

# Current Biology

## Giant Pandas Are Macronutritional Carnivores

### Highlights

- Giant pandas show seasonal foraging migration associated with bamboo phenology
- The macronutrient energy ratios of pandas' diets are similar to those of carnivores
- The absorbed macronutrient ratios of pandas are similar to those of the ingested foods
- The diet specialization of giant pandas might be less abrupt than it might appear

### Authors

Yonggang Nie, Fuwen Wei, Wenliang Zhou, ..., Qi Wu, Li Yan, David Raubenheimer

### Correspondence

weifw@ioz.ac.cn

### In Brief

Giant pandas feed on bamboo, yet they have both herbivore and carnivore traits. Nie et al. show that the macronutrient composition of the ingested and absorbed diets resembles the diets of carnivores, not of herbivores. This can explain why pandas have adapted incompletely to the plant diet and suggests that their shift to herbivory was easier than it might otherwise seem.



# Giant Pandas Are Macronutritional Carnivores

Yonggang Nie,<sup>1,2</sup> Fuwen Wei,<sup>1,2,3,5,\*</sup> Wenliang Zhou,<sup>1</sup> Yibo Hu,<sup>1,2</sup> Alistair M. Senior,<sup>4</sup> Qi Wu,<sup>1</sup> Li Yan,<sup>1</sup> and David Raubenheimer<sup>4</sup>

<sup>1</sup>Key Laboratory of Animal Ecology and Conservation Biology, Institute of Zoology, Chinese Academy of Sciences, Beijing 100101, China

<sup>2</sup>CAS Center for Excellence in Animal Evolution and Genetics, Chinese Academy of Sciences, Kunming 650223, China

<sup>3</sup>University of Chinese Academy of Sciences, Beijing 100049, China

<sup>4</sup>The Charles Perkins Centre, The University of Sydney, Sydney 2006, Australia

<sup>5</sup>Lead Contact

\*Correspondence: [weifw@ioz.ac.cn](mailto:weifw@ioz.ac.cn)

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## SUMMARY

Giant pandas are unusual in belonging to a primarily carnivorous clade and yet being extremely specialized herbivores that feed almost exclusively on highly fibrous bamboo [1]. Paradoxically, they appear inconsistently adapted to their plant diet, bearing a mix of herbivore and carnivore traits. Herbivore traits include a skull, jaw musculature, and dentition that are adapted for fibrous diets and a specialized “pseudo-thumb” used for handling bamboo [2, 3]. They have lost functional versions of the T1R1 gene codes for umami taste receptors, which are often associated with meat eating [3]. They also have an herbivore-like subcellular distribution of the metabolic enzyme alanine: glyoxylate aminotransferase [4]. But meanwhile, giant pandas have a digestive tract [5], digestive enzymes [6], and a gut microbiota composition that resemble those of carnivores and not of herbivores [6, 7]. We draw on recent developments in multi-dimensional niche theory [8] to examine this apparent paradox. We show that the pandas’ diet clustered in a macronutrient space among carnivores and was distinct from that of herbivores. The similarity with carnivore diets applied not only to the ingested diet but also to the absorbed diet, with the absorbed macronutrient ratios similar to those of the ingested foods. Comparison of the macronutrient composition of pandas’ milk with those of other species shows that the carnivore-like dietary macronutrient composition extends across the life cycle. These results cast new light on the seemingly incongruous constellation of dietary adaptations in pandas, suggesting that the transition from carnivorous and omnivorous ancestry to specialized herbivory might be less abrupt than it might otherwise appear.

