

# Withered on the stem: is bamboo a seasonally limiting resource for giant pandas?

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**Abstract** In response to seasonal variation in quality and quantity of available plant biomass, herbivorous foragers may alternate among different plant resources to meet nutritional requirements. Giant pandas (*Ailuropoda melanoleuca*) are reliant almost exclusively on bamboo which appears omnipresent in most occupied habitat, but subtle temporal variation in bamboo quality may still govern foraging strategies, with population-level effects. In this paper, we investigated the possibility that temporal variation in the quality of this resource is involved in population regulation and examined pandas' adaptive foraging strategies in response to temporal variation in bamboo quality. Giant pandas in late winter and early spring consumed a less optimal diet in Foping Nature Reserve, as the availability of the most nutritious and preferred components and age classes of *Bashania fargesii* declined, suggesting that bamboo may be a seasonally limiting resource. Most panda mortalities and rescues occurred during the same period of seasonal food limitation. Our findings raised the possibility that while total bamboo biomass may not be a limiting factor, carrying capacity may be influenced by subtle seasonal variation in bamboo quality. We recommend that

managers and policy-makers should consider more than just the quantity of bamboo in the understory and that carrying capacity estimates should be revised downward to reflect the fact that all bamboos are not equal.

**Keywords** Bamboo biomass · Diet · Energetic constraints · Foraging strategy · Population regulation

## Introduction

Foraging strategies are a central focus in animal ecology due to their pervasive influence on many other topics of importance, including habitat selection, home range, social interactions, reproduction, and population regulation (Stephens and Krebs 1986; Goss-Custard et al. 1995; Owen-Smith et al. 2010). Faced with seasonal variation in quality and quantity of available plant biomass, herbivorous foragers may switch to different plant resources to meet their nutritional requirements, which may offset the effects of restricted food availability. However, above strategies may be insufficient to eliminate its negative consequences on body condition and fitness (Jhala 1997; Wanless et al. 2005; Brown and Sherry 2006; Shrader et al. 2006). Thus, carrying capacity may be constrained by seasonally limited food resources, which constitute a cornerstone of population regulation (Lack 1954; Sinclair 1989; Goss-Custard et al. 1995; Saether et al. 1996).

The giant panda (*Ailuropoda melanoleuca*), reliant almost exclusively on low-quality but constantly available bamboo as a foraging resource, is a useful model to study foraging decisions and seasonally adaptive shifts in diet selection. The panda retains the simple digestive tract of its carnivore ancestors, and its genome does not code for enzymes needed to digest cellulose (Hu et al. 2010; Li et al. 2010; Wei et al. 2012), although this is to some degree compensated by gut microbes

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that aid in cellulose digestion (Zhu et al. 2011a; Wei et al. 2012). As for optimal diet selection, the panda appears to do by favoring certain species of bamboo, leaves over stems, and younger over older bamboo plants to maximize nutrient intake (Schaller 1985; Pan et al. 2001; Zhang et al. 2007a; Nie et al. 2015a). This omnivore-turned-herbivore specialist devotes approximately 14 h each day to foraging and is behaviorally and physiologically adapted to conserve energy (Nie et al. 2012a,b,c).

Although other life history characteristics interact with forage phenology in seasonally fluctuating environments, such as the energetically taxing breeding/lactation periods driving body condition in folivorous lemurs (Ganzhorn 2002), the panda, a species so nutritionally challenged, should optimize its diet to select the most nutritious plants or parts of the plant. It might also be especially sensitive to seasonally limiting food resources. Many species may adjust their intake rate, live off of stored body reserves, or broaden their diet to include less preferred foods when facing seasonally restricted food resources (Stephens and Krebs 1986; Owen-Smith 1994; Jhala 1997; Shrader et al. 2006). But the panda confronts ecological and evolutionary constraints that may limit each of these options. With time allocated to foraging at greater than 50% and the inherent limits of digestive tract capacity and passage time, the panda may not be able to increase daily food intake (Feng et al. 2009; Zhu et al. 2010a, 2011b; Qi et al. 2012) and to amass energy reserves in the form of body fat as readily as other herbivores and its ursid relatives (Schaller 1985). As a bamboo specialist, the panda does not switch among different plant species other than among two or more available species of bamboo (Schaller 1985). Instead, it must select among individual bamboos and bamboo parts that vary in nutritional quality (Wei et al. 1999). Thus, although bamboo is omnipresent throughout the year, seasonal variation in nutritional quality perhaps presents challenges to the panda which appears to have little margin of safety energetically (Schaller 1985; Sun et al. 2010; Nie et al. 2015b).

