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Li De-Pin<sup>a</sup>, Matthew B. Scott<sup>a,\*</sup>, Xiao Lin and Xiao Wen

# Age-gender feeding differences in dwarf blue sheep, *Pseudois schaeferi* (Cetartiodactyla, Bovidae) magnified by the expansion of an invasive plant species

**Abstract:** Understanding feeding habits and responses to habitat changes can be a critical step toward the conservation of threatened species. Pressured by hunting, habitat loss, and competition from livestock, the dwarf blue sheep (*Pseudois schaeferi*) of the Yangtze River gorge in the Eastern Himalaya is an IUCN-listed endangered species with a diminished range and population, and yet little is known of its basic biological requirements. Diet composition was quantified and compared between male and female adults, and juveniles of *P. schaeferi* on Rini Mountain, Yunnan, China from 10-min scan samples from October 2006 to February 2007. In total, 17 food species were identified though only six species (*Opuntia ficus-indica*, *Themeda triandra*, *Festuca durata*, *Polygonum thunbergii*, *Elsholtzia cypriani*, and *Excoecaria acerifolia*) made up nearly 90% of the diet. Although feeding niches of both adults and juveniles highly overlapped, significant quantitative differences in their food composition were found. Adult male and juvenile diets were the most dissimilar; adult sheep fed more frequently on the introduced succulent cactus, *O. ficus-indica*, whereas juvenile sheep fed more frequently on the herbs, *P. thunbergii* and *E. cypriani*, and the woody shrub, *Buddleja caryopteridifolia*. Field observations showed that *P. schaeferi* frequently used its broad curved horns to remove the spines of *O. ficus-indica*, presumably to gain access to the fleshy leaves. We suggest differences in the diets are the result of differential access to the cactus, but may also be influenced by nutritional requirements.

**Keywords:** Caprinae; conservation; diet; *Opuntia ficus-indica*; spine; Yunnan.

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## Introduction

One of the principal threats to species is the continued loss, fragmentation, and transformation of their habitats. As a consequence, the persistence of many species hinges on their ability to adapt their diets to modified and changing habitats, and for many species, successful conservation management will depend on having at least a baseline knowledge of feeding ecology (Korschgen 1980, Bagchi et al. 2004, Mishra et al. 2004, Liu et al. 2007a). The dwarf blue sheep (*Pseudois schaeferi*, Haltenorth 1963), a Caprinae, is confined to a narrow distribution along the steep rocky slopes of the upper Yangtze River gorge between c. 28°15'N and 31°0'N in Sichuan, Yunnan, and Tibet, China (Wang and Hoffman 1987, Wang et al. 2000, Harris 2008a). As a consequence of unrestricted overhunting, habitat loss, and competition with livestock, the distribution and abundance of dwarf blue sheep have sharply declined since the 1950s (Wang et al. 2000, Wang and Wang 2003), raising concern for the fate of the species, and providing rationale for the species to be listed by the IUCN as 'Endangered' (IUCN 2011). Pastoralism in the region is widespread, invasive weeds are abundant, infrastructural development is rapid, and pressure from locals on natural resources is pervasive. Still, remarkably little is known of the basic biological requirements of *P. schaeferi* and how these factors relate to its survival in a changing environment.

The relatively sparse distribution in difficult terrain has made data collection on *Pseudois schaeferi* challenging, so that few studies have been completed on the species. The best previous dietary information on

*P. schaeferi* relied on a few direct observations made in summer and late autumn, and information from local herders and hunters in Batang, Sichuan (Wu et al. 1990, Wang et al. 2000, Harris 2008a). Wu et al. (1990) observed *P. schaeferi* in spring and autumn eating a mixed diet of more than 20 plant species, including Solomon's seal (*Polygonatum* sp.), flaccid grass (*Pennisetum flaccidum*), eragrotis (*Eragrotis nigra*), yellow foxtail (*Setaria pumila*), primula (*Androsace erecta*), and clubmoss (*Selaginella sanguinolenta*). From their observations, Wang et al. (2000) suggest *P. schaeferi* derives most of its nourishment from graminoids, such as *P. flaccidum*, *S. pumila*, as well as the drought-tolerant *S. sanguinolenta*. These observations are congruent with those made of the bharal *Pseudois nayaur* (Hodgson, 1833), the only close relative of *P. schaeferi*, but which occupies a wide range of mostly treeless mountain habitats across the high ranges of the Himalayas from Pakistan to Inner Mongolia (Harris 2008b). *Pseudois nayaur* preferentially select habitats near cliffs (Mishra et al. 2004), where they preferentially graze on graminoids, and to a lesser degree on shrubs, trees, forbs, and lichens where graminoid availability is low or has been reduced (Harris and Miller 1995, Shrestha et al. 2005, Liu et al. 2007a, Suryawanshi et al. 2009). For *P. schaeferi*, no quantitative estimate of diet for the species has ever been completed, and nothing has been reported on the population at Rini Mountain, Yunnan.