## RESULTS

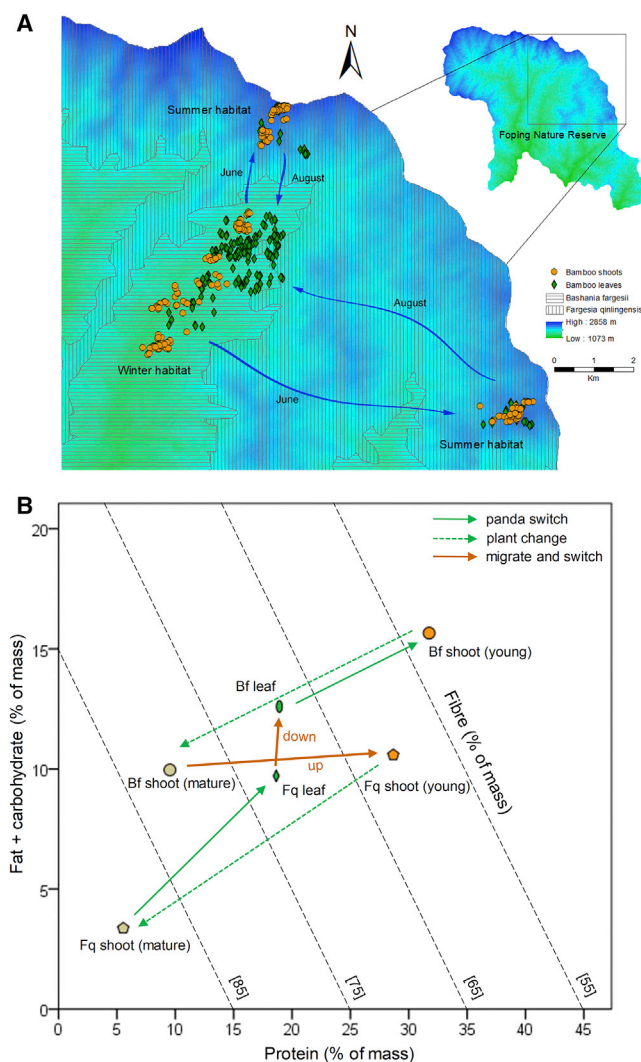
The giant panda is a specialist herbivore that feeds almost exclusively on highly fibrous bamboo [1], yet it bears a mix of herbivore

and carnivore traits [2–7]. We draw on recent developments in niche theory to test the hypothesis that the combination of herbivore- and carnivore-associated traits in giant pandas is not incongruous at all, but it reflects hitherto hidden dimensions of their diet. Machovsky-Capuska et al. [8] demonstrated using multi-dimensional nutritional modeling that dietary classifications might differ at the levels of foods eaten and the nutrient content of the diet. To illustrate, they show how the conventional dietary classification of “generalist” versus “specialist,” based on the range of foods an animal is capable of exploiting, might not align with its capacity to tolerate variation in nutrient intake. For example, an animal could benefit from eating a wide range of foods specifically because it has limited tolerance for nutritional diversity and eating many, nutritionally complementary, foods enables it to maintain the balance of nutrients eaten within narrow boundaries [9].

We predicted that the mix of herbivorous and carnivorous dietary traits in giant pandas can be explained within this dual-level niche framework. To test this, we measured the macronutrient composition of foods eaten by giant pandas in the wild and compared this with literature data on typical herbivore and carnivore diets. In order to ensure that our measures represented the overall diet of our study population, we sampled across the year and across locations in the annual migratory cycle. We also measured the nutrient content of feces associated with the analyzed foods to establish the extent to which the macronutrient profile of the absorbed diet resembled the ingested diet. Finally, to extend our study across all stages of the life cycle, we compared the milk macronutrient composition of giant pandas with those from other mammals using the literature data.

The giant pandas in our study showed seasonal foraging migration associated with the phenologies of the two dietary bamboo species (Figures 1A and 1B). For eight months of the year (usually late August–late April), pandas ate the leaves of *Bf* in the low habitat (Figure 1B) and switched to the young *Bf* shoots as these became available (Figure 1B). At the time of the switch, the dry weight protein concentration in *Bf* shoots was significantly higher than that in *Bf* leaves (32.09% versus 19.21%, estimated logit difference from linear model [est.] = 0.69, confidence interval [CI] = 0.60 to 0.77), and the fiber concentration was lower (53.19% versus 69.27%, est. = −0.69, CI = −0.78 to −0.58; Figure 1B). When the *Bf* shoots matured, their protein concentration decreased (32.09% versus 9.57%, est. = −1.50, CI = −1.67 to −1.37) and the fiber concentration





**Figure 1. Relationship between Movement by Giant Panda in Geographical and Nutritional Space and the Annual Pattern of Dietary Shifts between Leaves and Shoots of Two Bamboo Species**

(A) Seasonal foraging migration pattern of giant pandas.

(B) Right-angled mixture triangle [10] showing the mean dry weight contributions of protein (x axis), non-protein energy (y axis), and fiber (dashed diagonals) to replicate samples of the four food categories at different ages. Solid arrows show the temporal sequence of food switches within habitats (solid green) and associated with migration between habitats (orange). Dashed green lines show age-related changes in the composition of shoots, which for both species involved increasing concentration of fiber (displacement across negative diagonal lines toward the origin) and decreasing protein. “Down” and “up” show the altitude change of the foraging migration.

