

## Winter foraging strategy of the Chinese Grouse (*Bonasa sewerzowi*): ecological and physiological factors

Jie Wang · Yun Fang · Siegfried Klaus · Yue-Hua Sun

Received: 31 October 2009 / Revised: 24 May 2011 / Accepted: 30 May 2011 / Published online: 10 August 2011  
© Dt. Ornithologen-Gesellschaft e.V. 2011

**Abstract** Both the quality of food and the rate of food intake may influence an animal's food choice. We investigated the feeding choices of Chinese Grouse (*Bonasa sewerzowi*) among a group of trees/shrubs with similar morphologies but heterogeneous chemical compositions in a coniferous forest of the northeastern Qinghai-Tibet Plateau during two winters. The primary food was willow buds and twigs (foraging occurrence of 83%). The Kangding willow *Salix paraplesia* was most preferred, whereas the Sichuan willow *S. hylonoma* was most avoided, and feeding preference (foraging occurrence/food abundance) among the six main willow species was negatively correlated with the tannin content of the plant consumed rather than the protein, lipid, phosphorus, calcium, ash, fibre, or energy contents. The intake rates of dried biomass, energy, protein, fibre and tannin in different willow species were closely related to the bud sizes of these species. However, neither rate of intake nor total biomass acquired from a particular willow was related to the feeding preference of the Chinese Grouse. Therefore, we conclude that, rather than rate of food intake, the

major evolutionary determinant of Chinese Grouse diet has been to maximise the intake of nutrients while simultaneously minimising the intake of digestion inhibitors.

**Keywords** Willow · Food quality · Digestion inhibitors · Intake rate · Herbivorous bird

### Zusammenfassung

### Strategien der Winterernährung des Chinahaselhuhns (*Bonasa sewerzowi*) – ökologische und physiologische Faktoren

Nahrungsqualität und –aufnahmerate können die Nahrungswahl einer Tierart beeinflussen. Wir untersuchten während zweier Winterperioden die Auswahl der Nahrung des Chinahaselhuhns aus einer Gruppe von Baum- und Straucharten ähnlicher Morphologie aber von unterschiedlichem chemischem Gehalt. Das Untersuchungsgebiet ist ein Gebirgsnadelwald auf dem Qinghai-Tibet-Plateau. Die Hauptnahrung bildeten Knospen und Triebe von Weidenarten (83% Anteil). Die Kangding - Weide (*Salix paraplesia*) wurde am meisten bevorzugt, die Sichuan - Weide (*S. hylonoma*) am meisten gemieden. Die Nahrungsbevorzugung bezüglich aller sechs untersuchten Weidenarten war negativ korreliert mit dem Tannin-Gehalt, jedoch nicht mit dem Gehalt an Protein, Lipid, Phosphor, Calcium, Asche, Rohfaser und dem Energiegehalt. Die Aufnahmerate, bezogen auf den Gehalt an Trockenbiomasse, Energie, Protein, Rohfaser und Tannin der verschiedenen Weidenarten war mit der Größe der Knospen korreliert. Weder die Aufnahmerate noch die totale Biomasse, die von einer Weidenart gefressen wurde, entschieden über die Bevorzugung. Fazit: weniger die

Communicated by F. Bairlein.

J. Wang · Y. Fang · Y.-H. Sun (✉)  
Key Laboratory of Animal Ecology and Conservation Biology,  
Institute of Zoology, Chinese Academy of Sciences,  
100101 Beijing, China  
e-mail: sunyh@ioz.ac.cn

J. Wang  
Chengdu Institute of Biology, Chinese Academy of Sciences,  
Chengdu 610041, China

S. Klaus  
Max-Planck-Institute of Biogeochemistry,  
07745 Jena, Germany

Nahrungs-Aufnahmerate als vielmehr die Maximierung von Nährstoffaufnahme bei gleichzeitiger Meidung verdauungs-hemmender Stoffe bildeten beim Chinahaselhuhn die entscheidende evolutionäre Determinante.

## Introduction

To ecologists, factors such as food abundance and susceptibility to predation are dominant determinants of food selection (Whelan and Brown 2005). In contrast, digestive physiologists stress that efficient post-consumption processing has a strong influence on diet selection (Stephens et al. 2007). Until now, few studies have combined these ecological and physiological considerations to address questions of diet choice and foraging ecology (but see Karasov and Hume 1997; Levey and Martínez del Río 1999).