Population viability analysis suggests that carrying capacity may be one of the most important factors limiting panda population size, leading to suggestions for habitat management to increase carrying capacity (Zhou and Pan 1997). To guide habitat management, more fine-scale understanding of habitat requirements is needed (Linderman et al. 2005; Swaisgood et al. 2009, 2011; Zhu et al. 2010a,b; Zhang et al. 2011) and move understanding of foraging requirements beyond “they eat bamboo.” Indeed, anyone visiting panda habitat will quickly realize that pandas live in a virtual sea of food because bamboo is a highly conspicuous component of the understory and will wonder how bamboo could be a limiting factor regulating panda population size. However, panda populations remain lower than apparent carrying capacity predicted by bamboo abundance, biomass, and distribution (Schaller 1985; Linderman et al. 2005), raising the possibility

that carrying capacity may be not influenced by total bamboo biomass. Preferences for younger bamboo or different parts of the plant are associated with variation in nutritional quality (Schaller 1985; Sun et al. 2010; Nie et al. 2015b), shedding light on the failure of bamboo biomass to accurately predict population size. Thus, it is reasonable to hypothesize that panda populations are limited by the availability of high-quality bamboo forage. Previous research has established a possible link between seasonally limiting resources and behavioral and physiological components of their reproductive strategy, which could have population-level effects (Nie et al. 2012a,b,c).

Although rare, endangered, and exceedingly difficult to observe in the wild, pandas are fortunately somewhat unique in that they leave behind an accurate record of their foraging decisions in the form of bite-severed bamboo stems at foraging sites, presenting an excellent opportunity to examine their diet selection. In addition, they defecate prolifically (averaging nearly 50 feces/day, Schaller 1985), leaving long-lasting records of their foraging decisions, due to the fibrous nature and slow degradation of their feces. To investigate the possibility that temporal variation in the quality of bamboo resource is involved in panda population regulation, we conducted a field survey from November 2008 to April 2009 in Foping Nature Reserve, China. Two bamboo species, namely *Bashania fargesii* and *Fargesia qinlingensis*, dominate there. For many animal populations, seasonally limiting resources are believed to be important regulators, setting carrying capacity at the number of individuals that can be sustained through periods of seasonal resource restriction (Lack 1954; Sinclair 1989; Goss-Custard et al. 1995; Saether et al. 1996). Thus, our field survey was only conducted in *B. fargesii* forest because almost all pandas during that period stay in winter habitat and feed on this bamboo species (Zhang et al. 2014). Our goals are (1) to quantify bamboo availability in panda habitat and document changes in nutritional quality, (2) to uncover temporal variation in panda diet composition and investigate temporal preference for bamboo culms across ages, and (3) to examine range-wide records of mortality and rescues of weakened pandas to establish the possible link between mortality with seasonally restricted food resources. As winter progresses to early spring, the availability of preferred forage (younger bamboo and green leaves) will decline. We hypothesize that pandas' diet and foraging strategies would change to reflect these variations, which may, in turn, affect their survival.

## Materials and methods

### Study area

Spanning about 294 km<sup>2</sup>, Foping National Nature Reserve (N 33° 32'–33° 45', E 107° 40'–107° 55') in the Qinling

Mountains of Shaanxi Province, China, was established in 1978, primarily for the preservation of giant pandas (Zhang et al. 2007b). Elevation ranges from 980 to 2904 m, with annual mean temperature of 11.5 °C (average min = −3 °C in January, average max = 28 °C in July). Approximate annual rainfall is 930 mm and occurs mainly between July and September. Snowfall typically occurs in November at elevations >2000 m and about a month later at lower elevations (<2000 m). Snow begins to melt in early March and has completely melted at higher elevations by late March.

Vegetation below 2000 m is dominated by deciduous broadleaf forest, interspersed with mixed coniferous forest. Above 2500 m, the vegetation is primarily coniferous forest interspersed with subalpine shrubs and meadows (Ren et al. 1998). Foping Reserve understory provides ideal growing conditions for panda forage, principally the two bamboo species *B. fargesii* (occurring mostly <2000 m elevation) and *F. qinlingensis* (occurring mostly >2000 m), supporting the greatest density of giant pandas in the world (Zhang et al. 2007b).