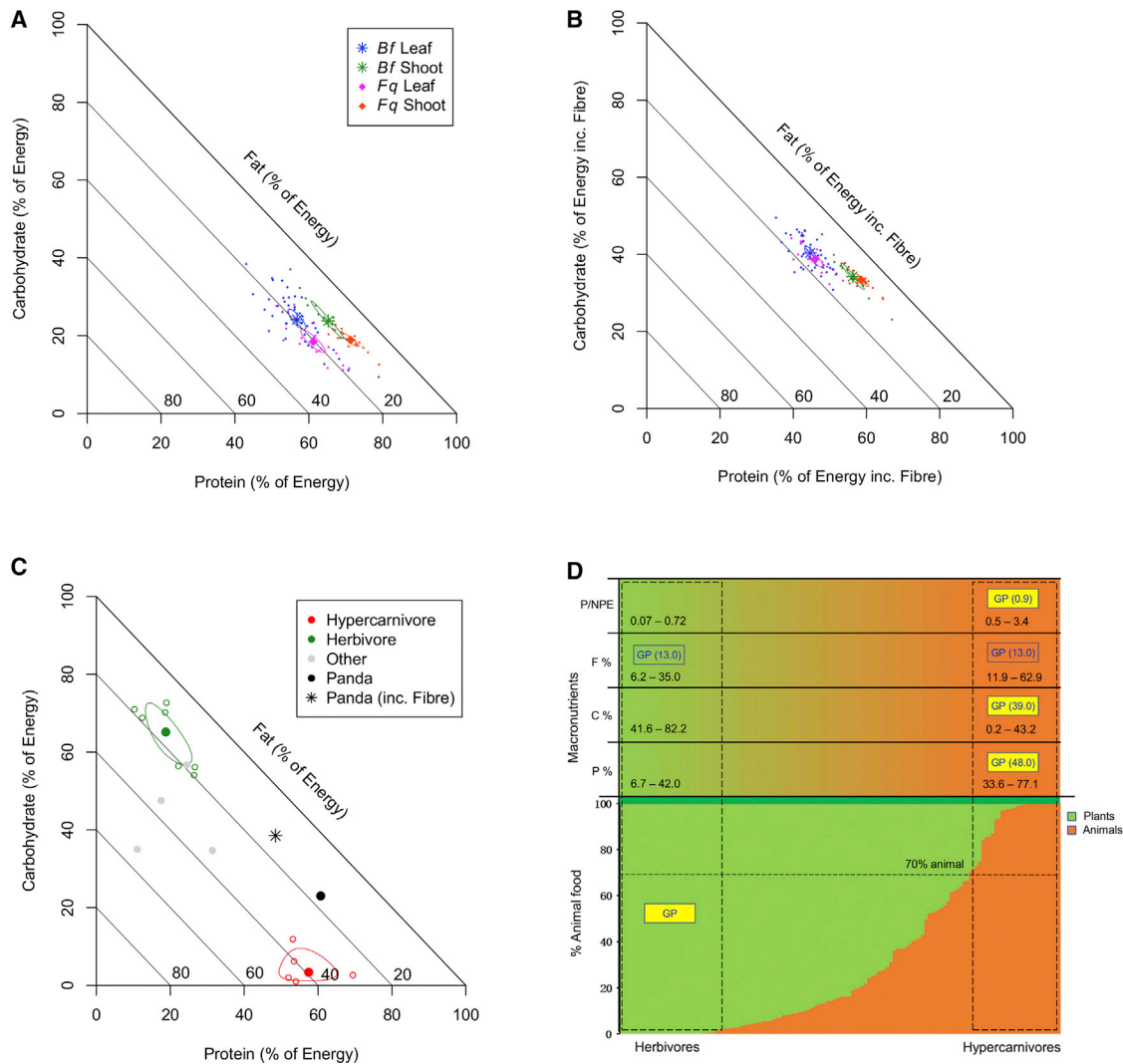
increased (53.19% versus 80.77%, est. = 1.31, CI = 1.17 to 1.43), at which point pandas migrated to the high elevation site and switched to higher-protein *Fq* shoots. As the *Fq* shoots matured and decreased in protein and increased in fiber concentration, the pandas switched to *Fq* leaves, which had significantly higher protein (18.84% versus 5.56%, est. = 1.38, CI = 1.27 to 1.50) and lower fiber than the mature shoots (72.40% versus 91.37%, est. = -1.40, CI = -1.50 to -1.27). When the new leaves of

the mature *Bf* shoots were available, the pandas returned to the low elevations and ate the new *Bf* leaves, which had similar protein content to the *Fq* leaves. Unlike protein and fiber, the total fat and carbohydrate concentrations did not show significant difference in leaves and shoots of *Fq* (8.76% versus 9.57%, est. = -0.11, CI = -0.28 to 0.05) and only minor differences of *Bf* (11.52% versus 14.72%, est. = -0.28, CI = -0.48 to 0.09; **Figures 1A and 1B**). Overall, these results are consistent with a sequence of diet switching that maximizes the proportion of macronutrients contributed by protein and decreases fiber.