The diets of herbivores, in contrast to carnivores, include low-quality and high-fibre items. To compensate for poor nutritional rewards, herbivore food resources must be more abundant and easier to procure (Hirakawa 1997). For avian herbivores, food quality is considered to be very important because of the severe limits on their digestive processing capabilities (e.g. Kenward and Sibly 1977; Sedinger and Raveling 1988), which in turn limit their ability to compensate for low nutritional quality by eating more food. The foods of herbivorous birds are poor in quality not only because plants are low in nutrients, but also because some components of plants are indigestible and produce secondary metabolites (e.g. Jakubas et al. 1989). The relative roles of these compounds versus the available nutrients in diet selection by grouse—birds of the subfamily Galliformes—are currently unclear (Sedinger 1997).

The Chinese Grouse (*Bonasa sewerzowi*), endemic to the alpine coniferous forest of the Qinghai-Tibet Plateau, is the smallest grouse in the world (Sun et al. 2005). It has been listed in Category I of the Nationally Protected Animals since the 1960s, and is listed in the China Red Data Book of Endangered Animals (Zheng and Wang 1998). General observations have suggested that willow (*Salix* spp.) buds and twigs might be the primary winter food of the Chinese Grouse (Sun 1996). Willows are a heterogeneous group with respect to their composition of primary and secondary plant compounds (Julkunen-Tiitto 1989; Stolter et al. 2005). Studies of food selection by avian herbivores have seldom been conducted at the willow species level (e.g. Williams et al. 1980). In this study, we investigated the winter diet selection of the Chinese Grouse (mainly focusing on the willows) in a conifer-dominated forest of the northeastern Qinghai-Tibet Plateau, considering both the ecological (food abundance and intake rate) and the physiological (energy, nutrients and digestion inhibitors) characteristics of the plants selected as food.

## Methods

### Study site

This study was conducted in a coniferous forest (250 ha) in the Lianhuashan Nature Reserve (34°55' N, 103°43' E), southern Gansu, central China. The forest is dominated by dragon spruce *Picea asperata* (36% of the trees) and Farges fir *Abies fargesii* (23%), mixed with willows (23%), Himalayan birch *Betula utilis*, and red birch *B. albo-sinensis* (together, 14%), mountain ash *Sorbus* spp., rose *Rosa* spp., and barberries. The understory species include honeysuckles, arrow bamboo, raspberry, forbs, grasses, and mosses. The forest occurs on north-facing slopes (2,800–3,200 m a.s.l.), whereas only grassland and scrubland, mainly sea buckthorn *Hippophae rhamnoides*, willow, and barberry, occur on south-facing slopes. Chinese willow *S. cathayana*, Rehder willow *S. rehderiana* var. *rehderiana*, Kangding willow *S. paraplesia*, Sichuan willow *S. hylonoma*, Dolia willow *S. rehderiana* var. *dolia* and Wallich willow *S. wallichiana* occur in many small patches in the forest, whereas other willow species are rare. Details of the study area are available in Sun et al. (2003).

### Observation of foraging occurrence and feeding rate

We observed the foraging activities of grouse in a conifer-dominated forest along small trails (approximately 3 km in length and 1.5–3 m in width). Food species can be identified reliably because the vegetation structure is simple and highly visible (without leaves), and most grouse are able to be approached within short distances (2–15 m, usually 3–7 m). Observation times averaged  $3.1 \pm 1.0$  h/day, and were spread evenly across each month for two winters (approximately 15–17 days monthly during 1 Nov–31 Mar. 2006–2007 and 2007–2008). A foraging occurrence was defined as one feeding bout of a grouse in a particular tree (or a shrub). The willows on which foraging took place were marked to collect bud samples.

Chinese Grouse always pecked rapidly while feeding arboreally. This pecking was occasionally interrupted by times of alertness or sitting for short periods of inactivity, and then usually switched to lengthy non-foraging periods (4–60 min, e.g. sitting, crouching, or preening). The peck rate was quantified as the number of pecks per minute by measuring the time taken by an individual to perform 100 pecks in a tree. Sometimes, a count of fewer than 100 bites occurring just before the birds flew was also included to increase sample size. Scans of the surroundings or movement between branches by birds (in general <30 s) were ignored for all measurements because they were associated with the need for birds to change positions to continue

pecking. However, if a bird did not perform these pecks continuously, such as when longer interruptions by head-up postures occurred (in general >1 min), the count was discarded to minimise opportunistic errors (Durant and Fritz 2006). We defined unsuccessful bites as those in which a grouse struck toward a food item with the beak but failed to touch or remove it (Hewitt and Kirkpatrick 1996).

#### Estimation of the biomass acquired in a particular willow and the intake rate

In some cases, we could follow a grouse to observe its activities for a long time (up to 145 min). During such periods, we continuously counted the number of pecks from a tree and determined the intake rate ( $\text{g min}^{-1}$ ) by multiplying the mean peck rate by the average bite size (Spalinger and Hobbs 1992).

