Migration Patterns of Two Endangered Sympatric Species from a Remote Sensing Perspective

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Abstract

Giant pandas (Ailuropoda melanoleuca) and golden takin (Budorcas taxicolor bedfordi) are large mammals that occur together throughout the southern part of the Qinling Mountains in China. Both species have the habit of altitudinal migration in a mixed forest-bamboo landscape. Although previous studies have reported that the migration patterns of giant pandas and golden takin seem different, little is known about these differences in relation to their food quality and quantity. We used radio-telemetry data from six giant pandas and three golden takin groups to determine whether differences in their migration patterns are related to satellite-derived plant phenology (a surrogate of food quality) and bamboo abundance (a surrogate of food quantity). Our results suggest that the altitudinal migration patterns of both the giant panda and the golden takin follow the phenological development of plants in the study area, and the difference between them seems to be attributable to the difference in the phenology of bamboo and non-bamboo plants, and thus the abundance and quality of food available to these two species.

Introduction

Altitudinal migration is exhibited by numerous species in many different mountainous regions throughout the world (Geist, 1971; Oosenbrug and Theberge, 1980; Festa-Bianchet, 1988; Mysterud, 1999; Igota et al., 2004). An understanding of the causes of animal migration may yield valuable insights into the variables that determine life histories, habitat requirements, and foraging strategies of species and individuals (Richter and Cumming, 2006). Altitudinal migration may be a strategy for animals to optimize living conditions throughout the year (Fryxell and Sinclair, 1988; Pettorelli et al., 2007). Traditionally, these conditions are either interpreted as the availability of abundant and high-quality foods (White, 1983; Albon and Langvatn, 1992; Hanley, 1997), or relevant environmental factors such as favorable temperatures, less snow depth, less predation, or the combination of the factors (Festa-Bianchet, 1988; Pan et al., 1988; Nelson, 1995; Mysterud et al., 2007). Previous studies have suggested that increased access to highly nutritious and abundant forage is one of the most important driving forces in the evolution of migration of large herbivores (Fryxell and Sinclair, 1988; Mysterud et al., 2001). Therefore, we are interested in determining how ecological factors affect patterns of altitudinal migration. In particular, we focused on how food availability (i.e., food quality and quantity) might cause differences in migration patterns between species.

Giant pandas (Ailuropoda melanoleuca) and golden takin (Budorcas taxicolor bedfordi) are both endangered mammals, and occur sympatrically throughout the southern part of the Qinling Mountains in China (Pan et al., 1988; Wu et al., 1990; IUCN, 2007). Many observers have reported that both species migrate altitudinally in a mixed forest-bamboo landscape in the Foping Nature Reserve (Pan et al., 1988; Wu et al., 1990; Yong et al., 2008); (a) to seek more abundant or nutritious forage, (b) to search for optimum temperature conditions, or (c) to escape insect
harassment. However, there is no quantitative research testing these hypotheses, as continuous field observations of environmental conditions are not easily available. Here, we focus on food quality and quantity, using remote sensing to estimate them, and examine the role they might play in the altitudinal migrations of these two sympatric species.

Crude protein content and digestibility of plants peak early in the growing season, and then rapidly decline as vegetation matures (Crawley, 1983; Van Soest, 1983). Higher forage quality is therefore associated with early phenological stages when new green leaves dominate biomass (Crawley, 1983; Van Soest, 1983; Prins and Ydenberg, 1985). Temperature is one of the key factors determining plant growth and is generally negatively correlated with elevation (Tang and Fang, 2006). Hence, in a mountain environment, plants at lower elevations tend to reach spring and summer phenological phases earlier than plants at higher elevations (Beck et al., 2007). The considerable spatial and temporal variation in plant quality is thus a direct result of seasonal changes at different elevation-climate zones. Plant phenology is therefore a good proxy for plant quality (Laycock and Price, 1970) and it is frequently described as the driving force in habitat use by vertebrate herbivores (Fryxell, 1991; Albon and Langvatn, 1992). However, high food quality does not always translate into high food abundance. According to classical theories on optimal foraging, a forager should maximize energetic gains and minimize energetic costs of foraging (MacArthur and Pianka, 1966). Under these conditions, animals will spend most time in habitats which are not only richest in food quality, but also highest in food abundance, and the selection of habitat is likely to reflect both these aspects of food availability.