The percentage of macronutrient energy contributed by protein was higher than those of the other two macronutrients combined (i.e., >50%) in shoots and leaves of both *Bf* and *Fq* (**Figure 2A**; **Tables S1 and S2**). We obtained an approximate estimate of the overall diet of the pandas in our study by taking the average composition of the four foods eaten (shoots and leaves of the two species), weighted by the proportion of the year they spend eating each food. This estimate suggests that panda's diet is 61% protein energy, 23% energy from carbohydrates, and 16% fat. Bamboo contains a large amount of hemicellulose and cellulose, which, if digested, could increase the fraction of energy coming from carbohydrates while decreasing that from protein and fat (**Figure 2B**). When the estimated digestible fraction of this fiber was included, we still estimate energy from protein at 48% of the total diet (carbohydrates, 39%; fats, 13%).

Contrasting these estimates with the diets of other species shows that pandas have a diet composition with protein and carbohydrate percentages similar to the means for hypercarnivores (i.e., animals that obtain >70% of their diets from animal foods [12]) and different from those of herbivores, and they have a fat percentage that overlaps those of herbivores and hypercarnivores in our sample (**Figure 2C**; **Table S3**). **Figure 2D** shows a synthesis of the giant panda dietary niche at the levels of foods and macronutrients. Although giant pandas fall among herbivores with respect to the foods they eat, the dietary protein content falls within the prediction intervals for hypercarnivores and outside that for herbivores, as did the carbohydrate content and the protein:non-protein energy ratio. The fat content of the giant panda diet fell within the prediction intervals both for hypercarnivores and for herbivores.

To establish the extent to which the absorbed diet of giant pandas resembled the ingested diet, we compared the macronutritional profiles of the plants eaten with matched feces. Although this approach does not measure absolute digestive efficiencies, it measures the relative efficiencies with which the different macronutrients are absorbed [10]. For example, if protein is preferentially eliminated relative to fat and carbohydrate, the percentage contribution of protein to macronutrients in the feces would be higher than its contribution to macronutrients in the food. Our analysis showed that the percentage contribution of protein to macronutrients in the fecal samples of giant pandas was either lower (shoots of *F. qinlingensis*, est. = -0.70, CI = -0.89 to -0.52; *B. fargesii*, est. = 0.38, CI = -0.66 to -0.10) or similar to (leaves of *F. qinlingensis*, est. = -0.16, CI = -0.34 to 0.02; *B. fargesii*, est. = 0.10, CI = -0.02 to 0.24) matched food samples (**Figure 3**; **Tables S2 and S4**). We could thus



**Figure 2. Macronutrient Energy Ratio of the Diets of Giant Pandas and Other Mammal Species and the Multi-Level Dietary Niche of Giant Pandas**

(A and B) Right-angled mixture triangles showing the composition of leaves and shoots of *Bashania fargesii* (Bf) and *Fargesia qinlingensis* (Fq) in terms of the percentage of energy from protein, carbohydrate, and fat. In (A), energy from digestible fiber has been excluded, while in (B), energy from digestible fiber was included. Small points give the composition of individual samples, while large solid points indicate means.

(C) Composition diets of species classified as functional herbivores, hypercarnivores, neither (other), and pandas (excluding and including energy from digestible fiber). For individual herbivore and hypercarnivore species, diet compositions are shown as small open points, while means of each species classification are shown as large solid points. In all panels, demarcated areas correspond to a 95% confidence interval for the mean.

(D) The bottom panel shows the proportions of plant and animal foods in the diets of mammal species (modified from [11]). Also shown is the threshold defining hypercarnivores (following [12], dashed horizontal line delineating 70% animal food). Top panels show the prediction intervals (black text) for the percentage of protein, digestible carbohydrate, fat, and the protein:non-protein energy ratio in the diets of hypercarnivores and herbivores in the data we extracted from the literature (see Figure S1). The boxes give the corresponding values for the giant panda diet. The diet of the giant panda corresponds with herbivory at the level of food proportions, but in terms of the percentage of energy contributed by protein and carbohydrate and the protein:non-protein energy ratio, it resembles that of hypercarnivores. The percentage of fat in the diets of giant pandas fell within the prediction intervals for both hypercarnivores and herbivores.

