CSIRO PUBLISHING

Wildlife Research, 2016, **43**, 671–680
http://dx.doi.org/10.1071/WR16011

Habitat use and selection by takin in the Qinling Mountains, China

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Abstract

Context. Understanding habitat use and selection by threatened ungulates is a crucial prerequisite to prioritise management areas and for developing effective conservation strategies.

Aims. The aim of our research was to determine the habitat use and selection of takins (*Budorcas taxicolor*) in the middle range of the Qinling Mountains, China.

Methods. The study was conducted from August 2013 to August 2015. Global positioning system (GPS) radio-tracking was used to monitor 10 collared takins to gain their location information. The Manly–Chesson selectivity index and Bonferroni-adjusted 95% confidence intervals were applied to determine which habitats were selected.

Key results. Habitat use and selection by takins showed obvious individual differences. At the landscape scale, all of the four most common habitat types were preferred by takins. However, all takins avoided artificially planted larch forest, and farmland and village. Available habitats within the home ranges also mostly included the four common habitat types. At the home-range scale, all individuals had significant habitat selectivity during the entire tracking period and each season. The habitat use and selection within the home range varied obviously with season and showed sexual differences to a certain extent.

Conclusions. The habitat selection by takins is scale-dependent. At the landscape scale, takins are most likely to occur at sites covered by forest. At both landscape and home-range scales, our results indicated that takins need more diverse forest habitats, but none of the four most common forest habitats is essential for survival of this species.

Implications. The present work has provided more insight into the habitat use and habitat selection of takins in mountainous forest landscapes. Many measures such as maintaining a diversity of forest habitats, avoiding habitat alteration by invasion of exotic plants, and increasing the area of available habitats by relocating the villages from within to outside of the reserve are recommended to conserve this large species.

Additional keywords: *Budorcas taxicolor*, conservation, habitat selection, scale, seasonality, ungulate.

Received 16 January 2016, accepted 26 November 2016, published online 27 February 2017

Introduction

Habitat selection is the process by which resources are selected by an animal from what is available (Boyce *et al.* 2003). Selective use of available resources could influence reproductive success and survival rate on the basis of the assumption that selected habitats provide higher fitness for animals (Rosenzweig 1981; Nicholson *et al.* 1997; Conradt *et al.* 1999; DeCesare *et al.* 2014). Actually, selection for locations with high forage abundance enhances individual fitness in large herbivores (Moen *et al.* 1997). Obviously, habitat-use and -selection studies are essential for understanding the biological requirements of animals to maximise survival fitness (Freitas *et al.* 2008). Therefore, the habitat selection is subject to considerable attention by ecological scientists. In addition, examinations of habitat selection could determine the most suitable areas for habitat protection and provide insight into animal distribution across environments (Edenius *et al.* 2002; Darmon *et al.* 2012; Braña *et al.* 2013; Corriale and Herrera 2014). Understanding habitat use and selection thus becomes a crucial prerequisite to prioritise areas for management and conservation (Morris 2003).

Most habitat-selection studies of ungulates have focussed on a variety of ecological and social factors, such as sex (Clutton-Brock *et al*. 1987; Oehlers *et al*. 2011), reproductive success (Switzer 1997; Pitman *et al*. 2014), population density (Pérez-Barbería *et al*. 2013; van Beest *et al*. 2014), forage availability and quality (Owen-Smith 2002; Hochman and Kotler 2006), resource distribution (Edenius *et al*. 2002; Kie *et al*. 2002), snow conditions (Mysterud *et al*. 1997), predation risk (Laundré *et al*. 2001; Walker *et al*. 2007) and intraspecific relationships (Putman 1996; Forsyth 2000). These factors influencing the habitat selection may be sensitive to scale (Mysterud *et al*. 1999; Mayor *et al*. 2009). Habitat selection, thus, is increasingly accepted as being scale-specific (Boyce 2006). Habitat use and selection may respond to different temporal scales, such as season (Mahoney and Virgl 2003; Sakuragi *et al*. 2003; Zengeya *et al*. 2014) and year (Rachlow and Bowyer 1998). At different spatial scales, ungulates, especially those large and mobile ungulates, may show different habitat-selection pattern (Bowyer and Kie 2006; Herfindal *et al*. 2009; Oehlers *et al*. 2011). Therefore, understanding scale-dependent habitat selection of an ungulate is essential in the face of temporal and spatial changes in the availability of forage resources.