This study aimed to redress the dearth of information on the diet of *Pseudois schaeferi* as a preliminary step in better understanding which food resources the species utilizes in its harsh environment, as well as to identify potential resource conflicts or threats to its existence. The principle objectives of this study were to quantify and compare winter diets of male and female, and adult and juvenile *P. schaeferi* based on direct field observations of *P. schaeferi*. We chose to collect data during the winter when quantity and nutritional quality of forage species was likely to be lowest and intraspecific competition for resources presumably higher than at other times of the year. Intraspecific gender and age-class comparisons of feeding choice can provide valuable biological information (Main et al. 1996), helping to determine the presence and causes of intraspecific competition and sexual segregation (Shank 1982, Bowyer 1984, Young and Isbell 1991, Bleich et al. 1997, Kie and Bowyer 1999), differences in physiological requirements (Harrison 1983, Dardaillon 1989), and learning modalities of feeding in young individuals (Bergerud 1972, Edwards 1976). We predicted the winter diet of *P. schaeferi*, like *Pseudois nayaur*, to be mixed, rich in browse species. We also predicted animals should prefer the same food (based on quality or

abundance), though believed some selection differences may occur due to body architecture (Hildebrand 1974), and allometric effects of metabolic requirements and digestive retention (McCullough 1979, Barboza and Bowyer 2000), or underlying nutritional requirements (Main et al. 1996, Bleich et al. 1997).

