Negrín, A., & Canales-Espinosa, D. (2011). Effects of lactation on the time-budgets and foraging patterns of female black howlers (*Alouatta pigra*). *American Journal of Physical Anthropology*, *145*, 137–146. <https://doi.org/10.1002/ajpa.21481>
- DiFeliceantonio, A. G., Coppin, G., Rigoux, L., Edwin Thanarajah, S., Dagher, A., Tittgemeyer, M., & Small, D. M. (2018). Supra-additive effects of combining fat and carbohydrate on food reward. *Cell Metabolism*, *28*, 33–44. <https://doi.org/10.1016/j.cmet.2018.05.018>
- Douhard, F., Lemaitre, J. F., Rauw, W. M., & Friggens, N. C. (2016). Allometric scaling of the elevation of maternal energy intake during lactation. *Frontiers in Zoology*, *13*, 32. <https://doi.org/10.1186/s12983-016-0164-y>
- Drewnowski, A., & Greenwood, M. R. C. (1983). Cream and sugar: Human preferences for high-fat foods. *Physiology & Behavior*, *30*, 629–633. [https://doi.org/10.1016/0031-9384\(83\)90232-9](https://doi.org/10.1016/0031-9384(83)90232-9)
- Droscher, I., Rothman, J. M., Ganzhorn, J. U., & Kappeler, P. M. (2016). Nutritional consequences of folivory in a small-bodied lemur (*Lepilemur leucopus*): Effects of season and reproduction on nutrient balancing. *American Journal of Physical Anthropology*, *160*, 197–207. <https://doi.org/10.1002/ajpa.22952>
- Dunham, N. T., & Rodriguez-Saona, L. E. (2018). Nutrient intake and balancing among female *Colobus angolensis palliatus* inhabiting structurally distinct forest areas: Effects of group, season, and reproductive state. *American Journal of Primatology*, *80*, e22878. <https://doi.org/10.1002/ajp.22878>
- Felton, A. M., Felton, A., Lindenmayer, D. B., & Foley, W. J. (2009). Nutritional goals of wild primates. *Functional Ecology*, *23*, 70–78. <https://doi.org/10.1111/j.1365-2435.2008.01526.x>
- Felton, A. M., Felton, A., Raubenheimer, D., Simpson, S. J., Foley, W. J., Wood, J. T., Wallis, I. R., & Lindenmayer, D. B. (2009). Protein content of diets dictates the daily energy intake of a free-ranging primate. *Behavioral Ecology*, *20*, 685–690. <https://doi.org/10.1093/beheco/arp021>
- Felton, A. M., Felton, A., Wood, J. T., Foley, W. J., Raubenheimer, D., Wallis, I. R., & Lindenmayer, D. B. (2009). Nutritional ecology of *Ateles chamek* in lowland Bolivia: How macronutrient balancing influences food choices. *International Journal of Primatology*, *30*, 675–696. <https://doi.org/10.1007/s10764-009-9367-9>
- Gosby, A. K., Conigrave, A. D., Lau, N. S., Iglesias, M. A., Hall, R. M., Jebb, S. A., Brand-Miller, J., Caterson, I. D., Raubenheimer, D., & Simpson, S. J. (2011). Testing protein leverage in lean humans: A randomised controlled experimental study. *PLoS ONE*, *6*, e25929. <https://doi.org/10.1371/journal.pone.0025929>
- Gosby, A. K., Conigrave, A. D., Raubenheimer, D., & Simpson, S. J. (2014). Protein leverage and energy intake. *Obesity Reviews*, *15*, 183–191. <https://doi.org/10.1111/obr.12131>
