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ORIGINAL PAPER

Seasonal migration by a large forest ungulate: a study on takin (*Budorcas taxicolor*) in Sichuan Province, China

**Tian-Pei Guan · Bao-Ming Ge · William J. McShea ·
Sheng Li · Yan-Ling Song · Chad M. Stewart**

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Abstract Migration in large mammals is a biological phenomenon that involves seasonal movements over a vertical or horizontal scale that encompasses distances of more than several home ranges. Takin are large bovid herbivores that conduct seasonal migrations. From 2006 to 2009, we utilized data from 9 GPS-collared animals and 22 trail event recorders to describe takin migration pattern at the level of both individuals and population. We found seasonal migration of takin over an elevation gradient which contained two migration cycles, with takin inhabiting the highest elevations in summer, lowest elevations in spring and autumn, and intermediate elevations during winter. These movements did not involve expansion of home range size but rather shifts in distribution. Habitat availability analysis based on five forest types indicated that takin showed significant monthly forest preferences. Based on both telemetry and trail monitors, mature forest with bamboo understory was the habitat favored by takin for more than 8 months of the year. Both methods also indicated that not all individuals migrated to the highest elevations during summer or the lowest elevations in winter. We also found that individual takin do not necessarily follow the same annual movement, as three out of the four animals with at least 2 years of data changed their migration pattern between years. Current protocols for annual surveys conducted at high-elevation meadows or low-elevation valleys are not adequate to detect all individuals. We suggest that surveys must include all potential habitats and include detection functions in order to accurately estimate takin numbers or relative changes in their density.

Keywords Elevation gradient · *Budorcas taxicolor* · Migration · Bamboo forest · Population estimation · Habitat availability analysis

Introduction

Seasonal migrations that progress from high elevations in summer to low elevations in winter are common for ungulates, based on studies with roe deer (*Capreolus capreolus*), sika deer (*Cervus nippon*, Sakuragi et al. 2003), red deer (*Cervus elaphus*, Morgantini and Hudson 1988), and moose (*Alces alces*, Ball et al. 2001). These seasonal elevation shifts are believed to be motivated by shifts in food resources (Dingle 1980; Fryxell et al. 1988; Mysterud 1999), mating opportunities (Liu et al. 2002; Wang et al. 2010), and environmental conditions (Dingle 1980; Fryxell et al. 1988) and to avoid predation (Fryxell et al. 1988). However, habitat loss and increasing human disturbance imposed

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T.-P. Guan
Ecological Security and Protection Key Laboratory of Sichuan Province, Mianyang Normal University,
Mianyang 621000, China

T.-P. Guan · Y.-L. Song
Ministry of Education Key Laboratory for Biodiversity Sciences and Ecological Engineering, College of life Science, Beijing Normal University,
Beijing 100875, China

B.-M. Ge
Jiangsu Provincial Key Laboratory of Coastal Wetland Bioresources and Environmental Protection,
Yancheng,
Jiangsu 224002, China

W. J. McShea · S. Li · C. M. Stewart
Smithsonian Conservation Biology Institute,
Front Royal, VA 22630, USA

Y.-L. Song (✉)
Key Laboratory of Animal Ecology and Conservation Biology,
Institute of Zoology, Chinese Academy of Sciences,
1 Beichen West Road, Chaoyang District,
Beijing 100101, China
e-mail: songyl@ioz.ac.cn

pressure on migration by creating barriers to spatial movement (Berger 2004). In order to protect their migrations from human interference, understanding the species-specific pattern and correlates for migration is indispensable for the effective conservation of many large mammals.

Takin (*Budorcas taxicolor)* are gregarious bovid herbivores (250–500 kg) that reside in the montane regions of Southeastern China, Myanmar, Northeastern India, and Bhutan (Wilson and Reeder 2005). Although primarily forest-dwelling ungulates, they were observed in large groups and engage in rutting behavior during June and August within alpine shrub/meadows (Wu et al. 1990). Although they were first reported by Hodgson in 1850 (Neas and Hoffmann 1987) and observed to live in habitats with rugged terrain with sharp elevational changes in forest types (Wu et al. 1990), knowledge of the pattern and causes of this migration is still limited (Zeng et al. 2003, 2008, 2010).

Although several studies have described seasonal movements by takin, different opinions have arisen. Zeng et al. (2008) reported that golden takin (*Budorcas taxicolor bedfordi*) used mid-elevation forest during the winter (mean elevation 2,100 m), low-elevation forest in spring and autumn (mean elevation 1,800 m), and high-elevation forests in summer (mean elevation 2,600 m) based on a 1-year study of three collared individuals and multiple sign transects. However, these results contrast with direct observations of takin in the Qinling, Minshan, and Gaoligong Mountains in more southern latitudes. These observations either reported a direct migration between high meadows in summer and low valleys in winter (Deng 1984; Wu et al. 2002; Ma 1999) or no major seasonal shifts (Ai 2003). These regional differences are possibly due to methodology, as the southern observations did not benefit from the use of radio telemetry or due to differences in sub-species observed. Furthermore, the study of Zeng et al. (2008) triangulated VHF signals within a complex terrain, a process prone to inaccuracies, as minor location errors in steep terrain can result in large errors in estimating elevation (White and Garrott 1986).