## Materials and methods

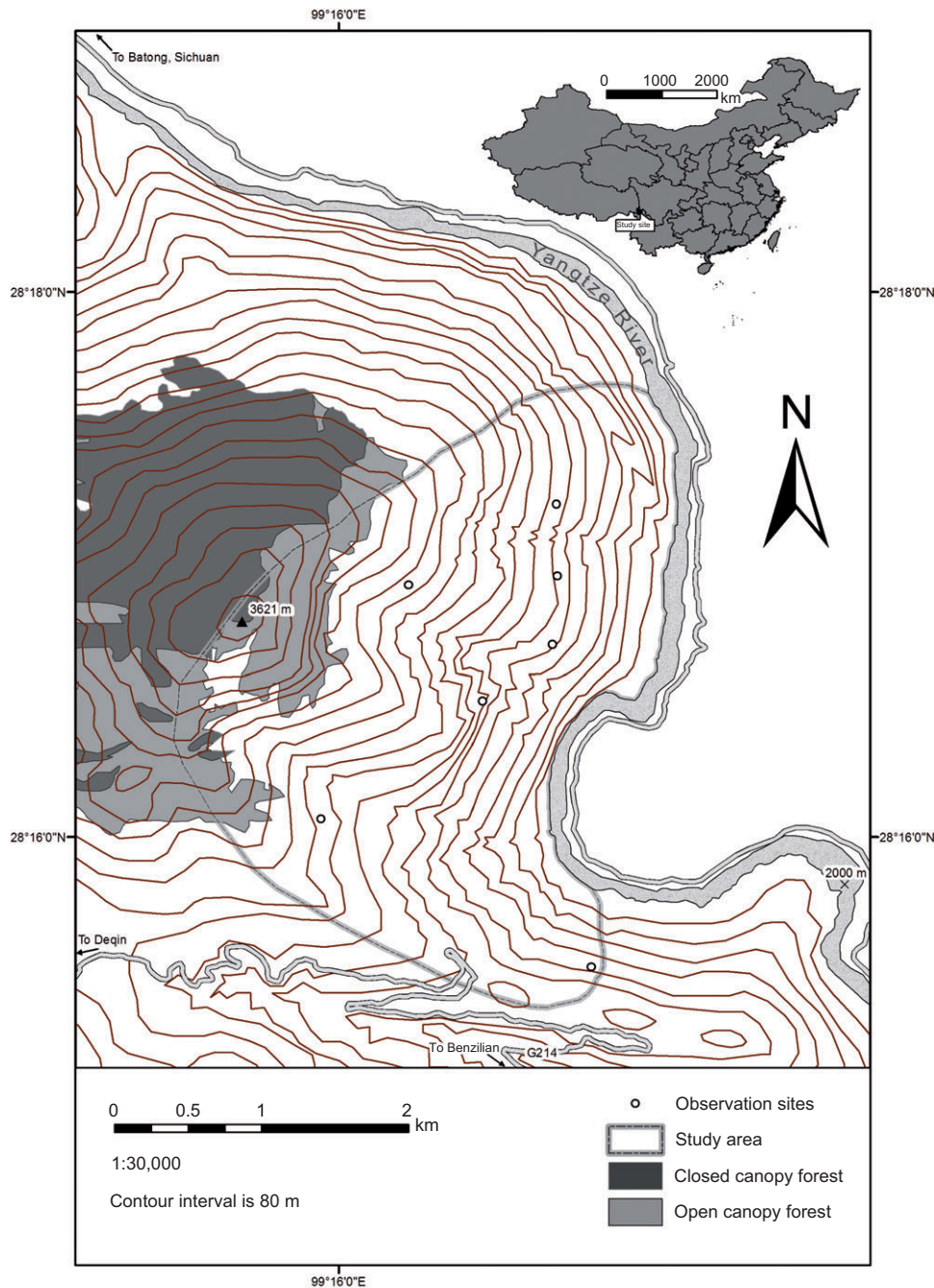
### Study area

Rini Mountain (3650 m asl, 28°15'–28°18'N, 99°16'–99°18'E) is a low conical hill situated above the Yangtze River in Baima Snow Mountain National Nature Reserve, Deqin County, Yunnan (Figure 1). Baima Snow Mountain is part of the extensive Hengduan Mountain Range that forms the high spine between the Jinsha (Yangtze) and Lancang (Mekong) Rivers in Yunnan and Tibet. Rini Mountain is separated from the main range by a low saddle and a mixed broadleaved-conifer forest belt (above 3200 m asl) of mainly *Pinus yunnanensis*, *Cupressus duclouxiana*, and *Quercus guajavifolia*. The lower and midslopes are rocky steep and unstable; massive cliffs, are interspersed by small pockets of sparse grassland, shrubland, scrub, and loose scree deposits. The scrub and shrubland vegetation within the main habitat used by the study group (2050–3300 m asl) mainly comprised the shrubs *Vitex negundo* var. *microphylla*, *Osyris quadripartita*, *Sophora davidii*, and the introduced cactus *Opuntia ficus-indica*. Scattered *Pistacia weinmanniifolia* grow along the river. The site is sparsely populated by sedentary agropastoralists who raise goats (*Capra hircus*), yak (*Bos grunniens*), and grow barley. Livestock are grazed within the habitat used by the *Pseudois schaeferi* study group (Li pers. obs.).

The site is characterized by a warm, arid climate, with mean annual temperatures from 14°C to 17°C, and with monthly means ranging between 24°C in July to 8°C in January (Jin 2002). Total annual precipitation is <350 mm, with 90% occurring as rainfall during the wet season (May–September). Annual mean evaporation is 3000–4000 mm (Jin 2002). Snow occurs regularly in winter down to ca. 3200 m asl (near lower treeline).

### Diet recording

After observing the herd for 10 days and speaking to local herders and hunters, seven prominently located sites (A–F) were selected for observing the Rini Mountain



**Figure 1** Study area of dwarf blue sheep (*Pseudois schaeferi*) at Rini Mountain, Yunnan Province, China.

*Pseudois schaeferi* population (Figure 1). The sites were located more-or-less evenly throughout the estimated home range of the study population and offered observational visibility to approximately 87% of the home range (Li unpublished data). The quantitative observations of behavior were made from 13 October 2006 to 27 January 2007 using a scan sampling method at 10-min intervals (Altmann 1974). During each 10-min observation, a visual scan was made of the group, recording the activity of

each visible individual at that instant ( $<5$  s/animal). The behavior types recorded during scan samples included resting/lying, standing/watching, moving, feeding, drinking, fighting, grooming, and defecating. When feeding behavior was recorded, the food plant species eaten were recorded at the species level and foraging class. The nomenclature follows eFloras (2008). For each scan record, the animal was classed as either adult male, adult female, or juvenile. Observations were made daily



from ca. 0800 h to 1830 h using a Nikon spotting scope (40×–60×) at distances, where possible to 300 m, though more typically observations were made between 50 and 200 m. The prohibitively steep and dangerous terrain precluded tracking the sheep on some occasions when they moved out of view. When the study group was disturbed by local herders, data collection was terminated until the following day.