The takin (*Budorcas taxicolor*) is a large ungulate mainly distributed in restricted mountainous areas of China (Wu *et al.* 1990; Zeng *et al*. 2002). Because of its population decline and habitat loss, takin is considered as a vulnerable species by IUCN and Category I species in the National Protected Animal List in China (Zeng *et al*. 2002; Song *et al*. 2008). Most takins live in groups larger than 10 individuals, and forage on various species of plants, including mosses, ferns, herbs, shrubs and trees (Zeng *et al*. 2001, 2002). Although takin groups are unstable and group composition can vary over time, most groups (79.6%) include both adult males and adult females (Zeng *et al*. 2002). They occur in a range of various habitats, including different forests and alpine meadow up to 4000-m elevation (Song *et al*. 2008). Home ranges of different takin groups may have a partial overlapping phenomenon (Song *et al*. 2000). Habitat use and selection of this species have received little study. Former researches based on line-transect surveys have shown that takins prefer coniferous forest, mixed coniferous and broadleaf deciduous forests (Song *et al*. 1995; Ma *et al*. 2001). However, we do not know how habitat selection of takins changes with spatial scale, and few studies have addressed habitat needs of this species at a landscape scale. Takin home ranges show seasonal variation (Song *et al*. 2000). This variation may affect habitat selection strategies for ungulates (Nicholson *et al*. 1997; Zengeya *et al*. 2014). Nevertheless, no studies have examined how habitat use and selection by takins respond to seasonal changes in the available resources at a home-range scale. Clearly, large gaps in our understanding remain regarding habitat use and selection of takins. Obtaining detailed information on habitat preferences of threatened species is a vital step in accomplishing their effective conservation (Gibbs *et al*. 1998).

Spatial and temporal variations in the quality of forage available to ungulates are typically pronounced, especially in regions with strongly seasonal climates (Zeng *et al*. 2010; Zengeya *et al*. 2014). Seasonal migrations exhibited by many ungulate species are interpreted as a strategy to achieve the maximum fitness on a large scale (Fryxell and Sinclair 1988; Mysterud *et al*. 2001). Takins have a habit of seasonal migration along an altitudinal gradient, resulting in seasonal variations of their home ranges (Zeng *et al*. 2008; Guan *et al*. 2013). Habitat selection of ungulates obviously coincides with seasonal variations of home range and corresponding food availability (Richard *et al*. 2014). Therefore, we predicted that large takins needed diverse habitats, and habitat selection would vary with the seasonal variation in their home ranges. In addition, adult male takins generally are ~40% heavier than are adult females (Zeng *et al*. 2002). For a sexually dimorphic ungulate, habitat requirements of male and female individuals may be different because of their difference in total metabolic-energy requirements (Barboza and Bowyer 2000). We further predicted that habitat selection of takins differed between the sexes.

We conducted a global positioning system (GPS) radio-tracking study to determine the habitat selection of takins in the middle range of the Qinling Mountains, China. Our study objectives were (1) to test whether habitat selection of takins was dependent on the spatial scale, (2) to determine how habitat selection within the home range of a large ungulate varied with seasons and (3) to discuss the implications of our results for conservation of the species.

Materials and methods

Study area

We conducted the present study in and around the Foping National Nature Reserve (33°30′N–33°50′N, 107°39′E–107°58′E), which is located in the middle range of the Qinling Mountains in Shaanxi Province of China (Fig. 1). The study area is ~827 km^2 and encompasses rugged mountains with an altitude ranging from 810 to 2904 m. The annual mean temperature is 11.5°C, and annual rainfall is ~920 mm. According to local climate data, June–August is termed summer, December–March is termed winter, with April–May and September–November forming the seasons of spring and autumn respectively (Zeng *et al*. 2010).

The study area is dominated by primary forest landscape, with shrub, subalpine meadow, and some farmland and villages. The forest types mainly included deciduous broadleaf forest, mixed coniferous–broadleaf forest and coniferous forest, showing an obvious vertical change along an altitudinal gradient from low to high (Ren *et al*. 1998; Zeng *et al*. 2008). The coniferous forest was dominated by farges fir (*Abies fargesii*) and Chinese pine (*Pinus tabuliformis*) intermixed with birch (*Betula* spp.). The understorey of the mixed coniferous–broadleaf forest and coniferous forest was formed mainly by arrow bamboo (*Fargesia spathacea*). Some artificially planted forest is distributed in low altitudes, mainly consisting of larch (*Larix gmelini*). The golden takin (*Budorcas taxicolor bedfordi*) is a large ungulate in this area. Sympatric ungulates include Chinese goral (*Naemorhedus goral*), serow (*Capricornis sumatraensis*), forest musk deer (*Moschus berezovskii*), wild boar (*Sus scrofa*), tufted deer (*Elaphodus cephalophus*) and Chinese muntjac (*Muntiacus reevesi*). Of further note, 298 local people of two villages reside within the reserve, but another 19 villages with 7720 people at low altitudes are distributed around the reserve (Fig. 2).