Previous radio telemetry studies were conducted on golden takin (Zeng et al. 2008), which occupy the northern edge of takin distribution and are considered a separate subspecies from Sichuan takin (*Budorcas taxicolor tibetana*) that are found within the more southern Minshan, Qionglai Mountain, and Liangshan regions (Wu 1986). These southern forests exhibit less severe winters (they are 1° south on latitude) and more habitat types over a broader elevation gradient (2,600 vs. 1,800 m gradient in North, Wu et al. 1990). Therefore, it would be interesting to know if the southern populations exhibited the same migration pattern observed in golden takin. The more complex terrain of the southern mountains precludes the use of VHF collars to accurately estimate elevation. Increased accuracy and sample size derived from GPS collars would facilitate analysis on habitat utilization and spatial movement (Barlow et al. 2011; Kittle et al. 2008; Tobler 2009).

If seasonal migration does occur in takin, it may be due to changes in forage quality and quantity; these changes should be detectable using remote sensing (Tucker and Sellers 1986). Zeng et al. (2010) presented a predictive model of takin migration based on seasonal changes in vegetation productivity (Normalized Difference Vegetation Index), slope, aspect, and solar radiation. They attributed the complex migration pattern to a combination of vegetation phenology driving downhill migration in early spring and fall and the uphill migration in later spring, while better thermal conditions at intermediate elevation motivates the use of middle latitudes during winter (Zeng et al. 2010).

Takin have class 1 protection status in China and are found within 25 national nature reserves (SFA 2010), where annual surveys are conducted using the assumption that predictable seasonal migrations bring all animals into observable areas at specific times of the year (Ge et al. 1989; Ma and Tian 2002). Population surveys in Foping Nature Reserve are conducted from April to July during a period of uphill migration and a sedentary period in alpine shrub/meadows and shrub forest (Zeng et al. 1998). Surveys in Tangjiahe Nature Reserve (Sichuan Province) and Niubeiliang Nature Reserve (Shanxi Province) are conducted in early winter based on the assumption that takin reside at low (Ge et al. 1989) or intermediate elevations (Ma and Tian 2002) in winter. These sight-based survey protocols assume all animals make the same movements, and the pattern is consistent between years.

The objectives of this study were to provide an accurate description of takin seasonal migration to guide management and to determine if: (1) takin in Minshan demonstrate seasonal migrations that match those reported in a more northern subspecies; (2) seasonal elevations selected by takin result in shifts in forest type; and (3) there are individual differences in migratory pattern that might make current survey protocols inadequate.

Materials and methods

Study area

This study was conducted in Tangjiahe National Nature Reserve (104°E, 32°N, hereafter referred as to Tangjiahe) from 2006 to 2009, which is located in northwest Sichuan Province, China (Fig. 1). Tangjiahe was established in 1978 for the protection of giant panda (*Ailuropoda melanoleuca*), golden monkey (*Rhinopithecus roxellana*), and takin, covering an area of 400 km^2. Located within a branch of Minshan, Tangjiahe has a rugged terrain with a broad elevation range from 1,100–3,864 m and is located within the main distribution region of takin in China (Hu 1994).

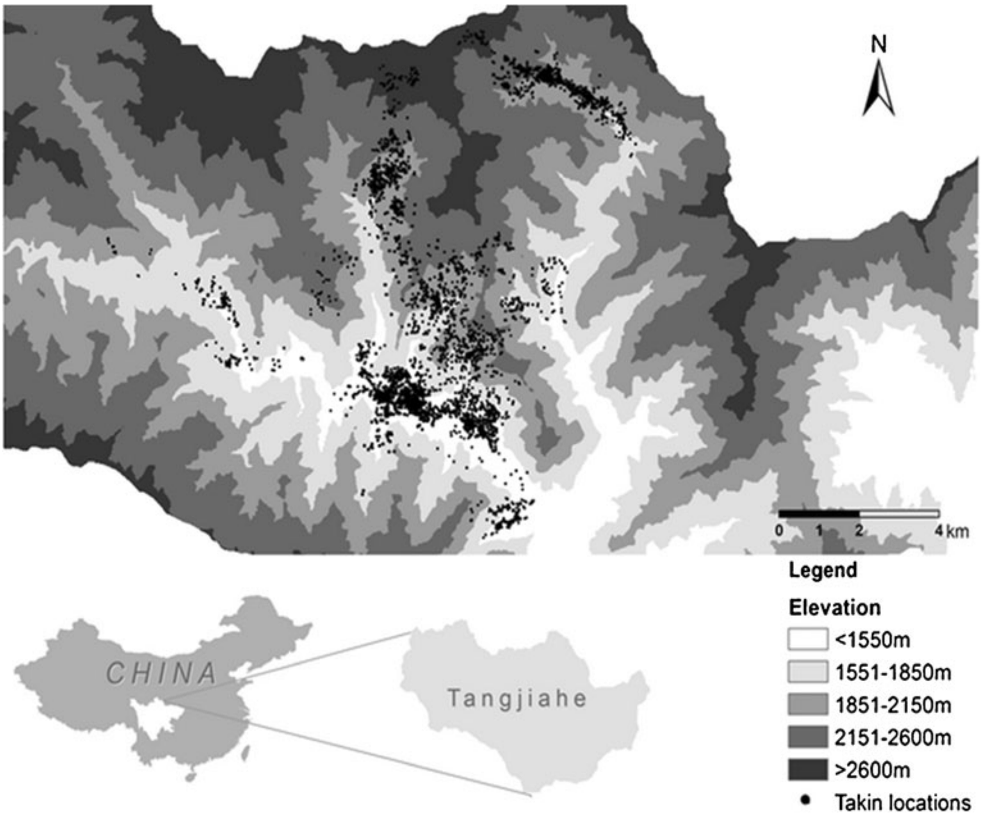


Fig. 1 Takin locations acquired from the nine GPS-collared animals in Tangjiahe Nature Reserve, China followed over a 2-year period (dates). Elevation bands shown correspond with forest types outlined in Fig. 2