## Data collection and statistical analyses

### *Temporal variation in bamboo availability*

Previous research has shown that brown and withered leaves are less nutritious than green leaves, and older stems are less nutritious than younger stems (Sun et al. 2010; Nie et al. 2015b). To examine temporal variation in quality and quantity of bamboo available, 10 transects were established, each running from the valley to the ridge along an elevational gradient. Within each transect, 5–10 plots were sampled, 1 every 50 m elevation gain. Plots were visited monthly from November 2008 to April 2009, the period of time when pandas reside at lower elevation sites, that is, winter habitat (Zhang et al. 2014). Bamboo culms in plots were divided into three age classes according to morphological features (sensu Qin et al. 1993). One-year-old bamboo culm usually has only primary branches, with the basal node sheath intact and not stained. Two-year-old bamboo culm usually has secondary branches, with stained basal node sheath that is not intact. All others were classified as the rest bamboo culms. To evaluate bamboo quality, we collected 15 bamboo samples for each age class per month, for a total of 45 samples per month. Each sample was comprised of a single whole bamboo culm, and leaves, branches, and stems were weighed separately. The leaves were divided into green and withered ones and counted and weighed separately. In the end, two-way ANOVA was used to evaluate the effect of month and bamboo age on the number and wet weight of green leaves and withered ones.

### *Selection of bamboo culms of different ages by month*

Panda foraging sites were located during random surveys and opportunistically identified by signs of panda foraging: bamboo stem cleanly severed, up to about 1 m above ground, leaving behind bamboo “stumps” (sensu Schaller 1985). No other animal forages on bamboo in this way, so the record of panda foraging is unambiguous. At each foraging site, 1.5 × 1.5 m<sup>2</sup> plots were established and we counted the number and type of culms selected and eaten and those remaining that were not selected. Meanwhile, we recorded locations of foraging sites (latitudes, longitudes, and elevations) and smashed all panda feces after survey. We categorized bamboo culms as 1-year-old, 2-year-old, or the rest as mentioned above. Preferential selection was determined by the percentage of each age class of bamboo culms eaten in the total eaten compared to its relative availability (percentage of bamboo of different ages present in the total before foraging). Distance between two consecutive plots was not less than 50 m. Approximately 30 plots were sampled each month.

Two-way ANOVA was used to test whether the effects of month and availability on the selection of bamboo of different ages were significant or not. To evaluate selection of bamboo culms across age classes each month, one-way ANOVA was used to test whether the difference in percentage before and after foraging was significant or not for bamboo culms in each age class.

### *Pandas' food habits*

During the field survey, we opportunistically collected approximately 30 fecal samples each month. All samples were collected from the same areas where above surveys were conducted. In total, 178 fresh feces were collected and oven-dried. Because bamboo passes through the panda digestive system relatively unchanged, it is easy to separate stem and leaf material (Hu et al. 1985; Wei et al. 1999). The proportion of leaves and stems in the diet was estimated by dry weight in feces. Correlation between percentage of dry matter of leaves in feces and that of wet weight of green was analyzed through Pearson's correlation coefficient when data were normally distributed or Kendall's tau-b correlation coefficient if not normally distributed.

### *Correlating temporal variation in mortality with restricted food*

Two datasets documenting panda mortality were reported here. The first is from known mortalities of pandas found dead in the Foping Nature Reserve between 2004 and 2010. The second is the records between 2000 and 2012 for all pandas found dead in the wild or rescued in Sichuan province, China. The fate of rescued pandas, which were sick, debilitated, or in

poor condition, varied, and although many of them died, others were treated and survived. Records indicated that they were in ill health and would likely have not survived without intervention. However, rescue and mortality data that support the food limitation hypothesis in panda mortality may result from other confounding factors, such as male-male mating competition that occurs during the spring. To shed light on these alternative hypotheses, we examined the effects of panda sex and age on rescue records. Chi-squared tests were adopted to test whether mortality and rescue records were associated with month, panda age, and sex.

All analyses were conducted through SPSS 13.0. The significance level was set at 0.05.

## Results

### Temporal variation in bamboo availability

Month and bamboo culm age influenced the available biomass of green leaves significantly (Table 1). For green leaves, percent of the total number and wet weight gradually decreased from November to April next year (Fig. 1a, b). Both measures of bamboo quality (% total green leaves and % weight of green leaves) decreased with increasing bamboo age.