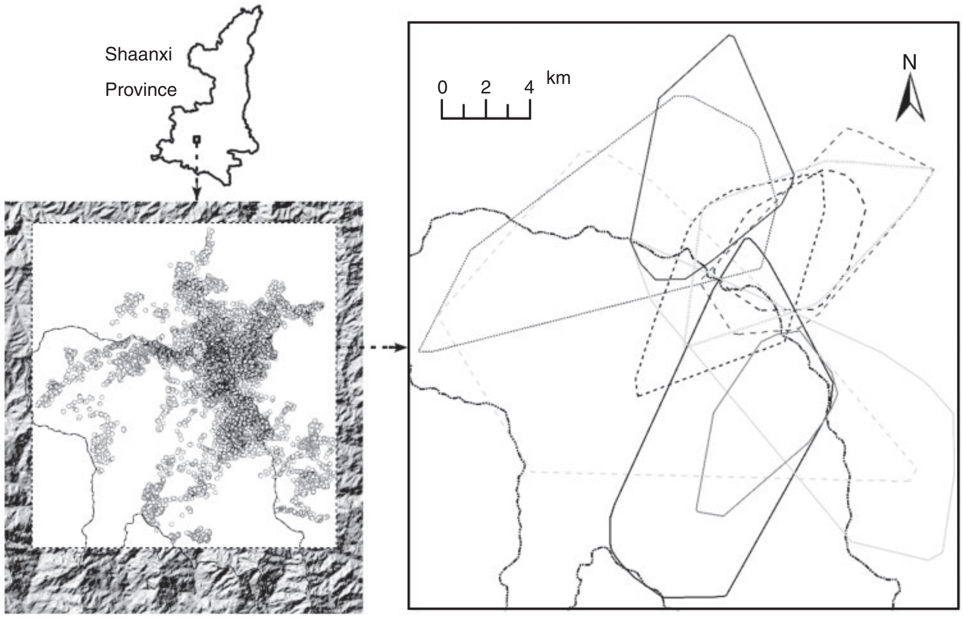

Fig. 1. Location of Foping National Nature Reserve (covered by the black boundary) in Shaanxi Province, China. Locations from 10 takins between 2013 and 2015, and their home ranges (solid line for male, broken line for female) generated by the minimum convex polygon with 100% of locations.

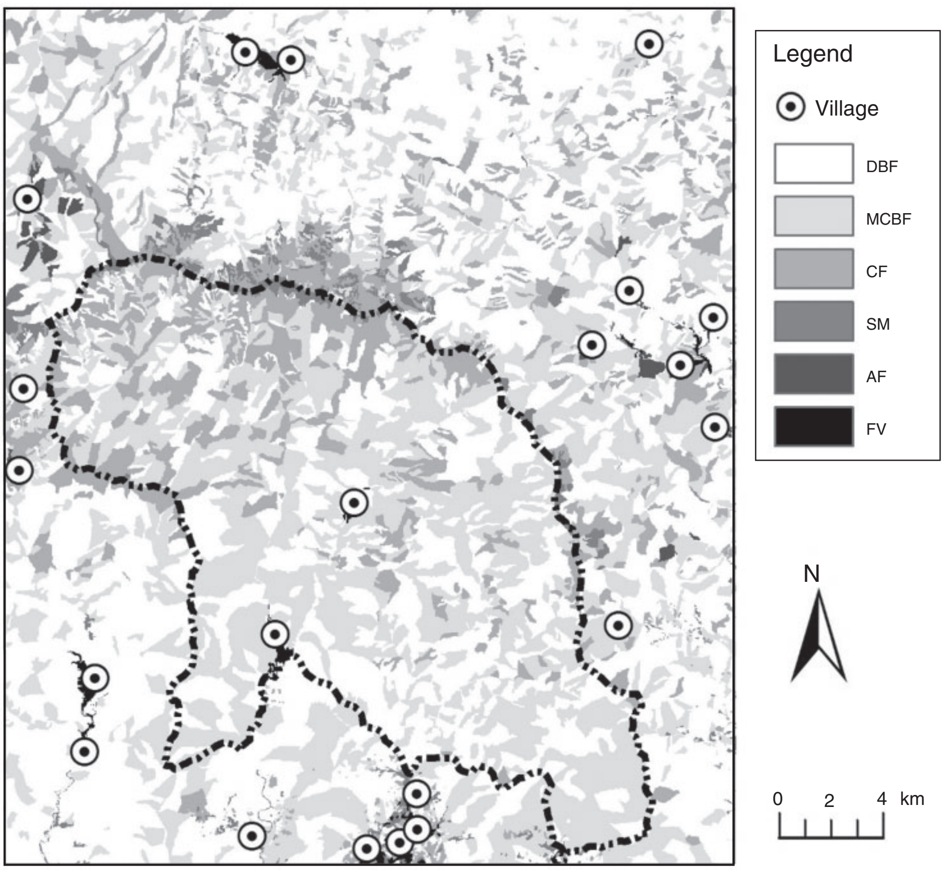

Fig. 2. Distribution of vegetation and the location of villages in and around the Foping National Nature Reserve (covered by the black boundary), China. Habitat types include shrub and meadow (SM), coniferous forest (CF), mixed coniferous–broadleaf forest (MCBF), deciduous broadleaf forest (DBF), artificial forest (AF) and farmland and village (FV).