The climate in Tangjiahe is temperate, with January the coldest month (mean temperature −1.2 °C) and July the warmest (mean temperature 19.7 °C). For home range analysis, we need to group location data into seasons, and we created four seasons (December to February as winter, March to May as spring, June to August as summer, September to November as autumn) according to common patterns of both snowfall and temperature. Winter was delineated from autumn and spring by the observation of snow at the higher elevation (>2200 m). Summer was delineated from spring and autumn by a mean daily maximum temperature >15 °C. The vegetation within Tangjiahe follows a distinct altitudinal gradient, exhibiting broadleaf forest at low elevation, coniferous forest at higher elevations, and alpine shrub/meadows above tree line (2,700 m). Bamboo (*Fargesia denudate Yi*, *Fargesia scabrida Yi*, and *Fargesia rufa Yi*) is common within the understory from middle elevation (1,900 m) to the edge of tree line (Hu 2005). There are no human settlements within the reserve boundary, but the lower elevations contained settlement sites prior to reserve establishment.

Takin capture

We captured three takin in 2006 and five takin in 2007.Two additional takin were captured in 2009. Our selection criteria was to capture adult individuals observed in groups, apparently in good health, with an effort to select individuals in different social groups and to create an equal sex ratio of study animals (Table 1). All takin were live-captured using a dart rifle to remotely deliver a 2-cc anesthetic cocktail consisting of 2 mg carfentanil citrate, 12 mg detomidine, and 280 mg ketamine. After sedation, animals were measured, ear-tagged, and we determined sex and physical condition. Each takin was fitted with a Lotek GPS 4400 M collar (Lotek Wireless Inc., Ontario, Canada) which weighed approximately 1.3 kg (less than 1 % of takin's body mass). All collars were pre-programmed to record four or six locations per day (Table 1) and equipped with a VHF transmitter for ground telemetry, an UHF transmitter for remote data downloading and uploading, and a mortality sensor with VHF signal. The pulse and body temperature of the anesthetized animal were monitored throughout the handling process, which was normally limited to <15 min, before an antidote was administered intramuscularly (200 mg naltrexone, 1,200 mg tolazoline, and 25 mg atipamezole). All animal handling protocols were approved by the National Zoo's Animal Care and Use Committee.

Takin GPS data

All ten collared animals were monitored monthly for mortality signals. We remotely downloaded the location data

Table 1 Summary for takin with GPS collars in Tangjiahe Nature Reserve, Sichuan Province, China, 2006–2009

Sex	ID	Age class	Date-On (mm/dd/yy)	Date-Off (mm/dd/yy)	Scheduled positioning frequency/day	Working days	Valid locations (%)
F	682	Adult	10-19-06	3-11-09	4	874	775 (22.2)
F	808	Sub-adult	10-22-06	3-09-09	4	869	1,419 (40.8)
F	1532	Adult	9-19-07	1-14-10	4	853	2,821 (82.41)
F	1534	Adult	9-21-07	1-14-10	4	854	2,731 (79.95)
M	195	Adult	9-20-07	12-26-07	4	97	310 (79.89)
M	683	Adult	4-04-09	6-16-09	6	73	373 (81.79)
M	1533	Adult	9-20-07	3-13-09	4	549	1,940 (88.34)
M	15311	Adult	9-20-07	1-08-08	4	112	379 (84.59)
M	15312	Adult	4-03-09	6-19-09	6	78	388 (85.09)

stored in the collar quarterly. We eliminated the locations without three-dimentional positioning and/or a PDOP value >10 for their poor positioning accuracy (D'eon and Delparte 2005). We extracted the elevation values of all selected locations from a fine-scale DEM (digital elevation model, 10×10 m) using ArcGIS 9.2 (ESRI Inc, CA, USA). To avoid the possible influence of the handling process on animal movements, we eliminated the data of the first 2 weeks after capture. Prior to analysis, we selected 1–2 GPS locations per day for each individual to minimize the autocorrelation between consecutive positions. A second location was only used when it met the criteria listed above and was >6 h from the previous location. We captured ten takin, but only nine individuals provided sufficient locations to be included in the analysis.

Trail monitor survey

To determine the seasonality and pattern of vertical movement for non-collared takin population, we used trail monitors to detect the occurrence of takin on patrolling trails that traversed the altitudinal gradients within the reserve. From October 2007 to November 2009, we evenly deployed 22 Trailmaster (TM1550) infrared trail monitors (Goodson & Associates, INC., Kansas, USA, hereafter referred to as TM) across a broad range of elevations (1,300–3,200 m). Each TM consisted of a transmitter and receiver that were set on opposite sides of animal trails, which were preselected based on reserve's routine patrolling routes. Monitors were set at a height of 1.2–1.3 m above ground, approximately the chest height of adult takin, and controlled so that the beam must be blocked for >0.5 s before it registered an event. Takin are the largest mammal within the reserve, it is possible a second large mammal, serow (*Capricornis sumatraensis*), could have sufficient height to trigger the TM, but their relative density is about 1/30 that of takin based on both sign transects (unpublished data) and camera-trapping (Wang et al. 2006) studies within the reserve. The monitors were checked quarterly to replace batteries and download data. Post hoc, the recorders were grouped into elevation bands whose limits were determined by the stratification of habitat types. Unfortunately, all recorders located in the lowest elevation band were stolen or damaged prior to providing data, and we discontinued placement within that band. However, we did conduct regular takin counts within the low-elevation band by surveying all visible takin during a daily commute (5 km) along a central road during morning (6:30–7:30) and evening (17:30–18:30) in 2009. We presented these observations as mean number of takin observed per day for each month of observations.