To test the adequacy of the scan sample size for representing the winter feeding diet, 388 feeding records (where the foraging species was positively identified) were analyzed using the methods outlined by Foster et al. (2010). The total number of species consumed was calculated for 10 randomly selected scans for an initial sample, and then repeated with each incremental addition of five scans to the sample up to 300 scans. This procedure was repeated for 100 sequences of random selections to create an iterative species accumulation curve (Foster et al. 2010).

## Habitat use

The habitat types were recorded for visible individuals every 30 min, classed as cliff cactus scrub, scree cactus scrub, scree scrub, cliff shrubland, and shrubland. For better visualization, the habitat was presented as percentages of the total records per age-gender class, and the differences in habitat use were tested for independence by a  $\chi^2$ -test.

## Food niche overlap

The frequency of feeding scans was used to evaluate the differences in the diet of adult and juvenile dwarf blue sheep. A  $\chi^2$  analysis was used to test for independence of age-gender class (male, female, juvenile) and most commonly selected food items (where the expected value was  $>1$ ), and foraging classes. A Fishers test of two proportions was used to test the usage of each food item. The relationship between the number of records age-gender class and habitat use was tested for independence by a  $\chi^2$ -test. For better visualization, habitat use was presented as percentages of the total records per age-gender class. Dietary overlap between adults and juveniles was calculated using the Pianka's index ( $O$ ) (Pianka 1973). Pianka's index formula is:

$$O_{jk} = \frac{\sum_{i=1}^n p_{ij} \times p_{ik}}{\sqrt{\sum_{i=1}^n p_{ij}^2 \times \sum_{i=1}^n p_{ik}^2}}$$

where  $p_{ij}$  (or  $p_{ik}$ ) is the proportion of food species (or plant category)  $i$  recorded in the diet of age class  $j$  (or  $k$ ), and  $n$  is the total number of diet items. Index values range from 0 (no overlap) to 1 (complete overlap). It is generally considered that values of Pianka's index ( $O_{jk}$ ) higher than 0.6 means that there is a biologically significant niche overlap for the resource(s) examined (Wallace 1981).

## Results

### Diet

In total, 630 scans were made recording some 1893 feeding records of *Pseudois schaeferi* from October to February; 734 on adult males, 626 on adult females, and 533 on juveniles. Of these records, 388 records were positively identified to species, and an additional 27 records, totaling 415, were identified to foraging class.

Based on these records, 17 plant species were eaten, though only six species (*Opuntia ficus-indica*, *Themeda triandra*, *Festuca durata*, *Polygonum thunbergii*, *Elsholtzia cypriani*, and *Excoecaria acerifolia*) made up nearly 90% of the observed identifiable diet (Table 1). Exotic succulent cactus prickly pear (*O. ficus-indica*) alone accounted for almost half of the observed feeding occurrences (Table 1). By foraging class, the diet was dominated by succulents (43%), with graminoids (18%), herbs (17%), and woody plants (21%) making up about equal proportions. The lycopods accounted for  $<1\%$  of the diet.

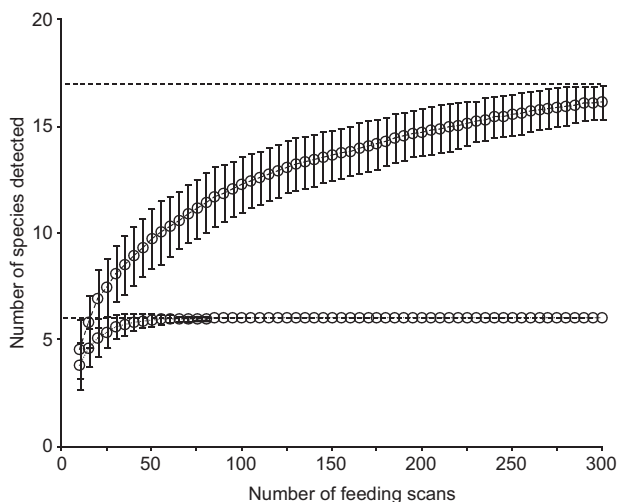
A species accumulation curve of 300 randomly selected scans showed some leveling, but did not reach an asymptote (Figure 2). However, as few as 30 scans were able to detect the six most common food items (i.e., those species making up  $>5\%$  of the items in the full sample).