#### Survey of food availability

We investigated the food availability of Chinese Grouse on 32 rectangular plots 100 m apart along the trails. Each plot was 20 m wide (parallel to a trail) and 40 m long (perpendicular to a trail) and was centred along trails. All deciduous trees (or shrubs) taller than 1.5 m were counted, and the availability (or relative abundance) of each food species was expressed as the ratio of the total trees in each plot. Smaller deciduous trees were omitted, as most of them were thin and solitary willows. Deciduous trees within the coniferous forest were not surveyed because they were often thin or dwarf (with deficient buds), sparsely distributed in small patches (<10 m<sup>2</sup>), and hence seldom fed on by grouse (as indicated by the records of radiotagged grouse).

#### Chemical analyses

Buds of each willow species (approximately 100 g) were sampled from at least 10 grouse-foraged trees in three phases of winter (November 2007, January and March 2008) and then dried to a constant weight at 50°C. The bud samples were homogenised to determine their energies (Parr 1281 bomb calorimeter, Moline, IL, USA), as well as their nitrogen (Foss Kjeltac<sup>TM</sup> 2100, Hilleroed, Denmark), lipid (Soxhlet), crude fibre (Ankom 200/220 fiber analyzer, Macedon, NY, USA), tannin (China Entry/Exit Inspection and Quarantine Association SN/T0800.9, 1999), calcium and phosphorus (Association of Official Analytical Chemists, 1995), and ash (combustion at 550°C) contents. We determined the buds' crude protein content by multiplying the Kjeldahl nitrogen values by 6.25 and the average size (mg) of the buds by weighing 300 dried buds.

#### Data analyses

The variation in bud size within species was neglected because of the large harvest of a grouse from a specific willow (approximately several hundred bites). Additionally, Chinese Grouse possibly do not omit smaller buds because they continuously peck buds from the tip to the base of branches at a high rate. The intake rates of dried biomass, energy, protein, lipid, crude fibre, tannin, calcium, phosphorus and ash were determined by multiplying the intake rate of each component by its average content in the buds. We pooled the chemical contents and bud sizes of all samples collected during the three phases of winter because buds are usually covered by snow or ice and are nearly in dormancy (the mean monthly air temperatures are  $-1.0$ ,  $-4.7$  and  $-11.0^\circ\text{C}$  in November and December 2007 and January 2008, respectively).

Two indices were utilized for comparisons of food selection. The “selection index” ( $S_i$ ) represents the ratio of foraging occurrence (%) to food abundance (%). The “standardized index” ( $P_i$ , also called the preference index) presents the selection indices in standardized form so that they add to 1. This index ( $P_i$ ) gives “the estimated probability that a randomly selected resource unit will be in category  $i$  if all categories are equally frequent in the original population of available resource units” (Manly et al. 1993). A chi-squared statistic with one degree of freedom was used to test for the selection of available food items against a hypothesis of no selection (Manly et al. 1993; Swenson 1993).

To test the potential effect of various factors on the feeding preference of Chinese Grouse, the average size of the food items, and the average contents and intake rates of nutrients, energy and digestion inhibitors in food items were all included in a Pearson correlation matrix. One-way ANOVA and Tukey's post hoc tests were used to test the difference in feeding profits (i.e. intake of food items or biomass) among willow species. All statistical tests were performed in SPSS 13.0 (SPSS Inc., Chicago, IL, USA) and considered significant within a level of  $\alpha = 0.05$  (two-tailed).

## Results

### Food choice

Chinese Grouse were observed feeding in 12 tree species (Table 1) with 389 occurrences (2–5 occurrences daily). The use of willow (83%) was greater than expected from its availability ( $\chi^2 = 42$ ,  $df = 2$ ,  $P < 0.001$ ; *Sorbus*, *Hippophae*, *Rosa* and *Viburnum* were combined because of their low expected values). The Himalayan birch was most available (35%) but was little used (2.1%, Table 1). Sea buckthorn was the most preferred among the nonwillow species, but it was not abundant (4.9%). Chinese Grouse

did not appear to choose strongly within the genera *Salix* ( $\chi^2 = 4.5$ ,  $df = 5$ ,  $P = 0.49$ ); however, the preference index for Kangding willow was four times greater than that for Sichuan willow (Table 1).

#### Nutrients, energy and digestion inhibitors in buds

The dry weight of buds varied greatly among willow species, with the Wallich willow buds being nearly 8 times heavier than the Dolia willow buds (Table 2). The level of nutrients, energy, and digestion inhibitors in willow buds

remained constant through the winter, as indicated by the small standard errors of the means, but varied greatly among species (Table 2).