Statistical analyses

We generated a forest classification of Tangjiahe based on a Landsat ETM+satellite image (path 129/row 037, obtained at 13th May, 2001, NASA) to examine the relationship between takin vertical movement and forest type. Four forest types were defined and classified during image processing; alpine shrub/meadow forest, coniferous forest, broadleaf forest, and riparian willow forest. The supervised classification of forest types was validated by using ground data from a reserve-wide vegetation survey of 329 circular plots (plot radius=20 m) conducted during 2007–2010. Since the distribution of understory bamboo cannot be accurately identified using Landsat image (Tuanmu et al. 2010), and bamboo is considered an important food resource for takin (Hu 1994; Wu et al. 1990; Zeng et al. 2001), we added a fifth forest category (bamboo forest) to the forest classification based on ground data from the third National Panda Survey (SFA 2006), and bamboo distribution was extracted from biodiversity monitoring transects that were conducted quarterly since 2005 (64 transects per year).

An accuracy assessment of the forest cover map found correct classifications to be robust: riparian willow forest

(n=127, 79.5 % correct), broadleaf forest (n=309, 77.2 % correct), coniferous forest (n=137, 82.5 % correct), and alpine shrub/meadow (n=55, 81.8 % correct). A separated accuracy assessment of bamboo were conducted within the whole elevation range (n=400, 82.5 % correct). For takin with >1 year of data, we considered each year as a spate analysis. We did not examine months where we had <30 locations for that month.

To test if takin select habitat in different months, we compared the locations of individual takin within each habitat band against a predicted distribution based on the proportion on each habitat band encompassed by their annual home range (minimum convex polygon) using a Chi-square test (Neu et al. 1974), with significant results further subject to a bonferroni test between categories. We considered each year as an independent sample for individuals with more than 1 year of data.

We calculated the median monthly elevation for all radio-collared takin by combining all validated data, including samples of animals collared for >1 year. We represented the monthly elevation using the median value, as it minimizes the influence of extreme values better than the arithmetic mean (Sokal and Rohlf 1995). To examine annual consistency and pattern in migration movements, we compared monthly elevation values across years for individuals using a non-parametric test (Mann–Whitney *U*) due to the failure of the data to meet criteria for a normal distribution (Kolmogorow–Smirnov test, $p<0.01$).

To determine whether elevation shifts were due to either an expansion of home range size or a shift in distribution, we calculated the mean seasonal home range. The seasonal home range size was determined for each animal with >50 valid locations by using Minimum Convex Polygon (MCP) which was executed by ArcGIS 9.2. We used 3-month seasons due to lack of sample size within all months, and we used the criteria of considering different years of data for the same animal as being different observations. One-way ANOVA and post hoc test were applied to test if difference of home range size might exist between seasons.

As an independent test of changes in elevation by the radio-collared takin, we used the average daily counts from the TMs as a measure of takin activity along the elevation gradient. Some weather events (i.e., fog and snow) were not consistent across elevations and produced false triggers, which were compensated by deleting daily records for all TMs whose number of events was >2 SD above the daily mean for all recorders (i.e., >36 events). An examination of the record counts at each elevation bands indicated they were not normally distributed and thus we selected a non-parametric test (Mann–Whitney *U*) to compare difference of record counts between habitat bands. All tests were conducted with SPSS (version 17.0), and we considered differences with probabilities of $p<0.05$ to be significant.

Result

Forest-type classification and elevation availability analysis

We examined a cumulative distribution curve for each forest type and identified five habitat bands that corresponded to the lower (<20 %) or upper limits (>85 %) of the cumulative distribution curve each forest type. We identified a low habitat band of riparian willow forest at <1550 m; a distribution of broadleaf forest from 1,550–1,850 m; mixed-bamboo forest from 1,851–2,150 m; coniferous forest with a bamboo understory (hereafter referred to as coniferous-bamboo forest) from 2,151–2,600 m; and a high-elevation forest of alpine shrub/meadow at >2,600 m (See Fig. 2). Across the entire study area, we estimated the availability of riparian willow forest (12.2 %), broadleaf forest (18.2 %), mixed-bamboo forest (23.0 %), and coniferous-bamboo forest (29.2 %), as well as alpine shrub/meadow (17.3 %).

Vertical movement of takin

From 2006–2009, 9 GPS collars were attached to 8 adult (three females and six males) and one sub-adult (female) takin. Five collars functioned for >1 year and four collars of these collars functioned for >2 years. In total, we obtained 144 months of location data from the nine individuals (mean duration of location data=16 months). Takin ranged from 1,250 to 3,000 m and exhibited distinct elevation change between seasons. They were recorded at their highest elevations in July and lowest elevations in October and April. Annually, there were two distinct vertical migrations cycles. The first migration occurred from November to March with takin moving up from low-elevation forests from November through December to mid-elevations (1,850–2,150 m) where they remain for 3 months (January, February, and March). From the end of March through April, takin returned to lower elevation valleys. The second migration occurred from May through October (see Fig. 3) as takin steadily increased in elevation until reaching their highest elevation (2,600–3000 m) during late June. Downhill migration began in late August/early September, with takin moving quickly to a lower elevation (<1,550 m) for approximately 2 months (September and October).

We calculated mean seasonal home range as 7.01± 1.26 km^2 (n=11) in spring, 6.69±1.64 km^2 (n=9) in summer, 3.98±0.55 km^2 (n=16) in autumn, and 3.63±0.62 km^2 (n=14) in winter (Fig. 4). As the shortest distances from lower to upper elevation bands was 5–10 km in our study area (Fig. 1), at no point did animals expand their home ranges to incorporate all elevations; and during autumn (p= 0.025, p=0.049) and winter (p=0.016, p=0.032), the animals confined their movement to significantly smaller home range sizes than during spring and summer.