- Gosby, A. K., Lau, N. S., Tam, C. S., Iglesias, M. A., Morrison, C. D., Caterson, I. D., Brand-Miller, J., Conigrave, A. D., Raubenheimer, D., & Simpson, S. J. (2016). Raised FGF-21 and triglycerides accompany increased energy intake driven by protein leverage in lean, healthy individuals: A randomised trial. *PLoS ONE*, *11*, e0161003. <https://doi.org/10.1371/journal.pone.0161003>
- Guo, S. T., Hou, R., Garber, P. A., Raubenheimer, D., Righini, N., Ji, W. H., Jay, O., & Li, B. G. (2018). Nutrient-specific compensation for seasonal cold stress in a free-ranging temperate colobine monkey. *Functional Ecology*, *32*, 2170–2180. <https://doi.org/10.1111/1365-2435.13134>
- Hall, K. D. (2019). The potential role of protein leverage in the US obesity epidemic. *Obesity*, *27*, 1222–1224. <https://doi.org/10.1002/oby.22520>
- Hewson-Hughes, A. K., Hewson-Hughes, V. L., Miller, A. T., Hall, S. R., Simpson, S. J., & Raubenheimer, D. (2011). Geometric analysis of macronutrient selection in the adult domestic cat, *Felis catus*. *Journal of Experimental Biology*, *214*, 1039–1051. <https://doi.org/10.1242/jeb.049429>
- Holmes, A. J., Chew, Y. V., Colakoglu, F., Cliff, J. B., Klaassens, E., Read, M. N., Solon-Biet, S. M., McMahon, A. C., Cogger, V. C., Ruohonen, K., Raubenheimer, D., Le Couteur, D. G., & Simpson, S. J. (2017). Diet-microbiome interactions in health are controlled by intestinal nitrogen source constraints. *Cell Metabolism*, *25*, 140–151. <https://doi.org/10.1016/j.cmet.2016.10.021>
- Hou, R., Chapman, C. A., Jay, O., Guo, S., Li, B., & Raubenheimer, D. (2020). Cold and hungry: Combined effects of low temperature and resource scarcity on an edge-of-range temperate primate, the golden snub-nose monkey. *Ecography*, *43*, 1–11. <https://doi.org/10.1111/ecog.05295>
- Hou, R., Chapman, C. A., Rothman, J. M., Zhang, H., Huang, K., Guo, S., Li, B., & Raubenheimer, D. (2020). Data from: The geometry of resource constraint: An empirical study of the golden snub-nosed monkey. *Dryad Digital Repository*, <https://doi.org/10.5061/dryad.wstqjq2jx>
- Hou, R., He, S., Wu, F., Chapman, C. A., Pan, R., Garber, P. A., & Li, B. (2018). Seasonal variation in diet and nutrition of the northern-most population of *Rhinopithecus roxellana*. *American Journal of Primatology*, *80*, e22755. <https://doi.org/10.1002/ajp.22755>
- Houlahan, J. E., McKinney, S. T., Anderson, T. M., & McGill, B. J. (2017). The priority of prediction in ecological understanding. *Oikos*, *126*, 1–7. <https://doi.org/10.1111/oik.03726>
- Huang, S. (2014). Noninvasive study of nutrient metabolism, stress and immune status in Sichuan golden monkey (*Rhinopithecus roxellana*) in the environment of captivity (Doctoral dissertation). Nanjing Agricultural University.