According to the Pearson correlation matrix, the degree of preference for different willow species was not related to the contents of energy, protein, lipid, calcium, phosphorus or fibre, but was significantly related to the tannin content in buds (Table 3), and the tannin content was not related to any other factors ( $P > 0.13$ ). Sichuan willow was the most avoided and had the lowest protein and phosphorous contents and highest fibre and tannin contents in its buds

**Table 1** The use of deciduous trees by foraging Chinese Grouse relative to their occurrence in the conifer-dominated forest at Lianhuashan, southern Gansu, over two winters (2006–2007 and 2007–2008)

Food species	Food item	Trees (%)		Preference index = standardised ratio of used to available
		Used (n = 389)	Available (n = 32 plots)	
Chinese willow <i>S. cathayana</i>	Buds, twigs	20.3	11.7 ± 1.9	0.114
Rehder willow <i>S. rehderiana</i> var. <i>rehderiana</i>	Buds, twigs	19.0	9.0 ± 1.4	0.139
Kangding willow <i>S. paraplesia</i>	Buds, twigs	13.1	4.1 ± 0.9	0.211
Sichuan willow <i>S. hylonoma</i>	Buds	7.5	9.8 ± 1.4	0.050
Dolia willow <i>S. rehderiana</i> var. <i>dolia</i>	Buds, twigs	4.9	4.4 ± 1.1	0.073
Wallich willow <i>S. wallichiana</i>	Buds	3.9	2.3 ± 0.7	0.112
Mountain ash <i>S. koehneana</i>	Fruits, buds	8.7	8.8 ± 1.2	0.065
Sea buckthorn <i>H. rhamnoides</i>	Fruits	4.9	3.0 ± 1.7	0.108
Himalayan birch <i>B. utilis</i>	Buds	2.1	34.7 ± 2.9	0.004
Red birch <i>B. albo-sinensis</i>	Buds	0.8	1.1 ± 0.5	0.048
Omei rose <i>R. omeiensis</i>	Buds	0.3	8.5 ± 2.0	0.002
Birchleaf viburnum <i>V. betulifolium</i>	Fruits	0.3	0.2 ± 0.1	0.073
Combined				
Willow <i>Salix</i> spp.		83	43 ± 3	0.700
Birch <i>Betula</i> spp.		3	36 ± 3	0.052
Others		14	21 ± 3	0.248

**Table 2** Energy, nutrients and digestion inhibitors in different willow buds (mean ± SE, n = 3) in Lianhuashan, southern Gansu, central China during the winters of 2006–2007 and 2007–2008

Willow species	Average size of buds (dry weight, mg)	Energy content (J mg <sup>-1</sup> )	Protein content (%)	Phosphorus content (%)	Lipid content (%)	Calcium content (%)	Ash content (%)	Fibre content (%)	Tannin content (%)
<i>S. cathayana</i>	3.0 ± 0.2	8.5 ± 0.1	14.2 ± 0.7	0.33 ± 0.01	4.3 ± 0.3	0.17 ± 0.01	5.6 ± 0.1	19.4 ± 0.4	3.4 ± 0.1
<i>S. rehderiana</i> var. <i>rehderiana</i>	5.4 ± 0.5	7.9 ± 0.0	15.6 ± 0.9	0.34 ± 0.02	5.1 ± 0.5	0.09 ± 0.00	4.1 ± 0.1	28.2 ± 0.3	3.4 ± 0.1
<i>S. paraplesia</i>	3.3 ± 0.3	8.5 ± 0.1	14.3 ± 0.6	0.30 ± 0.01	5.1 ± 0.2	0.11 ± 0.01	4.9 ± 0.4	27.7 ± 1.1	2.5 ± 0.3
<i>S. hylonoma</i>	3.9 ± 0.5	7.9 ± 0.0	9.7 ± 0.3	0.23 ± 0.01	3.0 ± 0.1	0.11 ± 0.00	4.0 ± 0.1	32.7 ± 0.6	3.6 ± 0.1
<i>S. rehderiana</i> var. <i>dolia</i>	1.4 ± 0.2	8.8 ± 0.1	15.8 ± 0.8	0.29 ± 0.02	6.7 ± 0.6	0.12 ± 0.00	5.3 ± 0.2	27.1 ± 0.6	3.4 ± 0.1
<i>S. wallichiana</i>	11.1 ± 2.3	8.0 ± 0.1	10.9 ± 0.2	0.25 ± 0.01	3.7 ± 0.3	0.07 ± 0.00	4.0 ± 0.4	31.6 ± 0.5	2.9 ± 0.3
<i>Betula utilis</i>	11.0 ± 1.0	8.8 ± 0.2	8.6 ± 0.6	0.19 ± 0.01	6.2 ± 0.2	0.05 ± 0.00	2.6 ± 0.2	9.9 ± 0.5	4.0 ± 0.1