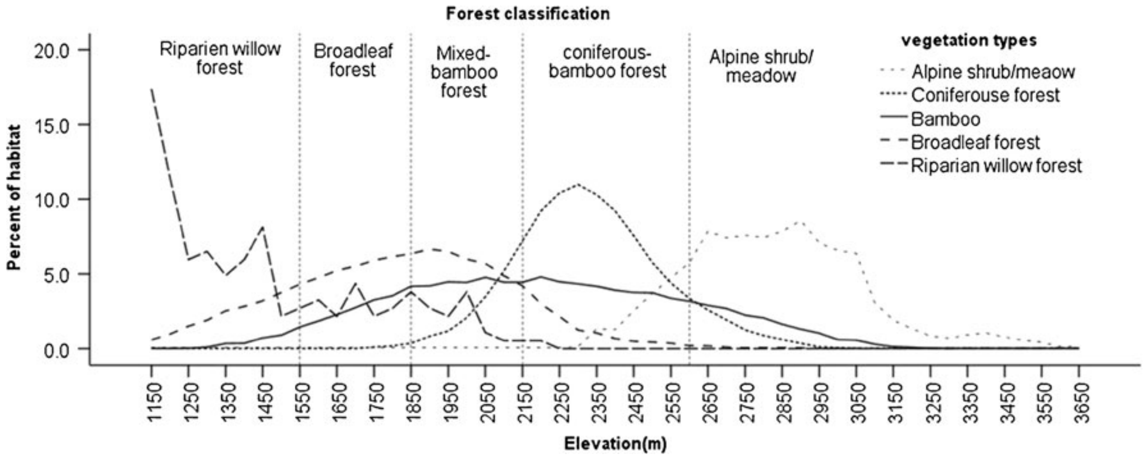


Fig. 2 Percentage area of the five major vegeta1tion types along the elevation gradient in Tangjiahe Nature Reserve, Sichuan Province, China. Classification based on cumulative distribution curves for each forest type, with 20 % or 85 % forming lower and upper boundaries of forest type

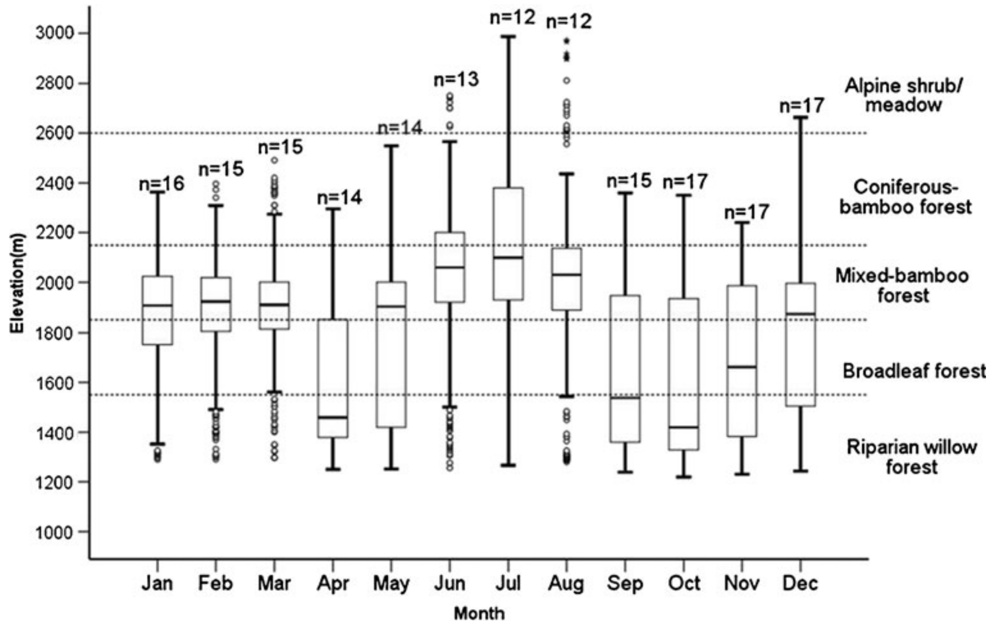
Twenty-two TM event recorders functioned for a total of 3,977 days (mean number of days per device=180). The average daily counts of TM devices (n=22) in the four forest types monitored showed that the relative activity of takin fluctuated between months and supported a seasonal migration (see Fig. 5). Recorders indicated that takin maintained their elevations from December through March and conducted uphill movement from March to April. We had to rely on visual observation for the lowest elevations, as our recorders were frequently stolen or damaged. No takin were observed from the central road during the winter (January and February), or summer (June and July), with consistent observations during spring (March and April), and again in autumn (September and October).

Population differences in forest type used by takin

We compared the habitat band selected by individual takin each month with a random distribution based on habitat availability analysis (Table 2). Most months showed habitat selection by individual takin, but in no month did all radio-collared takin select the same habitat type. For example, low-elevation willow forest was the most frequently selected habitat for three individuals, yet a fourth individual (Female 1534) was never found in that habitat.