- Irwin, M. T., Raharison, J. L., Raubenheimer, D. R., Chapman, C. A., & Rothman, J. M. (2015). The nutritional geometry of resource scarcity: Effects of lean seasons and habitat disturbance on nutrient intakes and balancing in wild sifakas. *PLoS ONE*, *10*, e0128046. <https://doi.org/10.1371/journal.pone.0128046>
- Jang, T., & Lee, K. P. (2018). Comparing the impacts of macronutrients on life-history traits in larval and adult *Drosophila melanogaster*: The use of nutritional geometry and chemically defined diets. *Journal of Experimental Biology*, *221*, jeb181115. <https://doi.org/10.1242/jeb.181115>
- Johnson, C. A., Raubenheimer, D., Rothman, J. M., Clarke, D., & Swedell, L. (2013). 30 days in the life: Daily nutrient balancing in a wild chacma baboon. *PLoS ONE*, *8*, e70383. <https://doi.org/10.1371/journal.pone.0070383>
- Kearney, M., Simpson, S. J., Raubenheimer, D., & Helmuth, B. (2010). Modelling the ecological niche from functional traits. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *365*, 3469–3483. <https://doi.org/10.1098/rstb.2010.0034>
- Kearney, M. R., Simpson, S. J., Raubenheimer, D., Kooijman, S. A. L. M., & Chown, S. (2013). Balancing heat, water and nutrients under environmental change: A thermodynamic niche framework. *Functional Ecology*, *27*, 950–965. <https://doi.org/10.1111/1365-2435.12020>
- Kohl, K. D., Coogan, S. C., & Raubenheimer, D. (2015). Do wild carnivores forage for prey or for nutrients? Evidence for nutrient-specific

- foraging in vertebrate predators. *BioEssays*, 37, 701–709. <https://doi.org/10.1002/bies.201400171>
- Krabbe, B. A., Arnan, X., Lannes, P., Bergstedt, C. E., Larsen, R. S., Pedersen, J. S., & Shik, J. Z. (2019). Using nutritional geometry to define the fundamental macronutrient niche of the widespread invasive ant *Monomorium pharaonis*. *PLoS ONE*, 14, e0218764. <https://doi.org/10.1371/journal.pone.0218764>
- Le Gall, M., & Behmer, S. T. (2014). Effects of protein and carbohydrate on an insect herbivore: The vista from a fitness landscape. *Integrative and Comparative Biology*, 54, 942–954. <https://doi.org/10.1093/icb/ucu102>
- Li, B., Chen, C., Ji, W., & Ren, B. (2000). Seasonal home range changes of the Sichuan snub-nosed monkey (*Rhinopithecus roxellana*) in the Qinling Mountains of China. *Folia Primatologica*, 71, 375–386. <https://doi.org/10.1159/000052734>
- Li, B., & He, P. (2007). *The biodiversity of Shaanxi Zhouzhi National Nature Reserve*. Shaanxi Science and Technology Press.
- Machovsky-Capuska, G. E., Priddel, D., Leong, P. H. W., Jones, P., Carlile, N., Shannon, L., Portelli, D., McEwan, A., Chaves, A. V., & Raubenheimer, D. (2016). Coupling bio-logging with nutritional geometry to reveal novel insights into the foraging behaviour of a plunge-diving marine predator. *New Zealand Journal of Marine and Freshwater Research*, 50, 418–432. <https://doi.org/10.1080/00288330.2016.1152981>
- Machovsky-Capuska, G. E., & Raubenheimer, D. (2020). The nutritional ecology of marine apex predators. *Annual Review of Marine Science*, 12, 361–387. <https://doi.org/10.1146/annurev-marine-010318-095411>
- Machovsky-Capuska, G. E., Senior, A. M., Simpson, S. J., & Raubenheimer, D. (2016). The multidimensional nutritional niche. *Trends in Ecology & Evolution*, 31, 355–365. <https://doi.org/10.1016/j.tree.2016.02.009>
- Moss, M. (2014). *Salt, sugar, fat: How the food giants hooked us*. W.H. Allen.
- Nagy, K. A. (1994). Field bioenergetics of mammals—what determines field metabolic rates. *Australian Journal of Zoology*, 42, 43–53. <https://doi.org/10.1071/ZO9940043>
- Owen-Smith, N. (2008). Effects of temporal variability in resources on foraging behaviour. In H. H. T. Prins & F. van Langevelde (Eds.), *Resource ecology: Spatial and temporal dynamics of foraging* (pp. 159–181). Springer.
- Parepa, M., Fischer, M., & Bossdorf, O. (2013). Environmental variability promotes plant invasion. *Nature Communications*, 4, 1604. <https://doi.org/10.1038/ncomms2632>
- Pinheiro, J. C., & Bates, D. M. (2000). *Mixed-effect models in S and S-PLUS*. Springer.
- Prins, H. H. T., & van Langevelde, F. (2008). *Resource ecology: Spatial and temporal dynamics of foraging*. Springer.