### Habitat use

The dwarf blue sheep used all five habitats, though more than 60% of the observed times were in cliff cactus scrub. The habitat use between age-gender groups among the five major habitat types at the site was significantly different than the expected (Pearson's  $\chi^2=97.388$ ,  $df=8$ ,  $p<0.001$ ). The adult males used the cliff cactus scrub habitat more than expected, while the juveniles and adult females used the scree scrub habitat more often than expected (Figure 3). A significant difference was also observed when comparing the adult male, female, and juvenile use

Food items	Life form	Adult		Juvenile		Z	p-Value
		N	F	N	F		
<i>Opuntia ficus-indica</i>	S	168	12.4	12	2.3	5.60	<b>&lt;0.001</b>
<i>Themeda triandra</i>	G	26	1.9	8	1.5	-0.78	0.487
<i>Festuca durata</i>	G	34	2.5	4	0.8	1.34	0.270
Unknown graminoid	G	3	0.2	0	0.0		
<i>Polygonum thunbergii</i>	H	25	1.8	21	3.9	-5.04	<b>&lt;0.001</b>
<i>Elsholtzia cypriani</i>	H	14	1.0	8	1.5	-2.21	<b>0.043</b>
Unknown herb	H	3	0.2	0	0.0		
<i>Buddleja caryopteridifolia</i>	W	1	0.1	3	0.6	-2.92	<b>0.021</b>
<i>Rosa soulieana</i>	W	2	0.1	0	0.0	0.68	1.000
<i>Bauhinia brachycarpa</i>	W	5	0.4	4	0.8	-2.02	0.066
<i>Campylotropis polyantha</i>	W	8	0.6	1	0.2	0.58	1.000
<i>Indigofera lenticellata</i>	W	1	0.1	2	0.4	-2.15	0.090
<i>Sophora davidii</i>	W	2	0.1	1	0.2	-0.66	0.461
<i>Vitex negundo</i> var. <i>microphylla</i>	W	7	0.5	2	0.4	-0.29	0.675
<i>Excoecaria acerifolia</i>	W	19	1.4	6	1.1	-0.72	0.433
<i>Osyris quadripartita</i>	W	1	0.1	0	0.0	0.48	1.000
<i>Rhamnus flavesces</i>	W	1	0.1	0	0.0	0.48	1.000
<i>Jasminum subhumile</i> var. <i>glabricymosum</i>	W	1	0.1	0	0.0	0.48	1.000
Unknown woody	W	16	1.2	5	0.9		
<i>Selaginella</i> sp.	L	1	0.1	0	0.0	0.48	1.000
Unknown		1022	75.1	456	85.6		
Trophic overlap, Pianka's Index, O							
species					0.63		
foraging class					0.69		

**Table 1** Feeding records (N) of adult and juvenile dwarf blue sheep at Rini Mountain, Yunnan Province, China based on 1893 feeding records in winter presented as relative frequency of occurrence (F, %). Foraging classes: S, succulent; G, graminoid; H, herb; W, woody shrub, tree, or liana; L, lycopod. Significant Fisher's exact test p-values (Z-test) shown in boldface. Fisher's exact test based on observations with identifiable species (n=388).



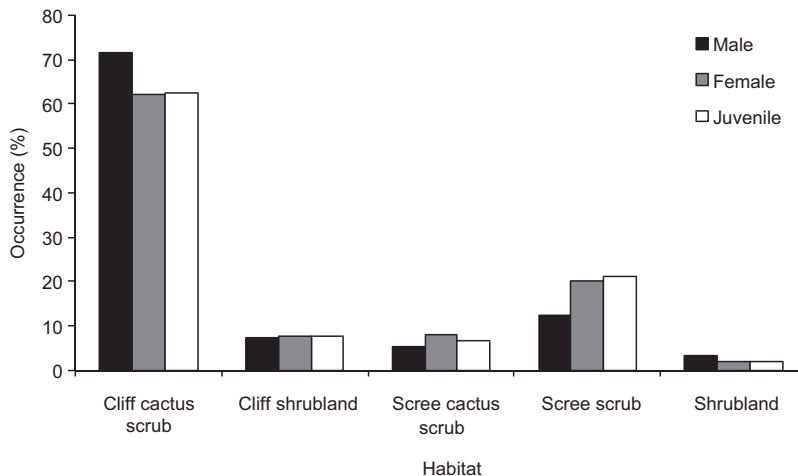
**Figure 2** Species accumulation curves for dwarf blue sheep winter diet at Rini Mountain, Yunnan Province, China. Mean ( $\pm$ s.d.) is shown for 100 random iterations. Dashed lines indicate the total recognized number of feeding species observed (upper lines) and of those with >5% relative occurrence (lower lines) detected in 388 feeding scans.

of cactus-dominated habitats in comparison with other habitats (Pearson's  $\chi^2=37.986$ ,  $df=8$ ,  $p<0.001$ ).