### Selection of bamboo culms of different ages by month

For 1-year-old and 2-year-old bamboo culms, the percentage foraged was always greater than the percentage available, indicating a preference for younger bamboo, although this result only attained statistical significance for 2 months (Table 2). Meanwhile, our data show a clear avoidance of the rest bamboo culms, with significantly less consumed than available for each month. There was a tendency for both available and foraged 1-year-old and 2-year-old bamboo culms to decrease from November to April, with a corresponding increase in the availability and consumption of the rest bamboo culms (Table 2, Fig. 2a, b). Two-way ANOVA indicated that availability had a large and significant effect on foraging on all bamboo age classes, whether analyzed with regard to temporal variation or not (Table 3). Thus, as higher quality young bamboo became less abundant, pandas relied more heavily on less nutritious older bamboo, consuming the highest proportion of older bamboo during March and April.

### Pandas' food habits

From November to April next year, the percentage of dry matter weight of leaves in feces decreased gradually from almost 100 to 82.3%. Meanwhile, that of stems and branches increased from near 0 to 17.7% (Table 4). When analyzed with

regard to availability, the percentage of dry matter weight of leaves in feces was positively correlated with that of wet weight of green leaves (Pearson's correlation  $r = 0.94$ ,  $P < 0.05$ ) on available bamboo, indicating greater selectivity for leaves over stems when leaves were green than when they were withered.

### Correlating temporal variation in mortality with restricted food

In Foping, 53.8% (7/13) of mortalities occurred in winter and 23.1% (3/13) were in early spring (April), with all but one of the remaining mortalities occurring in May, just after the period of restricted food supply (Table 5). Panda mortality in the reserve was higher in late winter and early spring than that in the remaining months ( $\chi^2 = 37.18$ ,  $df = 11$ ,  $P < 0.05$ ). For the 48 rescue records in Sichuan province, the highest number of rescue events occurred in March (37.5%, 18/48), followed by February (14.58%, 7/48), and then by April (10.42%, 5/48), May (10.42%, 5/48), and December (10.42%, 5/48). Similarly, rescue cases for pandas in Sichuan were not distributed evenly across months ( $\chi^2 = 69.50$ ,  $df = 11$ ,  $P < 0.05$ ), with higher frequencies occurring in late winter and early spring.

Contrary to predictions from the male-male competition hypothesis, females ( $N = 27$ ) were more likely to be rescued than males ( $N = 6$ ) ( $\chi^2 = 11.28$ ,  $df = 1$ ,  $P < 0.05$ ) and subadults were more frequently rescued than adults ( $\chi^2 = 9.79$ ,  $df = 3$ ,  $P < 0.05$ ;  $N = 4$  for cubs,  $N = 17$  for subadults,  $N = 7$  for adults,  $N = 10$  for elderly adults). Although this analysis does not take into account the demographic structure of the population, which is unknown, it does indicate that subadult females are likely the most vulnerable.

## Discussion

Bamboo availability has figured prominently in previous efforts to estimate carrying capacity for pandas, but all of these estimates have yielded carrying capacity estimates far larger than actual population size (Schaller 1985; Linderman et al. 2005). Our data strongly suggest that total bamboo biomass may not be the factor regulating carrying capacity, as there is subtle variation in bamboo quality. Reserves containing higher proportions of older bamboo, for example, may have lower carrying capacity than those containing much younger bamboo. Moreover, carrying capacity may be governed less by total biomass than by distribution and abundance of green leaves during the late winter-early spring season. Costs of search time to locate these higher quality food resources may also influence environmental carrying capacity in ways heretofore poorly understood.



**Table 1** Effects of month and bamboo age on available biomass of green leaves and withered leaves through two-way ANOVA