Takin location and home range

The present study was conducted from August 2013 to August 2015. In total, 10 adult takins (four males: M1–M4; six females: F1–F6) were captured and collared. Two males, M1 and M2, were caught in 2013, eight in 2014. All these collared takins lived in different groups with different group sizes. Each animal was captured via a dart rifle using immobilising anaesthetic. The anaesthetic was xylazine hydrochloride injection (Jilin Huamu Animal Health Product Co., Changchun, China), a solution of xylazine hydrochloride (100 mg mL^{-1}), delivered intramuscularly at a dose of 1.3–1.5 mL per 100 kg takin mass. The antidote to reverse the sedation was Suxing injection (Jilin Huamu Animal Health Product Co.), a solution of tolazoline (400 mg mL^{-1}), injected intramuscularly at an equal dose of the anaesthetic. An animal-capture protocol of the study was approved by the Animal Ethics Committee of the Institute of Zoology, Chinese Academy of Sciences, and the National Forestry Agency of China (Linhuxuzhun #(2012)1630).

All animals were fitted with GPS 7000M collars (Lotek Wireless Inc., Ontario, Canada). The GPS collar weighted ~950 g (less than 1% of the mass of takin) and was programmed to record a GPS location every 2 h for up to 3 years. The collar stored geographical and positional data associated with each data point captured, including date, time, latitude, longitude, altitude, dilution of precision (DOP) and validated class. We downloaded the stored data in the collars periodically, using a hand-held command unit. We kept only three-dimensional locations with a DOP of <10 to remove those less accurate locations (Adrados *et al*. 2002). From September 2013 to August 2015, validated GPS locations for the 10 animals averaged 4541.5 (range 3075–8315).

The validated locations were input to the geospatial modelling environment (GME). It is a platform designed to promote rigorous spatial analysis for spatial data (Beyer 2012). We used the GME to obtain home range of collared takins for each period, by using the minimum convex polygon with 100% of locations (MCP 100%) and Kernel home range with 95% isopleths (KHR 95%; Beyer 2012). For the present study, we obtained the home ranges of MCP 100% and KHR 95% of each individual during each season and the entire tracking period, and the MCP 100% home range generated by all tracking locations.

Habitat-selection analysis

We imported the validated locations and the home ranges in ArcGIS 10.1 (Environmental System Research Institute Inc., Redlands, CA, USA). According to a land cover and a vegetation cover from the State Forestry Administration of China, we also obtained a landscape map of the study area using the ArcGIS 10.1. The habitat variables in the landscape map were divided into six types, including shrub and meadow, coniferous forest, mixed coniferous–broadleaf forest, deciduous broadleaf forest, artificial forest, farmland and village (Fig. 2). To understand what type of habitat landscape was selected within the study area, we defined the home range generated by the MCP 100% of all tracking locations as available habitat, and used the proportion of each habitat variable used within the KHR 95% home range of each individual during the entire tracking period to evaluate its selectivity. To understand what type of habitat variable was selected within the selected landscape of the animals, i.e. their home ranges, we defined the MCP 100% home range of each individual in a given period as available habitat, and used the numbers of GPS locations in each habitat type in the period to evaluate habitat use and selectivity. Then, we could compare their individual differences in habitat selection.

We performed a log-likelihood χ^2 test to determine whether takin selectively used habitat initially (Manly *et al*. 2002), as follows:

$$\chi^2 = 2\sum_{i=1}^{k}\left[n_i^o \ln\left(\frac{n_i^o}{n_i^e}\right)\right], \qquad (1)$$

where k is the number of habitat types, n_i^o is the quantity of Habitat i used by takin in the period, and n_i^e is the expected quantity of Habitat i used. The null hypothesis is that takin used each habitat type in proportion to its relative abundance (randomly used). If the null hypothesis is rejected, at least one habitat experienced significant selection. We then determined which habitats within the home range were selected by applying the Manly–Chesson selectivity index (Eqn 2) and Bonferroni-adjusted 95% confidence intervals (Eqn 3) (Manly *et al*. 2002).

We obtained the selectivity index w_i as

$$w_i = \frac{o_i}{\pi_i}, \qquad (2)$$

where o_i is the proportion of Habitat i used within the given period, and π_i is the proportion of Habitat i available. For landscape-scale selection, habitat is preferred if the selectivity index is >1 and avoided if it is <1. The 95% confidence interval was

$$\hat{w}_i \pm z_{0.05/2k} \times se(\hat{w}_i), \qquad (3)$$

The standard error (Eqn 4) of a selectivity index was

$$se(w_i) = \sqrt{\frac{o_i(1-o_i)}{n\pi_i^2}}, \qquad (4)$$

where n is the total quantity of habitat type used by takin, i.e. the total number of the GPS locations in the given period. For home range-scale selection, Habitat i was preferred if the interval was >1 and avoided when it was <1. If the confidence interval includes 1, the habitat type was randomly used (Manly *et al*. 2002).