### Food niche overlap

According to the scan survey data, the diet of adults was significantly different from that of the juveniles based on the nine species with expected values  $>1$  (Pearson's  $\chi^2=52.508$ ,  $df=8$ ,  $p<0.001$ ) and foraging classes (Pearson's  $\chi^2=44.844$ ,  $df=3$ ,  $p<0.001$ ). The trophic niche overlap (O) was high, both by species and by foraging class (Table 1). The adult sheep fed more frequently on the introduced succulent cactus, *Opuntia ficus-indica*, whereas the juvenile sheep fed more frequently on the herbs, *Polygonum thunbergii* and *Elsholtzia cypriani*, and the woody shrub, *Buddleja caryopteridifolia*. These results were significant (Table 1).

Feeding niche differences also existed between age-gender classes. The adult male, adult female, and juvenile



**Figure 3** Habitat use by percent occurrence for dwarf blue sheep (*Pseudois schaeferi*) in winter at Rini Mountain, Yunnan Province, China.

dwarf blue sheep fed unevenly on the most common species (Pearson's  $\chi^2=90.996$ ,  $df=16$ ,  $p<0.001$ ). A similar result was found for the foraging class (Pearson's  $\chi^2=72.380$ ,  $df=6$ ,  $p<0.001$ ) (Table 2). The trophic niche overlap ( $O$ ) was high between males and females, and females and juveniles, both by species and by foraging class; however, feeding niche overlap was less than between males and juveniles (Table 3).

## Discussion

Our observations showed that dwarf blue sheep at Rini Mountain exhibit a narrow winter diet. The animals were observed to feed on 17 species, from which just six species formed the bulk of the diet (Table 1). This, however, is not extraordinary. *Pseudois nayaur* show a similarly narrow feeding breadth across its range, e.g., in Ninxia Hui Autonomous Region, Inner Mongolia (Liu et al. 2007a),

Qinhai Province (Harris and Miller 1995), India (Mishra et al. 2004), and Nepal (Shrestha et al. 2005), and dietary studies among various grazing animals show that a narrow feeding breadth is a common character even in more diverse habitats (e.g., Hayward 2005, Kowalczyk et al. 2011).

According to the classification set out by Hoffman (1989), the winter diet of the dwarf blue sheep at Rini Mountain was sufficiently mixed across the foraging classes to be grouped as an intermediate feeder. Wang et al. (2000) and Wu et al. (1990) each observed the dwarf blue sheep to have mixed diets, though specific proportions of the foraging classes were not given. Many specialist herbivores show considerable temporal variation in the contribution of foraging classes to their diets in response to environmental factors (Bodmer 1990, Brown and Doucet 1991, Liu et al. 2007a). *Pseudois nayaur* is, in its natural habitat, predominantly a grazer, preferring graminoids, though shifts its diet along the grazer-browser continuum as a result of seasonal availability, competitive exclusion by sympatric grazers, and local plant composition

Foraging class	Adult male		Adult female		Juvenile	
	N	F	N	F	N	F
Succulent	116	61.4	52	34.9	12	15.6
Graminoids	33	17.5	30	20.1	12	15.6
Herbs	19	10.1	23	15.4	29	37.7
Woody plants	21	11.1	43	28.9	24	31.2
Lycopods	0	0.0	1	0.60	0	0.0

**Table 2** Foraging class records (N) and frequencies (F) of adult and juvenile dwarf blue sheep at Rini Mountain, Yunnan Province, China based on 415 feeding observations made from 13 October, 2006 to 27 January, 2007.

	Adult (M)	Adult (F)	Juvenile
Adult male	1.00	0.93	0.56
Adult female	0.87	1.00	0.73
Juvenile	0.56	0.84	1.00

**Table 3** Pianka's food niche overlap ( $O$ ) (above the diagonal) found for adult male, adult female, and juvenile dwarf blue sheep at Rini Mountain, Yunnan Province, China, calculated from the 17 food items identified from scans. Below the diagonal are Pianka's food niche overlap ( $O$ ) calculated from the five foraging classes.