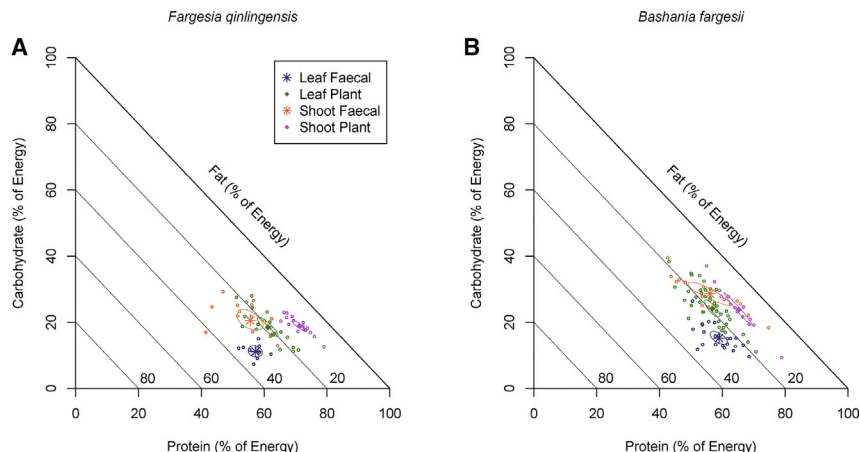
See also Tables S1–S3.

reject the hypothesis that differential elimination of protein alters the macronutritional profile of the absorbed diet to resemble more closely the diets of herbivores.

The macronutrient composition of panda milk falls among the carnivores, and it is substantially different from the milk of most herbivores in our sample, with the exception of a few species of Artiodactyls (Figure 4; Table S5). The percentage of energy

contributed by protein in giant pandas' milk is 21.9%, which does not significantly differ from the mean of terrestrial carnivores (15.1%, est. = 0.45, CI = −0.15 to 1.06) and is higher than the mean of marine carnivores (13.0%, est. = 0.63, CI = 0.31 to 0.94) and primates (11.8%, est. = 0.73, CI = 0.42 to 1.04) but similar to that of Artiodactyla (21.8%, est. = 0.003, CI = −0.21 to 0.21).





**Figure 3. Macronutrient Energy Ratio of the Plants Eaten with Matched Feces of Giant Pandas**

Right-angled mixture triangles showing the composition of leaves and shoots of (A) *Bashania fargesii* and (B) *Fargesia qinlingensis* in terms of the percentage of energy from protein, carbohydrate, and fat when sampled directly from the plant and when sampled from panda fecal matter. Small points give the composition of individual samples, while large solid points indicate means, with a 95% confidence interval for the mean demarcated. Note that in all cases, energy from digestible fiber has been excluded. See also Tables S2 and S4.

## DISCUSSION

Our results thus showed that the macronutrient composition of the diet of giant pandas is similar to that of carnivore diets and unlike that of herbivore diets. Most strikingly, the percentage of energy from protein was equivalent to that of hypercarnivores, even when we conservatively assumed high levels of hemicellulose and cellulose digestion [13, 14]. With about 50% of its energy coming from protein, the giant panda diet resembles that recorded for feral cats, *Felis silvestris catus*, (52%) and wolves, *Canis lupus*, (54%) [15, 16]. Equally high dietary protein energy values are implicit in results previously reported for giant pandas, but they have been obscured by the fact that dietary macronutrient content was expressed only as a percentage of dry weight and not also as a percentage of energy [17, 18].

Two separate factors contribute to the carnivore-like composition of giant panda diets. First, the macronutrient mixture was exceptionally high in protein (61% of energy), equivalent to the macronutrient composition of meat. Second, the short digestive tract and fast gut transit times are associated with low levels of fiber digestion. Therefore, compared with many herbivore diets, structural carbohydrates in the diets of giant pandas contribute only minimal non-protein energy.