Results

Landscape-scale selection

At a landscape scale, habitat composition of KHR 95% home ranges of the takins mostly contained the following four common types: shrub and meadow, coniferous forest, mixed coniferous–broadleaf forest, and deciduous broadleaf forest (Table 1). Although habitat selection of the takins had individual differences, all the four common habitat types were probably preferred by them. In all, 3 of 10 collared individuals used a little artificial forest mainly consisting of larch, but all takins avoided it. In addition, all takins did not use and avoided farmland and village at the landscape scale (Table 1).

Table 1. Habitat use and selection by takins (males: M1–M4; females: F1–F6) at the landscape scale
The π_i is the proportion of Habitat *i* available within the range, generated by the minimum convex polygon with 100% of all tracking locations. The w_i is the selectivity index of each individual for different habitat types in its home range, generated by the Kernel home-range estimate with 95% isopleths during the entire tracking period. Habitat types include shrub and meadow (SM), coniferous forest (CF), mixed coniferous–broadleaf forest (MCBF), deciduous broadleaf forest (DBF), artificial forest (AF) and farmland and village (FV). Habitat was preferred for $w_i > 1$ (+) and avoided for $w_i < 1$ (–)

Habitat type	π_i	w_i									
		M1	M2	M3	M4	F1	F2	F3	F4	F5	F6
SM	0.021	0.562–	1.948+	1.844+	3.785+	1.398+	0.825–	3.106+	0.898–	3.046+	1.036+
CF	0.166	0.523–	0.482–	1.015+	1.594+	1.154+	1.249+	1.904+	1.138+	1.405+	0.841–
MCBF	0.370	1.224+	1.300+	0.952–	0.753–	0.744–	0.868–	0.703–	0.873–	0.676–	0.852–
DBF	0.437	1.027+	0.910–	0.998–	0.860–	1.152+	1.039+	0.816–	1.072+	1.033+	1.198+
AF	0.005	0.000–	0.000–	0.864–	0.000–	0.000–	0.000–	0.093–	0.122–	0.000–	0.000–
FV	0.001	0.000–	0.000–	0.000–	0.000–	0.000–	0.000–	0.000–	0.000–	0.000–	0.000–

Home range-scale selection

Available habitat types within the MCP 100% home ranges of individuals mostly included the four common habitat types. Farmland and village landscape type occurred only in the home ranges of M1 and F3, but was not used by these individuals. Artificial (larch) forest occurred in the home ranges of M3, F3, F4 and F6, but was almost not used by them (Fig. 3). Habitat use of takins within the home ranges had large variation among individuals. Generally, takins used mostly mixed coniferous–broadleaf forest and deciduous broadleaf forest during the whole tracking period and each season. However, some individuals also showed a high percentage of use of shrub and meadow or coniferous forest. Habitat use of takins varied obviously with season, and the difference between the sexes existed to a certain extent (Fig. 3). In spring, males did not use shrub and meadow, whereas females did on a few occasions. In summer, males used deciduous broadleaf forest less than did females. In autumn, males used mixed coniferous–broadleaf forest more and coniferous forest less than did females. In winter, females hardly used shrub and meadow at all, and used coniferous forest more, whereas the inverse was true for males (Fig. 3).

The results of chi-square test showed that all individuals had significant habitat selectivity within the MCP 100% home range in the entire tracking period and each season (Table 2). This habitat selectivity had large individual differences, although all takins avoided artificial larch forest, farmland and village. During the study period, each of the four most common habitat types was probably preferred by takins, without obvious differences between the sexes. However, habitat selection of these takins varied with season, and the differences in habitat selection between the sexes occurred therewith. In spring, both males and females preferred mixed coniferous–broadleaf forest and deciduous broadleaf forest and avoided coniferous forest, whereas males avoided shrub and subalpine meadow, which were probably preferred by females. In summer, both males and females preferred shrub and subalpine meadow, and coniferous forest, whereas males avoided deciduous broadleaf forest which was preferred by females. In autumn, the four common habitat types were preferred by females, whereas males preferred mixed coniferous–broadleaf forest and avoided coniferous forest. In winter, males preferred deciduous broadleaf forest and avoided coniferous forest and mixed coniferous–broadleaf forest, whereas females preferred these three habitat types but avoided shrub and subalpine meadow, which was preferred by males (Table 2).

Discussion

In our study, we have provided information on habitat selection by threatened takins at spatial and temporal scales. Our results indicated that habitat selection by takins is scale-dependent. At a landscape scale, takins preferred primary forest, but avoided artificial larch forest, farmland and village. At a home-range scale, takins exhibited strong selectivity for the four most common habitat types, and had seasonal changes and sexual differences in the selectivity.