We examined the elevation changes observed for all our collared takin with respect to the forest classification and found that takin used the mixed-bamboo forest for 8 months of the year (Fig. 3). They were found within this forest type from December through March and sporadically in both

Fig. 3 The monthly median elevation of the nine radio-collared takin in Tangjiahe Nature Reserve, 2006–2009. *Thick black dashes* within the box are the median; each box is the interquartile range. *Circle* represents observations outside 1.5 x's the interquartile range and *asterisk* represents observations farther than 3 x's. *Dashed horizontal lines* indicate the transition points between forests types based on remote sensing and ground survey data



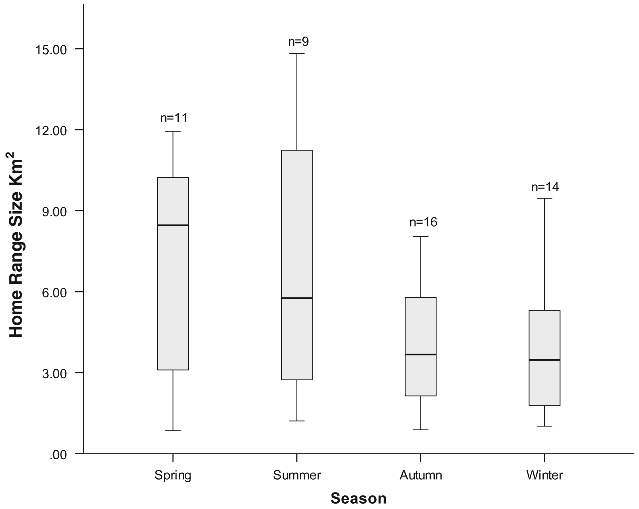


Fig. 4 Seasonal mean home range (minimum convex polygon) of takin in Tangjiahe Nature Reserve. We considered the same season in different years of the same animal as a different sample. We indicate sample size for each estimate. Home range size of spring (p=0.025, p=0.016) and summer (p=0.049, p=0.032) were significant larger than that of autumn and winter

spring and autumn months (see Fig. 5). During the onset of green vegetation in April and May and following the first frosts at higher elevations in September, October, and early November, takin spent most of their time within low-elevation forests composed primarily of willow and shrubs and abandoned agriculture. Only during July were takin observed at the highest elevations that included coniferous forest and alpine shrub/meadows, and only one male had its movement center in these forest types.

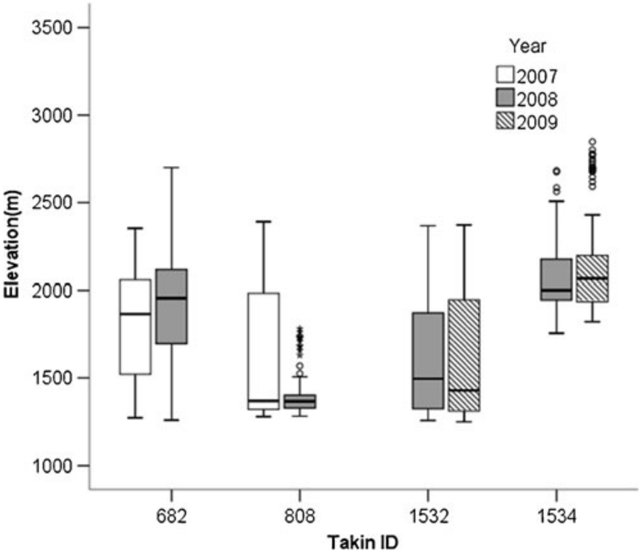


Fig. 5 The annual distributions of elevations used by four female takin at Tangjiahe Nature Reserve in Sichuan Provence, China with at least 2 years of observations. *Black dashes within the boxes* represented the Median; *each box* shows the interquartile range, with observation 1.5 times (*circle*) and 3.0 times (*asterisk*) the interquarile range

For the broader population, activity was followed with the TMs, and we found the highest detection rates within mixed deciduous/coniferous forest with a bamboo understory during the winter months (December through March) (see Table 3 and Fig. 6). The forest higher than 2,600 m (i.e., coniferous forest and alpine shrub/meadow) showed takin active only during the summer months of June through August. Relatively high detection rates within coniferous-bamboo forest indicate that this elevation was utilized by takin during winter (Table 3). Takin conducted an uphill migration in May as TM counts in alpine shrub/meadow significantly increased April to May while significantly decreasing within coniferous-bamboo forest (Table 3). However, all mid-elevation habitats maintained a low level of activity throughout the summer, indicating that all takin do not migrate to the alpine meadows during summer (Table 3).

Movement varied by individuals and years

Not all takin followed the annual movement described above (Fig. 5). Of four animals followed for at least 2 years, three takin (i.e. 808, 1,532, and 1,534) resided at significantly different elevations for >50 % of the comparable months (Mann–Whitney U test, $p<0.001$). For example, one individual (808) migrated from1,200 to 2,400 m during 2007 but maintained itself over a relatively narrow and lower elevation (1,200–1,800 m) in 2008. Takin 1534 was not detected below 1,700 m over 2 years of study (Fig. 5), indicating that the low-elevation forests are not utilized by all takin.

Discussion

We found a complex seasonal migration of takin that did not diverge significantly from the pattern reported by Zeng et al. (2008) for the northern subspecies of takin. However, we did detect variation between individuals and annual variation of the same individuals that indicates the migration pattern might be responsive to shifts in an individual's physiological state (i.e., pregnant, rearing cub, etc., Festa-Bianchet (1988) rather than solely the result of changes in elevation shifts in vegetation productivity (Zeng et al. 2010). In addition, based both on our radio-tracking data and activity monitors, we found that animals moved into the lower edge of the bamboo forests and some takin maintained themselves within this forest type throughout the year. Although encompassing only a small portion of takin habitat, alpine shrub/meadow and riparian willow forest were used extensively by takin in summer and autumn, respectively, which implies an important role of takin habitat requirements.