**Table 3** The relationships of the feeding preference indices of Chinese Grouse on different willows to various factors (Pearson test,  $n = 6$ ) at Lianhuashan, Gansu, central China, during the winters of 2006–2007 and 2007–2008

Potential factors	$r$	$P$
Energy and nutrient contents in food		
Energy	0.13	0.80
Protein	0.39	0.45
Phosphorus	0.49	0.33
Lipid	0.20	0.70
Calcium	-0.10	0.85
Ash	0.12	0.83
Digestion inhibitor content in food		
Fibre	-0.20	0.70
Tannin	-0.83	0.04*
Intake rate of		
Dried biomass	-0.02	0.97
Energy	0.00	1.00
Protein	0.12	0.82
Fibre	-0.06	0.90
Tannin	-0.02	0.97

\*  $P < 0.05$

(Table 3). In contrast, Kangding willow was the most preferred and had the lowest tannin content in its buds.

#### Peck rate and intake rate

According to our observations, grouse usually eat an entire bud with a single peck, and nearly 100% of cropping attempts were successful. We examined 40 eaten branches of three *Dolia* and two Chinese willows, and found that short twigs accounted for only 4.8% of 349 food items; thus, the average size of the buds represented the average size of the bites.

The peck rates of grouse, with the highest in Sichuan willow, varied greatly with willow species (Table 4). The peck rates on different willow species were unrelated to the average bud sizes ( $r = -0.09$ ,  $P = 0.87$ ). However, the intake rates of dried biomass, energy, protein, fibre and tannin in willows were all positively related to the bud size ( $r > 0.97$ ,  $P < 0.001$ ), suggesting that feeding on willows with larger buds was more efficient in food components (Table 4). Nevertheless, these rates were all unrelated to the preference indices of willows (Table 3).

Lengths of feeding periods and total bites were not significantly different among willow species, but biomass intake was dependent on the willow species consumed (Table 4). However, differences were not related to the preference of willows ( $r < -0.05$ ,  $P > 0.17$ ).

## Discussion

### Diet and willow preference

The observation of willow buds as the primary food for Chinese Grouse in winter is consistent with the results of crop content analyses: 65.7% of wet biomass and 94.8% of food items (W.J. unpublished data). Similarly, most grouse species appear to specifically feed upon only a few food species that are abundant and easy to procure in winter (Doerr et al. 1974, Moss and Hanssen 1980, Swenson 1993). Chinese Grouse may prefer fruits to buds because of the generally rich nutrients and good palatability of fruits. However, over 90% of mountain ash fruits fell to the ground before December, and birchleaf viburnum and sea buckthorn were very rare in the conifer-dominated forests (Table 1). Moreover, fallen fruits and spruce seeds were usually mixed with conifer needles, covered by snow, and eaten by pikas or passeriform birds.

We observed very few mammals (e.g. Roe Deer *Capreolus pygargus*) foraging on willow buds and twigs in the forest. The availability of willow (approximately  $390 \pm 42$  trees  $\text{ha}^{-1}$ , 4,000–40,000 buds per tree or shrub) is likely not limited for the Chinese Grouse in winter. Chinese Grouse appeared to forage selectively within the *Salix* genera in winter, and a few individual willows (mainly Kangding willow) were foraged repeatedly. Swenson (1993) reported that Hazel Grouse (*T. bonasia*) appeared not to distinguish between black alder (*Alnus glutinosa*) and grey alder (*A. incana*) when foraging, probably because neither was abundant in his study area (<6% of trees).

### Food quality

Birch was abundant in our study area (36%), but it was not a preferred food (3%) and yielded less food intake per feeding bout (<33 bites). The preference of willow over birch for Chinese Grouse was similar to what has been reported for Willow Ptarmigan (*Lagopus lagopus*), Rock Ptarmigan (*L. mutus*) and White-tailed Ptarmigan (*L. leucurus*) (Moss 1974), possibly because of the higher protein and phosphorous and lower fibre and toxin levels in willows (Table 2, Gardarsson and Moss 1970; Moss 1983). In addition, birch contains digestion-inhibiting resin (Moss 1973; Bryant and Kuropat 1980) and has lower digestibility than that of willow (Moss 1983). Hazel grouse primarily feed on alder in the Scandinavian boreal forest (Semenov-Tyan-Shanskii 1959; Swenson 1993), on birch in northern Finland (few alder available), and on a wider range of broad-leaved deciduous trees in temperate forests (Fujimaki 2002; Yang 1993), possibly because local willows in these habitats are too rare to be easily acquired (e.g. only 0.9% of trees, Swenson 1993).