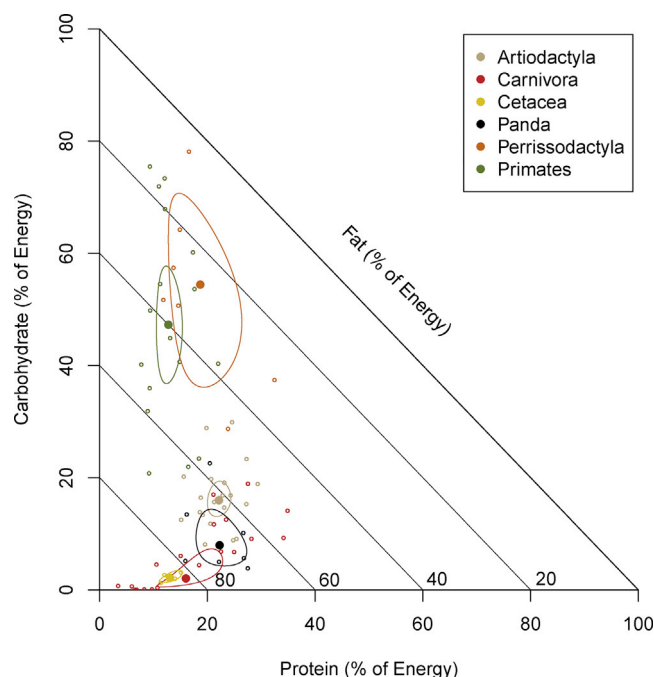
Our comparison of foods with matched feces demonstrates that the macronutritional similarity of giant pandas and carnivore diets applies both at the levels of the ingested and the absorbed diet. For *Fq* and *Bf* leaves, the energy ratio of protein was largely unchanged in the feces relative to the food, showing that protein was not preferably eliminated over carbohydrate and fat. For shoots of both species, protein in the food was higher than in matched feces, suggesting that the absorbed diet had an even higher contribution of protein to total macronutrients than did the ingested diet. This analysis establishes that protein was not selectively eliminated by pandas to reduce the high protein energy ratio of the diet, a strategy deployed by other herbivore species experimentally fed imbalanced high-protein diets [19]. Further, the relatively high absorption efficiency of protein concurs with previous results showing that protein measures for foods reflect available nitrogen and are not an artifact of unavailable, bound nitrogen, as has previously been noted of bamboo [20]. Although we did not measure urinary nitrogen, we suspect

that it would be high due to giant pandas catabolizing ingested amino acids via gluconeogenesis to supply glucose for energy metabolism and excreting the nitrogen residues. This is the same strategy employed by hypercarnivores [21].

Our analysis of milk composition reveals that the dietary similarity of pandas and other carnivores extends across the life cycle. Giant panda milk fell among that of other carnivores, both in terms of its high percentage of protein energy and low carbohydrate percentage. Pandas were not, however, the only herbivorous species for which this applied, with the same being true of bovids and cervids. The reasons these herbivores have milk compositions similar to those of carnivores are unclear, but one suggestion is that they reflect an adaptation for rapid growth [22]. The newborn cubs of the giant panda are very small, with an average body weight of 145 g, 1.6% of maternal mass [23], and they have one of the fastest growth rates of any mammal [17]. The similarity of giant panda milk with that of carnivores might also reflect the carnivorous macronutrient profile of the adult diet. Correlations between adult diet and milk composition exist among some marine carnivores, Cetacea, and primates [24, 25]. All else being equal, milk that matches the macronutrient composition of the maternal diet is, in terms of nutrient budgets, likely cheaper to produce, and it will prepare the infant for the macronutrient profiles encountered upon weaning.

The low metabolic rate of giant pandas warrants consideration in the context of the findings [26]. Data suggesting that carnivores have lower body temperatures and basal metabolic rates than herbivores have been interpreted as reflecting the relatively high thermal requirements of digesting fiber [27]. The low metabolic rates coupled with low efficiency of fiber digestion by giant pandas is consistent with this interpretation. On the other hand, reduced energy expenditure might be a necessary adaptation for an obligate herbivore that feeds on a diet with exceptionally low carbohydrate and fat content, given the important energetic role of fats and carbohydrates relative to protein in other herbivorous mammals (e.g., [28]).

It is interesting to speculate on the functional relationship between the carnivore-like digestive system of giant pandas and the percentage of energy from protein in their diet. A conspicuous adaptive challenge in the transition to herbivory by giant pandas concerns the dilution of macronutrients by the high levels of fiber in bamboo compared with those in animal-derived foods. Provided suitable bamboo is available, this is arguably less



**Figure 4. Macronutrient Energy Ratio of the Milk of Giant Pandas and Other Mammal Species**

Right-angled mixture triangles showing the composition (% of energy from protein, carbohydrate, and fat) of milk of belonging to different orders and to the panda. For individual species (and individual estimates in the case of panda), milk compositions are shown as small open points, while means are shown as large solid points (95% confidence intervals of means are demarcated). See also Table S5.

challenging than dealing with macronutritionally imbalanced diets. For example, studies using synthetic diets have shown that locusts (*Locusta migratoria*) adjust the amount eaten (up to five-fold) to compensate for dietary dilution with indigestible cellulose, but they are substantially less capable of dealing with macronutrient imbalance [29, 30]. In giant pandas, a short, carnivorous gut facilitates rapid throughput, and the high abundance and easy accessibility of bamboo enable large amounts to be eaten, compensating for low digestive efficiency. This rapid throughput system is incompatible with endogenous or microbial digestion of refractory carbohydrates, thus helping to explain the carnivore-like digestive enzymes and gut microbiota [6, 7].