Table 2 The monthly habitat selection by individual takin radio collared from 2006–2009 at Tangjiahe Nature Reserve

ID	Year	Month											
		January	February	March	April	May	June	July	August	September	October	November	December
808	2007	**A****	**C****	*–	**A*****	**A**,B,C**	A,B,**D*****	**A**,D*	**A*****	**A*****	**A**,B*	**A*****	**A*****
808	2008	**A**,B***	**A**,B***	**A**,B***	**A**,B***	**A**,B***	–*	–	**A**,B***	**A**,B,C***	**A**,B,C***	**A**,B**	**A**,B***
1532	2008	A,**C****	A,**C****	**B**,C,D***	**A**,B,C***	**A,B,C**,D*	–	A,B,**D****	–	**A**,B,D**	**A**,B,C,D***	**A**,B,C,D***	–
1532	2009	A,**B*****	A,**B,C,D***	–	**A*****	**A**,D*	–	A,**C**,**D****	A,**D*****	**A*****	**A*****	**A*****	**A**,**B**,C***
1533	2008	**A**,**C**,D***	**A*****	**A**,**C**,D***	**A*****	–**	**D****	B,C,**E*****	A,B,**E*****	**A**,B,D***	**A*****	**C*****	**C*****
1534	2008	–*	**B**,C**	**B**,C,D***	**C**,D**	**C**,D***	**C**,D**	C,**D****	B,**C**,D***	**B**,**C**,D***	–	B,**C**,D**	**C**,D***
1534	2009	B,C,**D**,E**	B,**C**,D,E**	**B**,D***	**B**,**C**,D***	**B**,**C**,D***	**C**,D***	D,**E*****	D,**E*****	**C**,D*	B,**C**,D,E***	B,**C**,D,E***	**C**,D**

We considered each year as an independent sample for individuals with more than 1 year of data. For each individual whose habitat selection was nonrandom during the month, we indicate the habitat they selected significantly more (bolded font) or less (non-bolded font) than predicted. Our habitat types are listed using letter codes (*A*=riparian willow forest, *B*=broadleaf forest, *C*=mixed-bamboo forest, *D*=coniferous-bamboo forest, *E*=alpine shrub/meadow). All tests were conducted using chi-square with a Bonferroni between each category (*$p<0.05$; **$p<0.01$; ***$p<0.001$)

Table 3 Mean daily event counts recorded by trail monitors throughout year in Tangjiahe Nature Reserve, Sichuan China (Dec-01-2008 to Jun-28-2010)

Forest type	January	February	March	April	May	June	July	August	September	October	November.	December.
Riparian forest*	0	0	0.89±0.42	0.92±0.39	0.12±0.04	0	0	0.40±0.24	0.89±0.29	1.50±0.36	0.23±0.09	0
Broadleaf	0	0.02±0.02	0.29±0.29	**0.24±0.15**	1.64±0.55	1.54±0.57	1.95±0.58	0.36±0.11	0.23±0.11	**0.26±0.18**	**0.65±0.42**	0.02±0.02
Mixed Bamboo	**2.76±0.90**	0.32±0.28	**1.93±0.85**	1.00±0.69	0.13±0.07	0.07±0.05	0.17±0.08	–	0.25±0.16	—	—	1.36±0.39
Conifer-Bamboo	**0.68±0.17**	0.52±0.18	0.76±0.23	0.73±0.30	**0.13±0.09**	0.47±0.18	0.16±0.05	0.71±0.035	1.02±0.36	0.51±0.21	0.51±0.20	0.42±0.13
Alpine shrub	0.01±0.01	**0.01±0.01**	1.40±0.65	**0.13±0.13**	1.91±0.59	**3.41±0.75**	1.83±0.69	1.23±0.47	**0.73±0.29**	0.03±0.02	0.17±0.17	0.24 ± 0.15

The forest types identified were broadleaf forest, mixed-bamboo forest, coniferous-bamboo forest, and alpine shrub/meadow forest and are listed from lowest to highest elevation. All values in this table are presented as mean±S.E. *Bolded font* indicates the marked month showed significant difference with the subsequent month ($p>0.05$). Due to the event recorder failures, we cannot provide sufficient data for all months, and indicate missing values as a dash (–)

*The mean counts of takin at lowest elevation band were derived from our monthly monitoring along the road within this elevation band through the year