**Table 4** Peck rate, intake rate and feeding characteristic (length, total bites, intake) comparisons of Chinese Grouse in different willow species at Lianhuashan, southern Gansu, central China, during the winters of 2006–2007 and 2007–2008

Willow species	Feed rate		Intake rate of					Feeding in a willow				Intake of biomass (g)
	Sample size	Peck rate (bites min <sup>-1</sup> )	Biomass (g min <sup>-1</sup> )	Energy (kJ min <sup>-1</sup> )	Protein (mg min <sup>-1</sup> )	Fibre (mg min <sup>-1</sup> )	Tannin (mg min <sup>-1</sup> )	Sample size	Length (min)	Food items (bites)		
<i>S. cathayana</i>	40	40 ± 1 <sup>b</sup> (25–57)	0.13	1.1	17.9	24.4	4.3	22	12 ± 2 (3–34)	468 ± 79 (107–1,618)	1.4 ± 0.2 <sup>ab</sup> (0.3–4.9)	
<i>S. rehdiana</i> var. <i>rehdiana</i>	79	36 ± 1 <sup>c</sup> (20–61)	0.20	1.6	31.2	56.3	6.8	28	14 ± 2 (2–35)	472 ± 62 (76–1,242)	2.5 ± 0.3 <sup>a</sup> (0.4–6.7)	
<i>S. paraplesia</i>	21	36 ± 2 <sup>c</sup> (22–53)	0.13	1.1	17.9	34.7	3.1	12	12 ± 2 (3–30)	365 ± 86 (46–1,117)	1.2 ± 0.3 <sup>b</sup> (0.2–3.7)	
<i>S. hylonoma</i>	19	48 ± 2 <sup>a</sup> (31–72)	0.19	1.5	18.2	61.2	6.7	8	11 ± 2 (3–20)	485 ± 109 (38–844)	1.9 ± 0.4 <sup>ab</sup> (0.2–3.3)	
<i>S. rehdiana</i> var. <i>dolia</i>	39	45 ± 2 <sup>ab</sup> (26–75)	0.06	0.5	9.5	16.3	2.0	12	16 ± 2 (10–30)	664 ± 138 (196–1,884)	0.9 ± 0.2 <sup>b</sup> (0.3–2.6)	
<i>S. wallichiana</i>	22	34 ± 2 <sup>c</sup> (18–58)	0.47	3.7	50.8	147.3	13.5	7	11 ± 2 (3–20)	382 ± 87 (55–662)	4.2 ± 1.0 <sup>ab</sup> (0.6–7.4)	
ANOVA, <i>F</i>		5.90							0.74	1.04	6.90	
<i>P</i>		0.00							0.59	0.40	0.00	

Data (mean ± SE) in the same column with no common superscript letters are significantly different (Tukey's  $P < 0.05$ )

The levels of energy, nutrients, and digestion inhibitors were significantly different among species. Detoxifying and excreting tannins requires nitrogen (Moss and Parkinson 1972); hence, the selection for nitrogen-rich food not only provides grouse with essential amino acids, but also facilitates detoxification (Moss 1983). We found a negative correlation between the tannin concentration and the feeding preference for willow species, indicating that Chinese Grouse could discriminate willow buds based on palatability (bitterness of tannins) and may quickly learn the characteristics of suitable food items (e.g. colour, shape, etc.). This would effectively reduce the number of feeding attempts on Sichuan willow and thus save energy. Nonetheless, Sichuan willow buds were generally avoided rather than completely rejected by Chinese Grouse. We found that 54% of the feedings in Sichuan willow occurred at dusk, when grouse typically feed voraciously to store large volumes of food in the crop (Svoboda and Gullion 1972) and continue to digest while roosting at night (Moss 1997). Therefore, we suppose that Chinese Grouse may become less selective with regard to forage species at dusk to maximise their intake.

#### Peck rate and intake rate

The peck rate of Chinese Grouse may be determined by the handling time, including the time to peck and the time to swallow. If the distance between buds was shorter and the branches were denser, grouse could peck faster. Likewise, Durant and Fritz (2006) found that the pecking rate of wintering European Wigeon *Anas penelope* was dominantly determined by the sward height. Chinese Grouse had a high peck rate in Sichuan willow for two reasons. Firstly, the foraging in Sichuan willow mainly occurred at dusk, when Chinese Grouse foraging voraciously to store food in crops. Secondly, the buds and branches are much denser in Sichuan willow.