- Raubenheimer, D. (2011). Toward a quantitative nutritional ecology: The right-angled mixture triangle. *Ecological Monographs*, 81, 407–427. <https://doi.org/10.1890/10-1707.1>
- Raubenheimer, D., Machovsky-Capuska, G. E., Chapman, C. A., & Rothman, J. M. (2015). Geometry of nutrition in field studies: An illustration using wild primates. *Oecologia*, 177, 223–234. <https://doi.org/10.1007/s00442-014-3142-0>
- Raubenheimer, D., & Simpson, S. J. (1997). Integrative models of nutrient balancing: Application to insects and vertebrates. *Nutrition Research Reviews*, 10, 151–179. <https://doi.org/10.1079/NRR19970009>
- Raubenheimer, D., & Simpson, S. (2006). The challenge of supplementary feeding: Can geometric analysis help save the kakapo? *Notornis*, 53, 100–111.
- Raubenheimer, D., & Simpson, S. J. (2018). Nutritional ecology and foraging theory. *Current Opinion in Insect Science*, 27, 38–45. <https://doi.org/10.1016/j.cois.2018.02.002>
- Raubenheimer, D., & Simpson, S. J. (2019). Protein leverage: Theoretical foundations and ten points of clarification. *Obesity*, 27, 1225–1238. <https://doi.org/10.1002/oby.22531>
- Raubenheimer, D., Simpson, S. J., Le Couteur, D. G., Solon-Biet, S. M., & Coogan, S. C. (2016). Nutritional ecology and the evolution of aging. *Experimental Gerontology*, 86, 50–61. <https://doi.org/10.1016/j.exger.2016.04.007>
- Raubenheimer, D., Simpson, S. J., & Mayntz, D. (2009). Nutrition, ecology and nutritional ecology: Toward an integrated framework. *Functional Ecology*, 23, 4–16. <https://doi.org/10.1111/j.1365-2435.2009.01522.x>
- Raubenheimer, D., Simpson, S. J., & Tait, A. H. (2012). Match and mismatch: Conservation physiology, nutritional ecology and the time scales of biological adaptations. *Philosophical Transactions of the Royal Society of London, Series B: Biological Sciences*, 367, 1628–1646. <https://doi.org/10.1098/rstb.2012.0007>
- Remonti, L., Balestrieri, A., Raubenheimer, D., & Saino, N. (2016). Functional implications of omnivory for dietary nutrient balance. *Oikos*, 125, 1233–1240. <https://doi.org/10.1111/oik.02801>
- Robbins, C. T., Fortin, J. K., Rode, K. D., Farley, S. D., Shipley, L. A., & Felicetti, L. A. (2007). Optimizing protein intake as a foraging strategy to maximize mass gain in an omnivore. *Oikos*, 116, 1675–1682. <https://doi.org/10.1111/j.2007.0030-1299.16140.x>
- Rothman, J. M., Chapman, C. A., & van Soest, P. J. (2012). Methods in primate nutritional ecology: A user's guide. *International Journal of Primatology*, 33, 542–566. <https://doi.org/10.1007/s10764-011-9568-x>
- Rothman, J. M., Plumptre, A. J., Dierenfeld, E. S., & Pell, A. N. (2007). Nutritional composition of the diet of the gorilla (*Gorilla beringei*): A comparison between two montane habitats. *Journal of Tropical Ecology*, 23, 673–682. <https://doi.org/10.1017/s0266467407004555>
- Rothman, J. M., Raubenheimer, D., & Chapman, C. A. (2011). Nutritional geometry: Gorillas prioritize non-protein energy while consuming surplus protein. *Biology Letters*, 7, 847–849. <https://doi.org/10.1098/rsbl.2011.0321>
- Ruivo, L. V., Stone, A. I., & Fienup, M. (2017). Reproductive status affects the feeding ecology and social association patterns of female squirrel monkeys (*Saimiri collinsi*) in an Amazonian rainforest. *American Journal of Primatology*, 79, e22657. <https://doi.org/10.1002/ajp.22657>
- Ruohonen, K., Simpson, S. J., & Raubenheimer, D. (2007). A new approach to diet optimisation: A re-analysis using European whitefish (*Coregonus lavaretus*). *Aquaculture*, 267, 147–156. <https://doi.org/10.1016/j.aquaculture.2007.02.051>
- Rydell, J. (1989). Feeding activity of the northern bat *Eptesicus nilssonii* during pregnancy and lactation. *Oecologia*, 80, 562–565. <https://doi.org/10.1007/bf00380082>
- Shik, J. Z., & Dussutour, A. (2020). Nutritional dimensions of invasive success. *Trends in Ecology & Evolution*, 35, 691–703. <https://doi.org/10.1016/j.tree.2020.03.009>
- Simpson, S. J., & Raubenheimer, D. (2012). *The nature of nutrition: A unifying framework from animal adaptation to human obesity*. Princeton University Press.