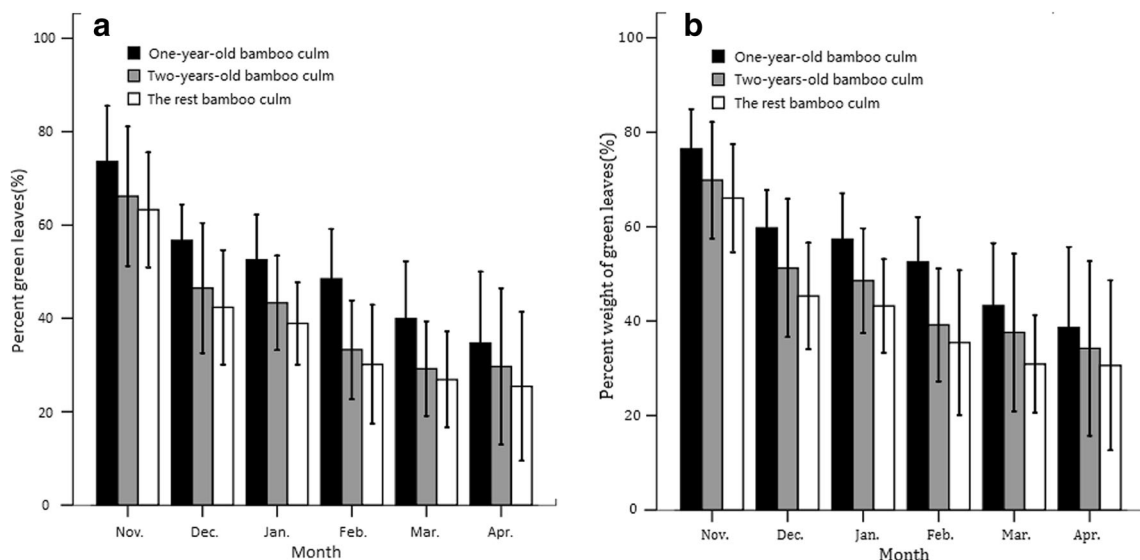
Items	Factors	df	F	P
Total number of green leaves	Month	5	33.10	0.00
	Bamboo age	2	30.60	0.00
	Month × bamboo age	10	3.04	0.00
Wet weight of green leaves	Month	5	11.12	0.00
	Bamboo age	2	7.21	0.00
	Month × bamboo age	10	1.09	0.37
Total number of withered leaves	Month	5	5.91	0.00
	Bamboo age	2	85.27	0.00
	Month × bamboo age	10	0.57	0.84
Wet weight of withered leaves	Month	5	7.14	0.00
	Bamboo age	2	53.1	0.00
	Month × bamboo age	10	0.44	0.93

**Foraging ecology of pandas**

Taken together, the study reported here suggests that bamboo may be a seasonally varying and limiting resource that influences individual foraging decisions, with possible population-level consequences. Strong temporal variation in the quantity and quality of bamboo available to pandas sets the stage for adaptive shifts in foraging strategies to offset seasonal energetic constraints. In our study, the proportion of withered leaves increased from approximately 30% to nearly 80% between November and February, suggesting that much greater foraging effort would be required to continue consuming green leaves during the late winter and early spring. Throughout the study, pandas favored leaves over stems; the latter comprised less than 5% of their diet until March–April, when consumption of stems increased sharply to about 18%,

as indicated by fecal samples. Correlation analyses indicated more directly that pandas responded to decreasing leaf quality by consuming less leaf and favoring more stems in their diet. For *B. fargesia*, green leaves contain more than eight times as much crude protein as stems (Sun et al. 2010). The increased consumption of low-quality stems suggests that reduced availability of leaves of high nutritional quality precipitated this diet shift.

Bamboo quality is also affected by bamboo culm age: Younger bamboo culm is more nutritious, having proportionately fewer withered leaves and higher protein/cellulose ratio (Schaller 1985; Pan et al. 2001; Sun et al. 2010) and a more optimal composition of key nutrients (Nie et al. 2015b). As winter progressed to spring, the availability of younger bamboo culms gradually diminished as pandas foraged preferentially, resulting in the availability of younger bamboo culms



**Fig. 1** Variation in available biomass of green leaves on *B. fargesii* bamboo across months and age classes (data presented by mean ± SD). Number of green leaves divided by total number of leaves (green plus

withered leaves) (*percent green leaves*). Weight of green leaves divided by total weight of leaves (green plus withered leaves) (*percent weight of green leaves*)