Our work on broad-scale habitat selection by takins has indicated that, at a landscape scale, takins are most likely to occur at sites covered by forest. Except for artificial larch forest, all other forest types were probably preferred by takins (Table 1). Obviously, as a large ungulate, takin's used space included more diverse habitats in their home ranges. At the landscape scale, habitat selection of takins might be determined by predation risk and resource abundance. Understorey of the artificial larch forest has little shrub and grass (Ban and Xu 1995). It is probably because of shortage of available forage that spoor of takins can hardly be found in the artificial larch forest in the study area and other distribution area of takins (Z.-G. Zeng, unpubl. data). Selection ratios in the present study also showed that takins did not use farmland and village, indicating that takins avoid human developments, as do also other ungulates (Nicholson *et al*. 1997; Pinard *et al*. 2012; Saïd *et al*. 2012; Yan *et al*. 2013; Luo *et al*. 2014). Human activities or disturbance, as a sort of anthropogenic 'predation risk', often modify the behaviour of ungulates (Saïd *et al*. 2012). However, farmland is probably used by takins, because sometimes some solitary individuals can be found to live in the farmland around villages (Zeng *et al*. 2003).

At the home-range scale, the ranges of only a few individuals covered a small quantity of artificial larch forest, farmland and village. Therefore, habitat use of takins within the home range showed strong selectivity for different primary forests, shrub and subalpine meadow. Similar to the early results of Song *et al*. (1995) and Ma *et al*. (2001), we detected that takins preferred coniferous forest, mixed coniferous–broadleaf forest, shrub and subalpine meadow. However, their habitat selection had

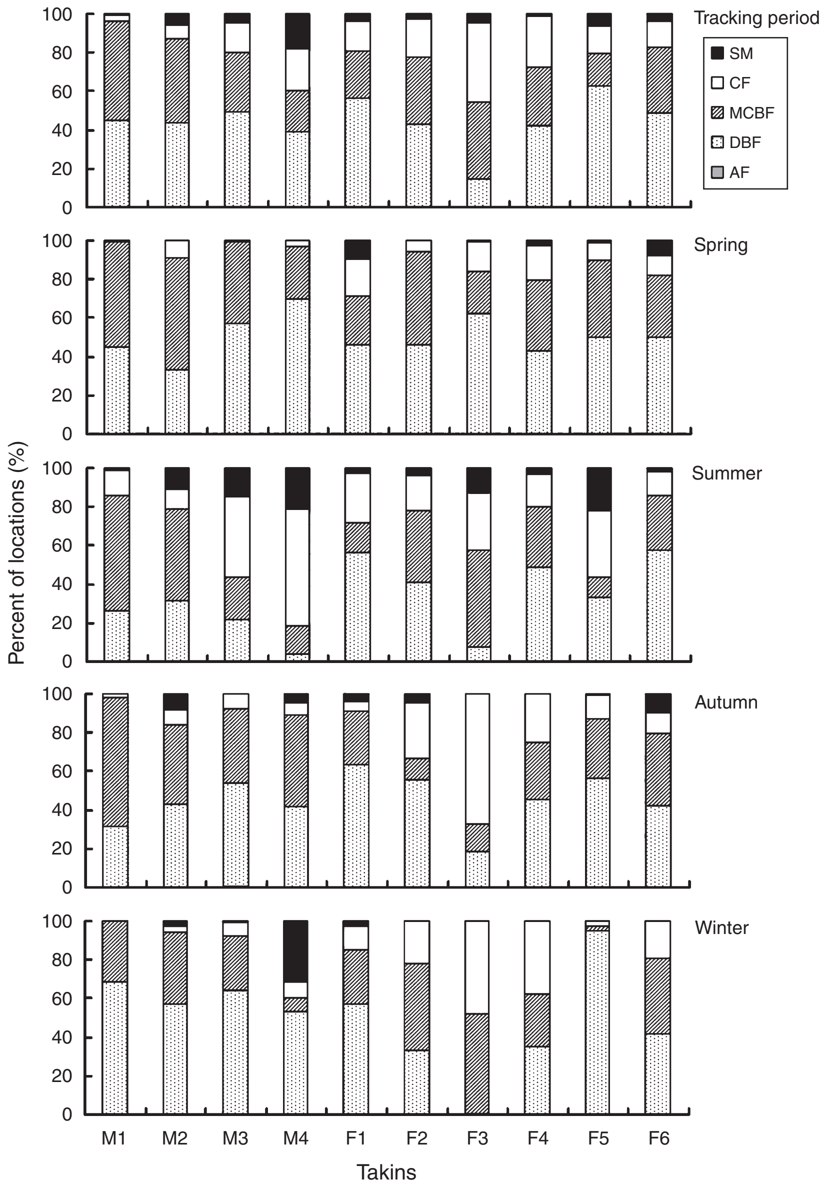

Fig. 3. Habitat use (percentage of locations) of 10 takins (males: M1–M4; females: F1–F6) in the Qinling Mountains, China, during the entire tracking period and each season. Habitat types mainly include shrub and meadow (SM), coniferous forest (CF), mixed coniferous–broadleaf forest (MCBF) and deciduous broadleaf forest (DBF). Only two M3 locations in autumn and one F6 location in spring were in the artificial forest (AF), so it is difficult to find the percentage of AF (0.07% by M3 and 0.02% by F6 during the tracking period, 0.14% by F6 in spring, and 0.34% by M3 in autumn) in the figure.