(Harris and Miller 1995, Miller and Schaller 1998, Schaller 1998, Mishra et al. 2004, Shrestha et al. 2005, Liu et al. 2007a, Suryawanshi et al. 2009). This shift is particularly pronounced in winter when graminoid resources become limited or where competition with domestic livestock or other wild ungulates occurs (Mishra et al. 2004, Liu et al. 2007a, Suryawanshi et al. 2009). Ultimately, the local plant composition determines the availability; for example, a complete lack of woody species in some areas totally precludes that component from entering the diet (Harris and Miller 1995, Miller and Schaller 1998).

Season, competitive exclusion by other grazers, and local plant composition are also likely to have been critical to defining the dietary pattern of dwarf blue sheep at Rini Mountain. While the winter food niche of both adults and juveniles overlapped, significant quantitative differences in the food composition were observed (Table 1). The adults, particularly the males, fed more frequently on the succulent, *Opuntia ficus-indica*, whereas the juvenile sheep fed more frequently on the herbs, *Polygonum thunbergii* and *Elsholtzia cypriani*, and the woody shrub, *Buddleja caryopteridifolia*. The adult females had an intermediate diet. Rumen samples of three poached animals also broadly support this disparity (Li unpublished data). The fleshy cladode of *Opuntia* spp. is highly palatable, high in soluble carbohydrates, Ca, K, and vitamin A, and a good source of water (Chavez-Ramirez et al. 1997, Hernández-Urbiola 2011), making *Opuntia* spp. an important food source for domestic, feral, and native species in the arid and semiarid parts of the world where it is found (Russell and Felker 1987, Biru and Bekele 2012). Graminoid density is exceedingly sparse in the dry winter months (Li unpublished data). Assuming the dwarf blue sheep have the same preference for graminoids and dietary plasticity as *Pseudois nayaur*, the animals may have shifted their diet to include cactus as a result of low graminoid abundance or quality or in response to a new resource. Numerous animal species are reported to browse *Opuntia* spp., though not always without ill consequences. Mouth injuries and chronic infection are common (Chavez-Ramirez et al. 1997). Some livestock will only browse the cactus when starving or preferentially browse where spines have been removed (Chavez-Ramirez et al. 1997). The observations in this study also recorded the adult sheep frequently raking their broad (ca. 9 cm diameter; Liu et al. 2007b) horns along the broad cladodes (flattened photosynthetic stems of Cactaceae) effectively removing spines from the fleshy cladodes before feeding. The juveniles with less-developed horns were never observed exhibiting this behavior and only rarely ate the cactus, usually targeting new growth. While the

behavior of rubbing cacti to remove the spines is known in the Caprinae, e.g., big horn sheep (*Ovis canadensis*) in North America (Warrick and Krausman 1989, Tarango et al. 2002), no records exist for this behavior in *Pseudois*, and no other native plant with a similar morphology or defense mechanism exists within the range of *Pseudois schaeferi* or *P. nayaur*. In the current study, domestic yaks and goats were observed to eat *O. ficus-indica*, as was the Chinese goral, *Naemorhedus griseus* Milne-Edwards, 1871, on one occasion, though none displayed the behavior of using their horns to remove the spines.

Intraspecific feeding niche partitioning of sexes is nearly ubiquitous in polygynous, sexually dimorphic ruminants. Intraspecific differences in the diet are particularly common where genders occupy seasonally different home ranges or habitats and have access to different resources (e.g., Shank 1982, Bowyer 1984, Young and Isbell 1991, Main et al. 1996, Bleich et al. 1997, Kie and Bowyer 1999). The males and females at Rini Mountain were not especially segregated in winter. The animals had highly overlapping home ranges during the breeding season and used habitats in similar proportions. Although all-male groups were still seen on occasion in October and early November, and the males chose cliff cactus scrub more often than the females and juveniles, most males were moving with the females and juveniles during the period of the study, and the differences in habitat use accounted for <10% of the observed time. This suggests that large-scale spatial segregation and habitat use differences are not likely to be the most important factors in determining the difference in winter diet.