**Table 2** Seasonal variation in selection of bamboo culms by giant pandas as determined at foraging sites

Month	One-year-old bamboo culm			Two-year-old bamboo culm			The rest bamboo culm		
	Available <sup>a</sup>	Percent foraged	<i>F(P)</i> <sup>b</sup>	Available	Percent foraged	<i>F(P)</i>	Available	Percent foraged	<i>F(P)</i>
November	19.00 ± 11.04	30.89 ± 19.89	8.45 (<0.05)	28.19 ± 11.93	43.67 ± 20.15	13.33 (<0.05)	51.26 ± 17.12	25.44 ± 18.60	32.33 (<0.05)
December	21.53 ± 13.31	27.51 ± 18.75	1.97 (0.17)	29.44 ± 12.24	35.19 ± 15.37	2.49 (0.12)	49.03 ± 17.62	37.30 ± 21.00	5.32 (<0.05)
January	21.47 ± 20.21	29.24 ± 25.44	1.60 (0.21)	29.76 ± 17.01	37.95 ± 21.18	2.54 (0.12)	48.77 ± 18.49	32.81 ± 20.86	9.17 (<0.05)
February	22.75 ± 12.45	30.31 ± 18.94	3.34 (0.07)	23.69 ± 12.75	27.97 ± 15.77	1.34 (0.25)	53.56 ± 16.52	41.72 ± 19.14	6.58 (<0.05)
March	9.52 ± 12.18	13.22 ± 16.76	0.93 (0.34)	19.22 ± 12.19	28.52 ± 21.89	4.00 (0.05)	71.26 ± 17.24	58.26 ± 26.31	4.95 (<0.05)
April	9.97 ± 8.6	11.72 ± 12.50	0.42 (0.52)	28.03 ± 14.59	38.73 ± 21.85	4.98 (<0.05)	62.00 ± 14.37	49.54 ± 24.43	5.80 (<0.05)

<sup>a</sup> Available refers to the percentage of bamboo culms of different ages present before panda foraging

<sup>b</sup> Test statistics from one-way ANOVA

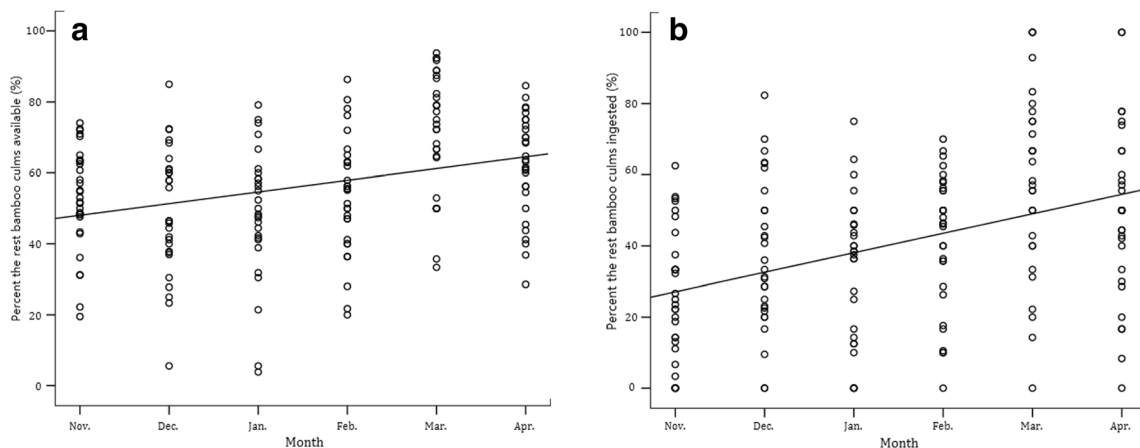
decreased and older bamboo culms increased, driving pandas to consume correspondingly greater quantities of the latter in March and April.

In a heterogeneous environment, an animal foraging at random can ingest fewer nutrients than a selective one (Illius and Gordon 1993). While pandas’ diet selection can be predicted by availability, suggesting random foraging, they also demonstrate clear evidence of preferences for individual bamboo plants or portions that contain higher nutritional value. As a species that must spend more than half of its activity budget foraging to meet its energetic needs, a plausible conclusion is that pandas’ diet selectivity is partially constrained by the need to maximize intake rate. Increased search time necessary to maintain consumption of green leaves and young bamboo at a high level during the limiting winter may entail too great a cost, causing pandas to accept less nutritious food resources to meet or offset immediate nutritional needs (*sensu* Stephens and Krebs 1986; Owen-Smith 1994). From these data, we cannot ascertain whether pandas also adopt other compensatory mechanisms, such as increased intake (Illius and Gordon

1993) or mobilizing stored energy reserves (Shrader et al. 2006), but there is no evidence that energy-limited pandas are able to store sufficient body fat to make the latter plausible (Schaller 1985; Nie et al. 2015a), raising the possibility that pandas’ adaptive diet shifts are insufficient to prevent loss of body condition and negative effects on fitness (Jhala 1997; Wanless et al. 2005; Brown and Sherry 2006).