Giant panda from being carnivorous evolved into an obligate bamboo grazer (Wei et al., 1999). Pandas meet their dietary requirements by consuming large quantities of bamboo to compensate for its low digestibility (approximately 20 to 26 percent energy in bamboo leaves and 40 to 44 percent in shoots) (Dierenfeld et al., 1982; Schaller et al., 1985). Therefore, generally, continuous dense bamboo forests with a high production of bamboo shoots provide the best feeding habitat for wild giant pandas. The golden takin, however, is a forest-dwelling herb-foraging ungulate with generalist foraging habits, feeding on more than 160 species of plants, including mosses, ferns, herbs, shrubs, and trees in the Qinling Mountains (Zeng et al., 2001). Although the diet of golden takin can vary over the seasons, it consists primarily of twigs, shoots, young stems, and leaves of plants (Zeng et al., 2001). However, plant diversity tends to be low, and seedlings, saplings, and young trees are scarce when dense bamboo dominates the understory (Veblen et al., 1977; Taylor and Qin, 1988; Yue et al., 1999). Hence, the areas of dense bamboo, favored by giant pandas, potentially form poor golden takin habitat (Zeng et al., 2001). We therefore predict that the spatial-temporal variation in plant phenology and bamboo abundance explains differences in the migration patterns of giant pandas and golden takin.

The ability to examine animal migration responses to environmental factors has often been hampered by a limited understanding of animal habitats. Indeed, it is difficult to obtain spatially continuous information on plant quality and abundance by using traditional field survey methods at large temporal and spatial scales (Krithna et al., 2008; Skidmore and Ferwerda, 2008). The rapidly increasing use of remote sensing data in ecological studies has recently changed this situation (Kerr and Ostrovsky, 2003; Hyde et al., 2006; Leyequien et al., 2007; Beck et al., 2008). Remote sensing generates a remarkable array of ecologically valuable measurements that include details on habitats (land-cover classification) and their biophysical properties (vegetation biomass and vegetation phenology). The normalized difference vegetation index (NDVI) combines reflected red and near infrared (NIR) radiation according to the simple equation: NDVI = (NIR - RED)/(NIR + RED), and is particularly useful because it shows spatial and temporal trends in vegetation productivity and distribution (Reed et al., 1994; Nemani et al., 2003; Krishnaswamy et al., 2009). Therefore, changes in NDVI are a good proxy for vegetation dynamics (Justice et al., 1985; Myneni et al., 1997; Nemani et al., 2003), and have been used extensively for monitoring vegetation phenology (Lloyd, 1990; Reed et al., 1994; White et al., 1997; Beck et al., 2006). As a result, NDVI is a useful tool for investigating the interaction between vegetation and animal activity, including migration (Boone et al., 2006; Ito et al., 2006).

The aim of this study is to examine the differences in altitudinal migration between giant pandas and golden takin in relation to spatial-temporal variations in their food quality and quantity. Satellite-derived plant phenology and bamboo abundance were adopted as surrogate measures of forage quality and quantity, respectively, for these two species.

**Materials and Methods**

**Study Site**

The study was conducted in the Foping Nature Reserve (Figure 1). This reserve is located on the southern slopes of the Qinling Mountains in southwest China (33°2’ to 33°45’ N, 107°40’ to 107°55’ E). It covers 294 km², and the elevation ranges from 1,000 to 2,900 m, with an annual mean temperature of 11.5°C. The lowest average monthly temperature is ~3°C, which occurs in January whereas the highest average monthly temperature is 28°C that occurs usually in July. Annual rainfall is approximately 930 mm and mainly concentrated in July, August, and September. The first snowfall usually occurs in November at the highest elevations and about a month later at lower elevations (below 1,500 m). Snow begins to melt in early March and has completely melted at higher elevations by late March.

The vegetation varies with elevation, and forests account for 96 percent of the total land area in the reserve. According to Ren et al. (1998), the major forest types are broadleaf deciduous (below 2,000 m), mixed coniferous and deciduous (2,000 to 2,500 m), and coniferous forests (above 2,500 m), with some interspersed subalpine shrubs and meadows at the top of the mountains (above 2,600 m). These forest types occupy 31 percent, 59 percent, 6 percent, and 2 percent of the total reserve, respectively (Liu, 2001). The dominant overstory tree species are Quercus spp., Populus spp., Betula spp., Acer spp., Pinus spp., Tsuga chinensis, and Abies fargesii. Two bamboo species, Bashania fargesii (below 2,000 m) and Fargesia mazziottiana (above 2,000 m), dominate the forest understory and form the principal food source for the giant pandas in the study area. Other common understory species include Lespedeza spp., Abelia spp., Liliea spp., Rosa spp., Aniscera spp., Spiraea spp., Rhododendron spp., Carex spp., and Kobresia spp.