The highest peck rate of Chinese Grouse in *Dolia* willow (75 bites min<sup>-1</sup>, Table 4) was very close to that of ruffed grouse in captivity, i.e. 0.78 s bite<sup>-1</sup> (Hewitt and Kirkpatrick 1996). However, the highest peck rates of Chinese Grouse in all willow species were higher than those of Ruffed Grouse in aspens, i.e. 47.4 bites min<sup>-1</sup> (Svoboda and Gullion 1972) and 50 bites min<sup>-1</sup> (Humpfner and Tester 1988), possibly because smaller food items (<12 mg vs. 90 mg) require less time to swallow. When consuming larger food items (e.g. Wallich willow buds), Chinese Grouse would stop foraging and sit still for approximately 4 s while the muscles in the crop region appeared to contract and relax. This behaviour was hypothesised to make room for subsequent bites (Hewitt and Kirkpatrick 1996), and may add to the energy consumption and discomfort of grouse. Moreover, because

food-processing rates are normally lower than intake rates, Chinese Grouse typically stopped foraging after 30–50 min, similar to Canada Goose goslings (*Branta Canadensis minima*, Sedinger and Raveling 1988). Hence, Wallich willow buds, though the most “profitable” foods (Table 4), were not preferred by Chinese Grouse (Table 1). However, we also found that most feedings on Wallich willow occurred on days of heavy snowfall, when Chinese Grouse typically increase the biomass acquired from an individual willow (up to 4.2 g in a single feeding bout, Table 4) with less energy expenditure.

### Foraging ecology

Most foraging studies have pooled different willow species as “*Salix* spp.” because of the logistical problems and/or difficulties with identification in the field. However, the feeding benefits to Chinese Grouse varied among willow species. Chinese Grouse did not vary their peck rate, but they avoided high tannin content while feeding, indicating that digestive constraints played more important roles than ecological factors in diet selection. The amount of dry matter actually digested by a bird increased up to the optimal intake but then decreased (Moss 1972). Given this behaviour, the only way in which a bird could increase its intake of digestible nutrients would be to select food that was particularly rich in nutrients and/or low in indigestible materials. Our results support the modified optimal diet model for herbivores (Freeland and Janzen 1974; Pulliam 1975; Westoby 1974), and suggest that maximising the intake of nutrients while simultaneously minimising the intake of digestion inhibitors represent the major determinants of the diet of Chinese Grouse.

**Acknowledgments** We thank X.-G. Sun for plant identification and the staff of the Lianhuashan Natural Reserve for field assistance. We especially thank S. J. Hannon, Y. Tao, J. F. Bendell, C.-X. Jia, J. E. Swenson, M. A. Gregg, N. Lu and five anonymous reviewers for helpful comments on the manuscript, and J. Martens for fieldwork guidance. This study was sponsored by the National Natural Science Foundation of China (grant 30620130110, 31071931).