In conclusion, our results build on a recent diet theory that predicts the classifications at the levels of foods and nutrients might diverge and cautions that the assumption of cross-level congruence can be misleading [8]. We provide an example of an animal that resembles different trophic niches at the food and macronutritional levels. This can help resolve long-standing questions concerning giant panda evolution, including the unusual transition to extreme specialized herbivory by a member of a carnivorous clade. In fact, the transition was likely more superficial than assumed, combining substantial adaptation to new food types with relatively smaller changes in macronutrient handling. Consistent with this are the dietary adaptations of giant pandas. Notable herbivore traits, including dental and cranial adaptations and the pseudo-thumb, are predominately concerned with food

processing. In contrast, the carnivore-like traits, including gut structure, digestive enzymes and the gut microbiota, are more closely associated with macronutrient processing. This suggests that giant pandas required minimal evolutionary modification from their ancestral state to deal with the macronutritional properties of bamboo and acquired principally food-handling and some micronutritional adaptations in the switch to this abundant food source.

## STAR★METHODS

Detailed methods are provided in the online version of this paper and include the following:

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- EXPERIMENTAL MODEL AND SUBJECT DETAILS
- METHOD DETAILS
  - Foraging observation and sample collection
  - Nutritional analysis
  - Macronutrient energy analysis and comparison
- QUANTIFICATION AND STATISTICAL ANALYSIS

## SUPPLEMENTAL INFORMATION

Supplemental Information can be found online at <https://doi.org/10.1016/j.cub.2019.03.067>.

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## AUTHOR CONTRIBUTIONS

F.W. and Y.N. designed research; Y.N., W.Z., Y.H., Q.W., and L.Y. performed research; Y.N., A.L.S., D.R., and W.Z. analyzed data; Y.N., D.R., and F.W. wrote the paper.

## DECLARATION OF INTERESTS

The authors declare no competing interests

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## STAR★METHODS

### KEY RESOURCES TABLE

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Critical Commercial Assays		
Plant Soluble Sugar Assay Kit	Solarbio Science & Technology	Cat#: BC0705
Plant Starch Assay Kit	Solarbio Science & Technology	Cat#: BC0035
Software and Algorithms		
R ver. 3.5.2	R Foundation	<a href="https://www.r-project.org">https://www.r-project.org</a>
Other		
Macronutrient energy ratio data	This paper	Available in <a href="#">Supplemental Information</a>

### CONTACT FOR REAGENT AND RESOURCE SHARING

Requests for further information should be directed to and will be fulfilled by the Lead Contact, Fuwen Wei ([weifw@ioz.ac.cn](mailto:weifw@ioz.ac.cn)).

### EXPERIMENTAL MODEL AND SUBJECT DETAILS

We conducted this study in a key panda reserve, Foping National Nature Reserve, in the Qinling Mountains, China. The Qinling Mountains is the northern most mountain range that wild giant pandas populate with a population of 345 individuals. In an area of 294 km<sup>2</sup>, the Foping Nature Reserve harbors the highest population density in the world. The Foping reserve, which spans elevations from 980 to 2904 m, has two dominant bamboo species, *Bashania fargesii* (hereafter, *Bf* or *B. fargesii*) and *Fargesia qinlingensis* (hereafter, *Fq* or *F. qinlingensis*), at mean elevations of 1600 and 2400 m, respectively. These two bamboos comprise the diet of giant pandas in this area, which switch between leaves and shoots of these species in synchrony with their phenology. With approval from the State Forestry Administration of China, we conducted a long-term study of the giant panda ecology in this area by fitting pandas with GPS/VHF collars (Lotek Wireless Inc., Ontario, Canada). This enabled us to locate and track the giant pandas for behavioral observations. The GPS collars were programmed to attempt a location fix every 3 h. To show the seasonal foraging migration pattern of giant pandas in this area, we randomly chose the GPS data of two GPS collared pandas. These GPS data include the locations recorded automatically by GPS collars when giant pandas migrated seasonally for bamboo shoot and leaf utilization.