Instead, differential selection of food resources between age-gender classes is likely to have arisen from allometric effects of gut capacity and metabolic rates (McCullough 1979, Barboza and Bowyer 2000), physiological requirements (Harrison 1983, Darailon 1989, Bleich et al. 1997), or differences in accessibility resulting from body architecture (Hildebrand 1974), e.g., the dimensions of the incisor arcade, the placement of new vegetative growth, the distribution of the spines on the plant, or the smaller horn size. The allometric hypothesis proposes that the males have a larger ratio of ruminal volume to body mass, and a lower metabolic rate per unit of body weight than the females or subadults and, therefore, are able to accommodate and digest bulkier forage of lower quality (McCullough 1979, Bowyer 1984, Barboza and Bowyer 2000). This leads to an expected greater retention time in the larger males. The greater retention time is associated with an ability to utilize slower digesting matter, such as mature plant fiber and crystalline celluloses, and reduces protein



intake requirements due to the greater capacity for the recycling of urea (Wales et al. 1975, Barboza and Bowyer 2000, Parker et al. 2005). The smaller individuals, on the other hand, constrained by gut size, must ingest more energy-rich, quickly digestible diets because they need more energy per kilogram. However, cactus is likely to differ from most other available winter forages in having high digestible energy, low levels of fiber, and very low protein contents (Ramírez et al. 2000, Hernández-Urbiola et al. 2011). The ability to accommodate more matter in the rumen may enable the recovery of more nitrogen from microbial activity and reduce the minimal density of protein required in the diet of the males. Thus, males would be enabled to consume proportionately more cactus. However, whether the high-energy content of the cactus provides carbohydrates that sustain microbial activity and facilitate endogenous recycling of nitrogen is unknown. Protein needs would presumably be particularly important in the developing juveniles and lactating or pregnant females, thus a rich diet of cactus could present nutritional challenges (Dardaillon 1988, Parks et al. 2005, Guevara et al. 2009). Several studies of domestic sheep have shown that the growth rates of juveniles decrease with increasing levels of *Opuntia* spp. in the diet, unless supplemented with protein (Ben Salem et al. 2002, Tien and Beynen 2005, Mendez-Llorente et al. 2008). Conversely, the young animals and lactating females may benefit more from the high water content of cactus. Several studies in arid environments have shown that the *Opuntia* spp. greatly reduces water consumption in domestic sheep (Mendez-Llorente et al. 2008). The larger-bodied mammals have lower rates of water loss than the smaller-bodied ones (Gordon et al. 1982), so that the females, particularly the lactating females, and the juveniles would probably have successively higher water requirements than the males, which should, in the absence of other variables, cause them to consume proportionately more cactus.

The winter diet of *Pseudois schaeferi* at Rini Mountain has undoubtedly changed with the invasion of the highly palatable exotic succulent *Opuntia ficus-indica*. *Opuntia ficus-indica* is a long-domesticated crop species estimated to have originated in central Mexico sometime in the last 9000 years (Griffith 2004). Probably due to its ease in clonal propagation, edibility, and drought tolerance, *O. ficus-indica* was both intentionally and unintentionally established around the world by early explorers and sailors (Griffith 2004), with sometimes catastrophic ecological and economic consequences (Richardson et al. 2000). In many of its destinations, e.g., South

Africa, Australia, Pacifica, its invasive qualities enabled it to rapidly spread and, in several instances, gaining complete dominance of the ecosystem (Richardson et al. 2000). *Opuntia ficus-indica* was first introduced in China around 1645 as a hedge and for its edible young joints and fruit (eFloras 2008). Since then, it has become well established in the upper Yangtze River valley, becoming a conspicuous element of the arid dryland ecosystem, particularly on the steep and sparsely vegetated rocky slopes below 2800 m asl. No other records exist of *P. schaeferi* or its close relative *Pseudois nayaur* consuming *O. ficus-indica*, although *O. ficus-indica* extends as far north as Batang. The literature conspicuously lacks information on the species in Yunnan, and it is not clear whether its naturalized distribution has reached an equilibrium, to what extent native and domestic animals are contributing to its spread, or how it is interacting with the ecosystem. Our results give the first evidence that the winter diet of the adult dwarf blue sheep was highly enriched by this exotic and frequently invasive species, and given the ecosystem-level issues caused by *O. ficus-indica* in parts of its range, highlight the need for a better understanding of the interactions between the dwarf blue sheep, *O. ficus-indica*, and the environment. While wild native ungulates are commonly reported foraging on exotic species (e.g., Parks et al. 2008), to our knowledge, the diet of no other wild population of threatened or endangered ungulate depends so much on an invasive exotic species. While *O. ficus-indica* cactus is now an integral winter forage crop for the dwarf blue sheep at Rini Mountain, and may be directly contributing to their survival, the long-term physiological needs of the species and the balance of ecosystem-level interactions are still troublingly unclear.

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