**Bamboo forage as a seasonally limiting resource influencing population regulation**

Most records on dead or rescued pandas (about 70%) in this study were located besides streams in valley, on farmland, or in villages, similar to that reported by Hu (2001). These areas are usually characteristic of little bamboo cover, potentially eliminating the possibility that dieback in the bamboo understory may have increased the probability that dead or rescued pandas are detected in winter. Our data on foraging indicate that pandas in late winter and early spring consumed a less optimal diet, as the availability of the most nutritious and



**Fig. 2** Availability (a Pearson’s correlation,  $r = 0.35$ ,  $P < 0.00$ ) and ingestion (b Pearson’s correlation,  $r = 0.39$ ,  $P < 0.00$ ) of the rest bamboo culms (beyond 2 years old) at foraging sites by month

**Table 3** Effects of month and bamboo age on selection of bamboo culms by giant pandas through two-way ANOVA

Bamboo age	Factors	df	F	P
One-year-old	Month	5	1.68	0.17
	Availability	89	11.24	<0.05
	Month × availability	47	1.92	<0.05
Two-year-old	Month	5	1.55	0.21
	Availability	95	2.90	<0.05
	Month × availability	53	0.54	0.97
The rest	Month	5	3.21	<0.05
	Availability	116	4.04	<0.05
	Month × availability	34	1.49	0.17

preferred bamboo declined, suggesting that bamboo may be a seasonally limiting resource with population-level effects. Consistent with this point, most panda mortalities and rescues occurred during the same period of food limitation. Other factors such as injuries sustained during male-male competition may contribute to these results, but the strength of this seasonal mortality pattern is difficult to explain without reference to limiting food resources. In addition, our data on panda rescues also indicate that mortality may be higher for females and subadults than for adults and males, although this could in part reflect demographic structure. These data are inconsistent with the hypothesis that seasonal mortality patterns are driven by male-male competition, which occurs coincident with the period of restricted food resources. Both females and subadults are at a competitive disadvantage to the larger males, raising the possibility that rescued individuals from these age-sex classes are dispersing in an attempt to locate better foraging resources, resulting in specific female-biased dispersal pattern in wild pandas (Zhan et al. 2007).

If seasonally restricted food availability affects individual survival, it may also impact other life history variables relevant to fitness. The mating season for giant pandas occurs in late February to early April, a period that coincides with the period of most restricted food availability. Panda mating is energetically expensive, with males and females increasing

**Table 5** Giant panda mortality records for Foping Nature Reserve (2004–2010) and rescue records for Sichuan province, China (2001–2012)

Month	Foping Nature Reserve	Sichuan province
November		5 (10.42%)
December		1 (2.08%)
January		4 (8.33%)
February	1 (7.69%)	7 (14.58%)
March	6 (46.15%)	18 (37.50%)
April	3 (23.08%)	5 (10.42%)
May	2 (15.38%)	5 (10.42%)
June		
July		1 (2.08%)
August		
September		2 (4.17%)
October	1 (7.69%)	
Total	13	48

home range and movement in search of mates (Schaller 1985; Pan et al. 2001; Zhang et al. 2014). Males in particular search out several estrous females and compete vigorously with other males for mating access (Schaller 1985; Nie et al. 2012b). Metabolically expensive, testosterone increases energy expenditure. Most seasonally polygynous male mammals elevate testosterone throughout the mating season, but male pandas display elevated testosterone levels only for brief periods when they are with estrous females, with testosterone levels falling to non-breeding season baseline during periods when estrous females are absent (Nie et al. 2012a), suggesting that male pandas cannot afford the increased energetic costs associated with sustained elevated testosterone in support of mating. In addition, chemical communication, a prerequisite for courtship and reproduction (Swaigood et al. 2000), also peaks during the mating season and appears well designed to minimize energetic costs of this important signaling system (Nie et al. 2012c). The rigors of mating and competition in concert with restricted food supplies for an energy-limited species such as the panda may interact synergistically to reduce reproductive success or increase mortality.