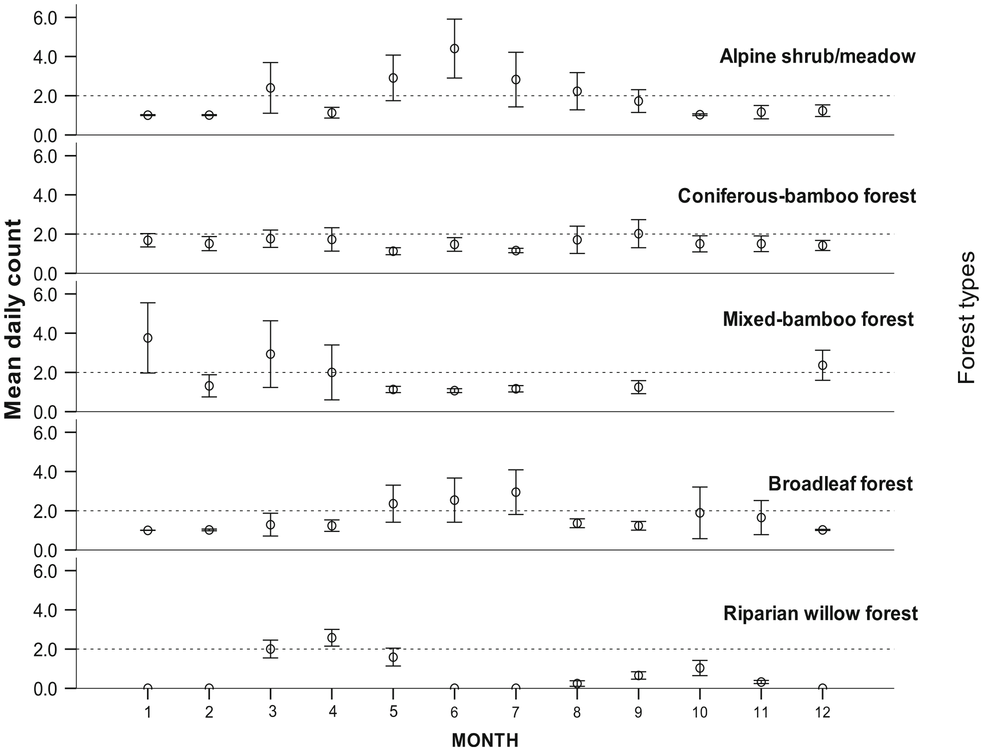


Fig. 6 Mean daily counts derived from trail monitors deployed along elevation gradient at Tangjiahe Nature Reserve, Sichuan China. The missing data in August, October, and November were due to device failure. Due to frequently stolen and destroyed devices at lowest elevation band, the mean daily counts within riparian willow forest were derived from counting all visible takin during a daily commute (5 km) along a central road during morning (6:30–7:30) and evening (17:30–18:30) in 2009

Individual variation in migration pattern found in this study has been reported for multiple ungulates, such as elk (*C. elaphus*, Morgantini and Hudson 1988), moose (*A. alces*, Ball et al. 2001), mule deer (*Odocoileus hemionus*, Nicholson et al. 1997), pronghorn (*Antilocapra americana*, Deblinger and Alldredge 1984), and sika deer (*C. nippon*, Sakuragi et al. 2003).The individual differences are generally found to be based on population asymmetries, such as age, sex, experience, and dominance positions (Lundberg 1987; Sakuragi et al. 2003). We observed no obvious gender or age differences in the migration pattern, but we were not able to track the reproductive status of all individuals and are unaware of their social status. The lack of previous reports on takin variable migration pattern may be due to the relatively small sample size of these studies (Zeng et al. 2008). We used both improved location data (larger sample size from collars with GPS accuracy) and TM event recorders as two independent measures of takin movements.

The causes for the observed migration pattern are not clear, but takin use bamboo as a food resource and thermal shelter during winter (Wu et al. 1990;Hu 1994; Zeng et al. 2001), and the distribution of bamboo was confined to intermediate elevations in this reserve. Although snow cover impacted migration in other ungulates (Ball et al. 2001; Telfer and Kelsall 1984), we do not consider it a key factor motivating takin migration; although we have no detailed data on snow cover in Tangjiahe, we do know that snow cover was least at the lowest elevations, yet takin did not maintain that elevation during the winter months. The migration pattern observed from most ungulates which move along an elevation gradient is for winter residency at the lowest elevations (Ball et al. 2001; Morgantini and Hudson 1988). In our study system, green forages and better thermal cover occured within the mid-elevation bamboo groves. For takin, the movement out of these groves to the lower elevation only occurred when herbaceous vegetation growth started within the lower valleys. The movement uphill throughout the spring generally follows this flush of green vegetation. Exploratory movements during the spring seem to result in larger home range sizes observed during this season among our animals. Our observations match those of Zeng et al. (2008) for more northern populations.

High-elevation alpine shrub/meadows were believed to be important habitat for takin because all previous observations at the study area have assumed that takin aggregate in the alpine shrub/meadows during the summer months for breeding (Wu et al 1990; Ge et al. 1989). However, only one of our nine collared takin established an elevation range that centered in the alpine shrub/meadows, with most animals making periodic movements from the lower forests into the meadows, which indicated that many takin remain within dense bamboo forest during summer, where they may or may not be engaging in mating activities. Two collared female takin (1,534 and 808) did engage in mating activity during the study period (based on production of offspring), but the location data of 808 showed it never migrated to the meadows during the mating season.

Therefore, evidence does not indicate that alpine shrub/meadow is an indispensible habitat of successful reproduction by takin.

Compared with alpine shrub/meadows, bamboo forest more heavily used by takin, as our collared takin inhabited bamboo forest for at least 8 months of each year. However, within this region, bamboo forest is shared with the giant panda (Hu 2001) and a spatial overlap has the potential for competition over food resources (Wu et al. 1990; Hu 2001). We do not know the degree of diet overlap or if there are limits in the amount of suitable bamboo within these forests, but visual observations are that takin feed primarily on grasses and forbs within these forests during the non-winter months (Guan et al. 2012).

Our findings are important for improving takin conservation and management because most takin surveys have been based on sighting all animals within a single habitat band. Summer surveys of alpine shrub/meadows (Deng 1984; Ge et al. 1989) are not adequate because they miss those animals that do not move to the high-elevation habitat. Zeng et al. (2008) recommended that surveys be conducted in winter months while takin were resident within bamboo forests, but this habitat has the densest understory and the least probability of sighting takin, even during the winter months. Understanding takin migration patterns is essential for estimating populations and assisting wildlife managers to select appropriate management strategies. Based on our results, it is reasonable to suspect that the population size of takin in these reserves may be underestimated. We recommend that takin surveys not attempt a total census but incorporate either mark/recapture modeling from DNA samples (Mowat and Strobeck 2000; Boulanger et al. 2004) or distance sighting methods that account for differences in detection probability (MacKenzie and Kendall 2002; Nichols et al. 2000) and include a broad range of elevations. Our results indicate that our understanding of takin migration is not sufficient to effectively manage the species beyond the obvious role of importance of maintaining bamboo forest, as well as alpine meadows, within these nature reserves.

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