obviously individual differences (Table 2). Each of the four most common habitat types was preferred by takins at the home-range scale, further indicating that takins need more diverse habitats. In addition, preferred habitats varied among individuals, suggesting that none of these four habitats is essential for survival of this species.

Our results showed that habitat selection within the home range of takins significantly differed among seasons. This may be determined by seasonal migratory behaviour of takins and seasonal change of environmental conditions, such as available food resources and temperature along an altitudinal gradient (Zeng *et al*. 2010). Seasonal migration is a habitat-selection strategy adopted by many ungulates as a response to spatial variation of available resources (Nicholson *et al*. 1997; Zweifel-Schielly *et al*. 2009; Beck *et al*. 2013). This strategy allows them access to habitats of highest quality (Nicholson *et al*. 1997; Zeng *et al*. 2010). In spring, most takins preferred deciduous broadleaf forest and mixed coniferous–broadleaf forest because the animals moved downhill to obtain new green food in their understorey. Vegetation sprouts earlier at

Table 2. Habitat selection by takins (males: M1–M4; females: F1–F6) within their home ranges, generated by the minimum convex polygon with 100% of locations

The following table shows the selectivity index, w_i, of individuals for different habitat types, including shrub and meadow (SM), coniferous forest (CF), mixed coniferous–broadleaf forest (MCBF) and deciduous broadleaf forest (DBF). Only two M3 locations in autumn and one F6 location in spring were in the artificial (larch) forest, and no locations were within farmland and village for all individuals, so these two types avoided by takins are not shown in the table. Habitat was preferred for confidence interval $w_i > 1$ (+) and avoided for $w_i < 1$ (–). Habitats without markings were randomly used. For the values of chi-square test: *$P < 0.05$, **$P < 0.01$, ***$P < 0.001$

Takin ID	Habitat type	Entire tracking period	Spring	Summer	Autumn	Winter
M1	SM	0.442–	0.000–	1.901	0.000–	0.000–
	CF	0.303–	0.031–	1.101	0.163–	0.000–
	MCBF	1.101+	1.184+	1.284+	1.435+	0.681–
	DBF	1.093+	1.083+	0.637–	0.763–	1.659+
χ^2-value		749.87***	323.46***	199.40***	514.02***	1258.85***
M2	SM	3.682+	0.177–	7.004+	5.439+	1.577+
	CF	0.867–	1.099	1.258+	0.974	0.408–
	MCBF	0.926–	1.216+	1.003	0.866–	0.786–
	DBF	1.008	0.776–	0.733–	0.991	1.321+
χ^2-value		500.28***	66.76***	492.93***	275.22***	258.97***
M3	SM	1.721+	0.078–	5.985+	0.000–	0.280–
	CF	0.973	0.012–	2.638+	0.486–	0.460–
	MCBF	0.760–	1.055	0.545–	0.953	0.683–
	DBF	1.218+	1.398+	0.528–	1.313+	1.583+
χ^2-value		190.87***	206.49***	661.62***	82.96***	287.95***
M4	SM	3.552+	0.000–	4.196+	0.919	6.210+
	CF	1.068	0.143–	2.966+	0.302–	0.400–
	MCBF	0.952	1.215	0.667–	2.119+	0.320–
	DBF	0.748–	1.335+	0.075–	0.801–	1.018
χ^2-value		788.01***	191.91***	1502.09***	277.94***	991.35***
F1	SM	2.227+	5.260+	1.447	2.302+	1.322
	CF	0.976	1.256	1.647+	0.317–	0.807–
	MCBF	0.738–	0.762–	0.463–	0.837–	0.861–
	DBF	1.134+	0.922	1.133+	1.273+	1.139+
χ^2-value		195.64***	111.85***	168.61***	143.34***	29.87***
F2	SM	0.932	0.000–	1.578+	1.659	0.000–
	CF	1.100+	0.310–	1.005	1.615+	1.210+
	MCBF	1.010	1.382+	1.052	0.323–	1.295+
	DBF	0.956–	1.037	0.925–	1.242+	0.742–
χ^2-value		11.69**	121.29***	16.89***	280.04***	144.75***
F3	SM	1.242+	0.103–	3.269+	0.000–	0.000–
	CF	1.678+	0.652–	1.236+	2.787+	1.992+
	MCBF	0.998	0.544–	1.251+	0.345–	1.293+
	DBF	0.467–	1.929+	0.248–	0.580–	0.016–
χ^2-value		793.54***	204.70***	597.14***	634.36***	1003.33***
F4	SM	0.844	1.549	2.166+	0.000–	0.059–
	CF	1.595+	1.105	1.004	1.525+	2.324+
	MCBF	0.890–	1.071	0.936	0.862–	0.784–
	DBF	0.888–	0.905	1.016	0.957	0.739–
χ^2-value		221.47***	10.15*	18.87***	62.81***	331.89***
F5	SM	0.922	0.202–	3.283+	0.076–	0.000–
	CF	0.468–	0.289–	1.144+	0.409–	0.083–
	MCBF	0.652–	1.548+	0.405–	1.185+	0.111–
	DBF	1.680+	1.334+	0.891–	1.510+	2.526+
χ^2-value		1058.38***	277.90***	339.72***	260.16***	1991.04***
F6	SM	1.673+	3.226+	0.910	4.122+	0.091–
	CF	0.832–	0.645–	0.736–	0.662–	1.162
	MCBF	0.979	0.932	0.808–	1.082	1.137+
	DBF	1.049+	1.070	1.248+	0.910–	0.893–
χ^2-value		96.98***	70.51***	104.76***	161.93***	77.92***