- Simpson, S. J., Raubenheimer, D., Charleston, M. A., Clissold, F. J., & the ARC-NZ Vegetation Function Network Herbivory Working Group. (2010). Modelling nutritional interactions: From individuals to communities. *Trends in Ecology & Evolution*, 25, 53–60. <https://doi.org/10.1016/j.tree.2009.06.012>
- Solon-Biet, S. M., Walters, K. A., Simanainen, U. K., McMahon, A. C., Ruohonen, K., Ballard, J. W. O., Raubenheimer, D., Handelsman, D. J., Le Couteur, D. G., & Simpson, S. J. (2015). Macronutrient balance, reproductive function, and lifespan in aging mice. *Proceedings of the National Academy of Sciences of the United States of America*, 112, 3481–3486. <https://doi.org/10.1073/pnas.1422041112>
- Sorensen, A., Mayntz, D., Raubenheimer, D., & Simpson, S. J. (2008). Protein-leverage in mice: The geometry of macronutrient balancing and consequences for fat deposition. *Obesity*, 16, 566–571. <https://doi.org/10.1038/oby.2007.58>
- Speakman, J. R. (2008). The physiological costs of reproduction in small mammals. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 363, 375–398. <https://doi.org/10.1098/rstb.2007.2145>

- Takahashi, M., Rothman, J. M., Raubenheimer, D., & Cords, M. (2019). Dietary generalists and nutritional specialists: Feeding strategies of adult female blue monkeys (*Cercopithecus mitis*) in the Kakamega Forest, Kenya. *American Journal of Primatology*, 81, e23016. <https://doi.org/10.1002/ajp.23016>
- Tirado Herrera, E. R., & Heymann, E. W. (2004). Does mom need more protein? Preliminary observations on differences in diet composition in a pair of red titi monkeys (*Callicebus cupreus*). *Folia Primatologica*, 75, 150–153. <https://doi.org/10.1159/000078304>
- Toft, S., Cuende, E., Olesen, A. L., Mathiesen, A., Meisner Larsen, M., & Jensen, K. (2019). Food and specific macronutrient limitation in an assemblage of predatory beetles. *Oikos*, 128, 1467–1477. <https://doi.org/10.1111/oik.06479>
- van Soest, P. J., Robertson, J. B., & Lewis, B. A. (1991). Methods for dietary fiber, neutral detergent fiber, and non-starch polysaccharides in relation to animal nutrition. *Journal of Dairy Science*, 74, 3583–3597. [https://doi.org/10.3168/jds.s0022-0302\(91\)78551-2](https://doi.org/10.3168/jds.s0022-0302(91)78551-2)
- Wilder, S. M., Norris, M., Lee, R. W., Raubenheimer, D., & Simpson, S. J. (2013). Arthropod food webs become increasingly lipid-limited at higher trophic levels. *Ecology Letters*, 16, 895–902. <https://doi.org/10.1111/ele.12116>

How to cite this article: Hou R, Chapman CA, Rothman JM, et al. The geometry of resource constraint: An empirical study of the golden snub-nosed monkey. *J Anim Ecol*. 2021;00:1–15. <https://doi.org/10.1111/1365-2656.13408>