### METHOD DETAILS

#### Foraging observation and sample collection

Behavioral observations were performed by following individual pandas from short distance (usually 10–20 m) to examine their seasonal pattern of movement and food selection. We recorded which species, tissues and ages of bamboo were eaten, and concurrently collected food and fresh feces from the feeding patch. Food and feces were immediately placed in clean zip-lock bags, the residual air compressed out, and placed on ice for transport, to prevent bacterial contamination and loss of volatiles. A feeding patch was defined as an area with a size of about 300 × 300 m within which a panda was observed feeding for at least 24 h, and this is much longer than the gut passage time,  $8 \pm 3$  h [13]. The food and fecal samples were coded by the feeding patch and transported to lab for nutritional analysis immediately. All samples were ground to powder with a common multifunctional laboratory mill (KMS-800Y) and oven dried at 55°C before laboratory analyses.

#### Nutritional analysis

Fiber was measured by analyzing the dried samples for neutral detergent fiber (NDF), acid detergent fiber (ADF) and acid detergent lignin (ADL) according to the method developed by Vansoest et al. [31] via sequential analysis using Fibertec 2010. We used the Kjeldahl method to analyze N concentrations with a Kjeltac 8400. Crude protein was calculated by multiplying N × 6.25. This coefficient is standard for bamboo (e.g., [17]), and reliably estimates available protein because bamboo does not contain protein-binding tannins [20]. The fat was determined by Soxhlet extraction method with the automated Soxhlet extractor, Soxtec 8000. We calculated the non-structural carbohydrate as the total content of the soluble sugar and starch. The soluble sugar and starch were determined using Plant Soluble Sugar Content Detection Kit and Starch Content Detection Kit (Beijing Solarbio Science & Technology Co., Ltd., Beijing, China) with the anthrone method [32]. The colorimetry of samples was treated with enzymatic-reader at 620 nm (Synergy H1 Hybrid Multi-Mode Microplate Reader, Biotek Instruments, Winooski, VT, USA). The macronutrients were converted to percent metabolizable energy using conversion factors of 4 kcal/g for protein and carbohydrate, and 9 kcal/g for fat.



### Macronutrient energy analysis and comparison

To compare the energy ratio of macronutrients in giant pandas' diets with that of other mammals, we searched the available literature for studies that presented the proportional protein:fat:carbohydrate composition of the diets of species spanning strict carnivores to herbivores (see the species in [Figure S1](#)). Previous studies indicated that pandas could digest a fraction of ingested hemicellulose and cellulose, so we also did a comparison by adding possible digested hemicellulose and cellulose to the carbohydrate. To do so, we used an average of published digestion coefficients of 22% and 8% for hemicellulose and cellulose, respectively [[13](#), [14](#)]. We used Right-angled Mixture Triangles (RMTs), [[11](#)] to examine the relationship of proportional macronutrient compositions in the diets of giant pandas and published estimates of the other species. To estimate the relative digestive extraction efficiencies by giant pandas of protein, fat and carbohydrate, we compared the energy ratios of macronutrients in food and the associated feces using a proportional depletion framework based on RMTs [[10](#)]. We also calculated and compared the energy ratio of macronutrients in the milk of giant pandas and other mammals using published measures (see [Table S5](#)), and displayed these compositions using RMTs. In all cases mean compositions and 95% confidence intervals presented on RMTs are transformations of 3-dimensional estimates using linear models of additive log ratios fitted using the *compositions* package in R [[33–35](#)].

### QUANTIFICATION AND STATISTICAL ANALYSIS

We used linear models (LMs) of logit transformed proportions [[36](#)] to make estimates and comparisons between percentages of specific macronutrients (e.g., proportions of protein versus carbohydrate) or categorical predictors (e.g., leaves versus shoots or feces samples versus associated food samples, or taxonomic groups). Where we considered only a single macronutrient (usually percentage energy from protein), we used standard LMs implemented using the 'lm' function in the base package in R. For comparisons of greater than one percentage (usually energy from protein, carbohydrate and fat), we used multi-response LMs with a fully specified residual covariance matrix (to account for inter-dependence among proportions; following the method in Senior et al., 2016 [[37](#)]). Multi-response linear models were implemented using the Bayesian modeling function 'MCMCglmm' in the R package *MCMCglmm* [[38](#)]. For standard LMs and multi-response LMs we present estimates with 95% confidence and 95% credible intervals (CIs), respectively, and interpret estimates with 95% CIs not spanning zero as statistically significant [[39](#)]. Where needed, predicted distributions of macronutrient ratios of diets of species falling within specific classifications (e.g., herbivores and hypercarnivores) were estimated as 95% prediction intervals (PIs) from LMs generated using the "predict" function in R.