lower altitudes because threshold temperatures for spring phenology are reached earlier here (Zeng *et al*. 2010). Early phenological stages of plants generally have a high nutritional quality in terms of energy and protein (van Soest 1994; van der Wal *et al*. 2000). In summer, most takins preferred coniferous forest, shrub and subalpine meadow at high altitudes, in which vegetation sprouts later and the abundance of young forage and temperature is increasing. The twigs and leaves of the arrow bamboo in the understorey of coniferous forest also constitute important forage for takins (Zeng *et al*. 2001). In autumn, each of the four most-used habitat types was preferred by takins. The decrease of temperature and the forage quality and quantity at a higher altitude may force animals to move down in early autumn (Zeng *et al*. 2008). Therefore, some takins preferred deciduous broadleaf forest and mixed coniferous–broadleaf forest again by moving downhill in autumn in search of unwithered forage (Zeng *et al*. 2010). In winter, most takins preferred deciduous broadleaf forest, mixed coniferous–broadleaf forest and coniferous forest at intermediate and low altitudes, because the forest provides sufficient shelter for animals from heavy snow and cold wind, especially on south-facing slopes (Wu *et al*. 1990). In addition, the mixed coniferous and broadleaf forest is also an important habitat of takins for giving birth (Wang *et al*. 2005). In conclusion, habitat selection of takins appears to coincide with seasonal changes of vegetation phenology and corresponding food availability, at least from spring to autumn.

Habitat selection by takins also showed an obvious difference between the sexes, especially in spring and winter. Sexual difference in habitat selection, i.e. habitat segregation, has been found in other sexual dimorphic ungulates (Nicholson *et al*. 1997; Bowyer *et al*. 2004; Oehlers *et al*. 2011; Unterthiner *et al*. 2012; Ranglack and Toit 2015). Many hypotheses such as the nutritional-needs hypothesis (NNH), the reproductive-strategy hypothesis (RSH; or the predation hypothesis) and the gastrocentric hypothesis have been put forward to explain the habitat segregation (Mysterud 2000; Oehlers *et al*. 2011). For an ungulate, the NNH predicts that males, being larger, can accept lower diet and habitat quality than do females. This may be the reason that some male takins prefer shrub and subalpine meadow at high altitudes in harsh winter (Table 2). In addition, the RSH suggests that males should seek high-quality forage so as to improve body condition for their future reproductive success, whereas females should select habitats that maximise their ability to raise young. This may be the reason that all male takins preferred deciduous broadleaf forest and mixed coniferous–broadleaf forest for new-green food in spring (Table 2). However, the underlying causes of sexual difference in takin habitat selection are not yet fully understood and require further study.

Our findings indicated that temporal and spatial changes in habitat selection by takins should be considered in conservation of the threatened species. There are several important implications for takin conservation and habitat management. First, the maintenance of a diversity of forest habitats is recommended to conserve this large species. Second, since deciduous broadleaf forest was preferred by takins, especially in spring, conservation measures for this kind of habitat at low altitudes are very important. Third, wildlife managers should be aware of the potential impacts of invasion by exotic plants, because the presence of artificial larch forest was altering the habitat that was suitable for a large ungulate. Last, the villages within the reserve are suggested to be relocated outside the reserve, because a decrease in human disturbance and the recovery of the farmland around villages can effectively increase the area of available habitats of this species. Overall, our study has provided more insights into the habitat use and habitat selection of the takin.

Acknowledgements

This research was supported by the National Natural Science Foundation of China (Grant No. 31372146 and No. 31172112).

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