### References

- Bryant JP, Kuropat PJ (1980) Selection of winter forage by subarctic browsing vertebrates: the role of plant chemistry. *Annu Rev Ecol Syst* 11:261–285
- Doerr PD, Keith LB, Rusch DH, Fischer CA (1974) Characteristics of winter feeding aggregations of ruffed grouse in Alberta. *J Wildl Manage* 38:601–615
- Durant D, Fritz H (2006) Variation of pecking rate with sward height in wild wigeon *Anas penelope*. *J Ornithol* 147:367–370
- Freeland WJ, Janzen DH (1974) Strategies in herbivory by mammals: the role of plant secondary compounds. *Am Nat* 108:269–289
- Fujimaki Y (2002) Food habit of hazel grouse in Hokkaido, Japan. *J Yamashina Inst Ornithol* 34:73–79
- Gardarsson A, Moss R (1970) Selection of food by Icelandic ptarmigan in relation to its availability and nutritive level. In: Watson A (ed) *Animal populations in relation to their food resources*. Blackwell, Oxford, pp 47–69
- Hewitt DG, Kirkpatrick RL (1996) Forage intake rates of ruffed grouse and potential effects on grouse density. *Can J Zool* 74:2016–2024
- Hirakawa H (1997) Digestion-constrained optimal foraging in generalist mammalian herbivores. *Oikos* 78:37–47
- Huempferner RA, Tester JR (1988) Winter arboreal feeding behavior of ruffed grouse in east central Minnesota. In: Bergerud AT, Gratson MW (eds) *Adaptive strategies and population ecology of northern grouse*. University of Minnesota Press, Minneapolis, pp 122–157
- Jakubas WJ, Guillion GW, Clausen TR (1989) Ruffed grouse feeding behavior and its relationship to secondary metabolites of quaking aspen flower buds. *J Chem Ecol* 15:1899–1917
- Julkunen-Tiitto R (1989) Phenolic constituents of *Salix*: a chemotaxonomic survey of further Finnish species. *Phytochemistry* 28:2115–2125
- Karasov WH, Hume ID (1997) The vertebrate gastrointestinal system. In: Dantzler WH (ed) *Handbook of physiology*. Oxford University Press, New York, pp 409–480
- Kenward RE, Sibly RM (1977) A woodpigeon (*Columba palumbus*) feeding preference explained by a digestive bottle-neck. *J Appl Ecol* 14:815–826
- Levey DJ, Martínez del Río C (1999) Test, rejection and reformulation of a chemical reactor-based model of gut function in a fruit-eating bird. *Phys Biochem Zool* 72:369–383
- Manly BFJ, McDonald LL, Thomas DL (1993) *Resource selection by animals: statistical design and analysis for field studies*. Chapman and Hall, London
- Moss R (1972) Food selection by red grouse (*Lagopus lagopus scoticus* (Lath.)) in relation to chemical composition. *J Anim Ecol* 41:411–428
- Moss R (1973) The digestion and intake of winter foods by wild ptarmigan in Alaska. *Condor* 75:293–300
- Moss R (1974) Winter diets, gut lengths, and interspecific competition in Alaskan ptarmigan. *Auk* 91:737–746
- Moss R (1983) Gut size, body weight, and digestion of winter foods by grouse and ptarmigan. *Condor* 85:185–193
- Moss R (1997) Grouse and ptarmigan nutrition in the wild and in captivity. *Proc Nutr Soc* 56:1137–1145
- Moss R, Hanssen I (1980) Grouse nutrition. *Nutr Abstr Rev Ser B* 50:555–567
- Moss R, Parkinson JA (1972) The digestion of heather (*Calluna vulgaris*) by Red Grouse (*Lagopus lagopus scoticus*). *Br J Nutr* 27:285–298
- Pulliam HR (1975) Diet optimization with nutrient constraints. *Am Nat* 109:765–768
- Sedinger JS (1997) Adaptations to and consequences of an herbivorous diet in grouse and waterfowl. *Condor* 99:314–326
- Sedinger JS, Raveling DG (1988) Foraging behavior of cackling Canada goose goslings: implications for the roles of food availability and processing rate. *Oecologia* 75:119–124
- Semenov-Tyan-Shanskii O (1959) *Ekologiya terevinykh ptits*. Trudy Laplandskogo Gosudarstvennogo Zapovednika 5:1–318
- Spalinger DE, Hobbs NT (1992) Mechanisms of foraging in mammalian herbivores: new models of functional response. *Am Nat* 140:325–348
- Stephens DW, Brown JS, Ydenberg RC (2007) *Foraging: behavior and ecology*. University of Chicago Press, Chicago
- Stolter C, Ball JP, Tiitto RJ, Lieberei R, Ganzhorn JU (2005) Winter browsing of moose on two different willow species: food selection in relation to plant chemistry and plant response. *Can J Zool* 83:807–819

- Sun Y-H (1996) Winter ecological study on the Chinese Grouse (*Bonasa sewerzowi*). *Acta Zool Sinica* 42(Suppl):96–100
- Sun Y-H, Swenson JE, Fang Y, Klaus S, Scherzinger W (2003) Population ecology of the Chinese Grouse, *Bonasa sewerzowi*, in a fragmented landscape. *Biol Conserv* 110:177–184
- Sun Y-H, Fang Y, Swenson JE, Klaus S, Zheng GM (2005) Morphometrics of the Chinese Grouse *Bonasa sewerzowi*. *J Ornithol* 146:24–26
- Svoboda PJ, Gullion GW (1972) Preferential use of aspen by ruffed grouse in northern Minnesota. *J Wildl Manage* 36:1166–1180
- Swenson JE (1993) The importance of alder to hazel grouse in Fennoscandian boreal forest: evidence from four levels of scales. *Ecography* 16:37–46
- Westoby M (1974) An analysis of diet selection by large generalist herbivores. *Am Nat* 108:290–304
- Whelan CJ, Brown JS (2005) Optimal foraging and gut constraints: reconciling two schools thought. *Oikos* 110:481–496
- Williams JB, Best D, Warford C (1980) Foraging ecology of ptarmigan at Meade River, Alaska. *Wilson Bull* 92:341–351
- Yang B-R (1993) On food features and nutrient analysis of hazel grouse in bud-feeding periods. *Acta Zool Sinica* 39:48–55 (in Chinese)
- Zheng G, Wang Q (1998) China red data book of endangered animals, Aves. Science Press, Beijing (in Chinese)