**Table 4** Seasonal variation in the composition of fresh feces left by giant pandas

Month	Wet weight of fresh feces (g)	Dry weight of fresh feces (g)	Percent of dry matter of leaves in fresh feces (%)	Percent of dry matter of stems and branches in fresh feces (%)
November	157.3 ± 8.9	48.2 ± 3.1	≈100	≈0
December	127.5 ± 11.0	39.5 ± 2.8	98.5 ± 1.5	1.5 ± 1.4
January	147.6 ± 9.9	43.2 ± 3.0	96.6 ± 1.4	3.4 ± 1.4
February	146.8 ± 8.5	47.1 ± 2.7	96.7 ± 1.8	3.3 ± 1.7
March	140.9 ± 9.8	44.5 ± 3.0	87.3 ± 5.2	12.3 ± 5.1
April	146.7 ± 10.0	46.8 ± 2.4	82.3 ± 5.9	17.7 ± 5.9

Advancing the hypothesis that bamboo is a seasonally limiting resource for pandas does not eliminate other hypotheses for ecological variables affecting carrying capacity in the species. Old-growth trees as a source of maternity dens, for example, are another factor that may limit the population size in reserves with a history of logging (Zhang et al. 2007b; Hong et al. 2015, 2016). On longer timeframes, the pattern of bamboo flowering and die-off may also influence population size, especially in areas where surrounding anthropogenic development precludes adaptive migration to lower elevations where different species of bamboo may provide alternative food sources following bamboo die-off of species in the pandas' current range (Reid et al. 1989). These ecological factors undoubtedly work together to establish carrying capacity for pandas.

### Policy and management applications

One of the most important contributions of ecological research is to obtain a better understanding of habitat requirements and factors determining the carrying capacity of the environment, enabling the development of management strategies better targeted to address factors influencing population size and sustainability. Identifying seasonally limiting resources is particularly important because conservation or management of these resources is likely to have the most dramatic effects on populations (Lack 1954; Sinclair 1989). In the case of the panda, our results highlighted that young bamboo stands may be of greater importance for panda conservation in the reserve, and special conservation efforts should be paid to the areas where abundant young bamboo stands exist. In addition, managers should consider more than just the quantity of bamboo in the understory and that carrying capacity estimates should be revised downward to reflect the fact that all bamboos are not equal.

The knowledge that younger bamboo is preferred, more nutritious, and retains more green leaves during the lean winter period than older bamboo is important for management policy and planning. Local communities sometimes collect new bamboo shoots for food, a practice which may reduce availability of pandas' preferred food, and should be controlled in protected areas. It is plausible that in many reserves that have undergone panda population restrictions in the past, the bamboo forage has suffered from lack of "grazing lawn" effects (sensu McNaughton 1984; Knapp et al. 1999; Verweij et al. 2006). Absent panda foraging, bamboo stands may age and become less valuable as a foraging resource for pandas. Carefully controlled management actions to cut older bamboo stands and allow younger bamboo to regenerate, if done in a hypothesis-testing adaptive management framework, may be advisable (Swaisgood et al. 2011).

The availability of younger bamboo decreases during the winter and early spring, and the nutritional quality of all

bamboo declines. Thus, management actions should be more restrictive of human activity during this period, particularly activities that might disturb pandas away from valuable young bamboo stands. In addition, it can be anticipated that the reintroduction or translocation of captive pandas during this period of limiting resources would entail higher mortality rates and may induce greater social competition and should be avoided.

Understanding foraging ecology of pandas is critical not just for better management of pandas today but also for assessing the pervasive effects of climate change on bamboo production and the bamboo-obligate panda (Tuanmu et al. 2013). After inclement winter, pandas in Foping Reserve begin to extensively feed on new shoots of *B. fargesii* since May every year, which are nutritious and easily digestible (Nie et al. 2015b). Extensive intake of new bamboo shoots can help pandas to improve their body conditions (Hu 2001; Nie et al. 2015b). Wang et al. (1991) reported that temperature ranks the first factor controlling the growth of *Fargesia denudate*. Tian (1989) found that as temperature increases when winter progresses to early spring, new shoots of *B. fargesii* sprout more and more. Under this circumstance, global warming to some extent can promote new shoots of *B. fargesii* to sprout earlier, which, in turn, can be beneficial for pandas to survival during late winter and early spring. Thus, our findings highlight that climate change models will benefit from a more nuanced understanding of panda foraging ecology, allowing more accurate predictions under different future scenarios.

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