The Foping Nature Reserve was established in 1978, and is dedicated to the conservation of the giant panda and associated habitat. It is one of the few Chinese reserves with intact ecosystems, and is renowned for having the highest density of giant pandas in China. An estimated 76 giant pandas and 480 golden takin live in the reserve (Zeng et al., 1998; State Forestry Administration, 2006). Other herbivores that coexist with giant pandas and golden takin are serow (Capricornis sumatraensuis), goral (Naemorhedus goral), musk deer (Moschus berezovskii), tufted deer (Elaphodus cephalophus), and Chinese muntjac deer (Muntiacus reevesi). Large predators, such as tiger (Felis tigris amoyensis) and wolf (Canis lupus) once occurred in the
region, but are now considered to be functionally extinct. Dholes (*Cuon alpinus*) and occasionally leopards (*Panthera pardus*) are still found in the study area, but the size of their populations remains uncertain.

No roads were constructed in the reserve until 2000. About 300 local people resided within the nature reserve during 1998. They were concentrated in five village groups along the river valleys, where the elevation is below 1,500 m. The major land-use activity is farming.

**Collection of Animal Movement Data using Radio Telemetry**

Six giant pandas (three males and three females) and three golden takin (one male and two females) were fitted with radio collars (MOD-500, Telonics, Inc., Mesa, Arizona) and tracked for different periods (Liu *et al*., 2002; Zeng *et al*., 2008). Tracking of giant pandas started in January 1992 and ended in December 1995, while golden takin were tracked from July 1995 to August 1996. At the conclusion of the study, collars were removed from the animals. No evidence of discomfort or skin lesions was observed upon recapture of collared giant pandas and golden takin. The golden takin is gregarious and their group composition can vary over time. The three groups of golden takin with one radio-collared individual each had an average size of about ten individuals (Zeng *et al*., 2002). As the location data showed that the three radio-collared individuals did not meet each other, it was assumed that we were able to obtain information on the movement of approximately 30 individuals through these collared individuals.

A total of 59 and 38 receiving towers across the radio tracking region were used to monitor the giant pandas and golden takin, respectively. The collared animals were located using a tracking system consisting of a TR-2 receiver and a two-element directional H-antenna. Locations were obtained daily by triangulation (White and Garrott, 1990). At least three signal bearings from different towers were used to form an error polygon. The center of the polygon represented the animal’s location. We used these locations when the associated error polygons measured less than 1 ha. As a result, we obtained 1,437 radio-telemetry locations for giant pandas and 487 locations for golden takin (see Figure 1). We subsequently extracted altitudinal data by overlaying the coordinates of animals on a digital elevation model (DEM) with a 25 m horizontal resolution. Because altitudinal migration patterns of giant pandas and golden takin become visible at a ten-day scale, rather than at a monthly or seasonal scale, we divided each month into three ten-day periods (TD) (Liu *et al*., 2002; Zeng *et al*., 2008). The first, second, and the last ten days of the month were used as time units, i.e., 36 TDs (ten-day periods) per year.

**Mapping of Plant Phenology using MODIS NDVI**

Changes in NDVI through time reflect phenological development in vegetation (Krishnaswamy *et al*., 2004; Beck *et al*., 2006). Moderate Resolution Imaging Spectroradiometer (MODIS) data can be used to produce NDVI time series at a spatial resolution of up to 250 m, making them useful for local and regional studies. For this study, MODIS 250 m NDVI data (MOD13Q1) over part of the Foping Nature Reserve were downloaded. The dataset provides 23 NDVI images per year at 16-day intervals, where every pixel value is produced by taking the maximum value for the composite of near-daily data (Huete *et al*., 2002). From the data collected in the five years between 2001 and 2005, the best one-year time series, consisting of 23 images, was composed, i.e., for each pixel and compositing period, the five available NDVI values were extracted and the mean of the three values of highest quality, based on the quality flags provided in the MOD13Q1 product, was calculated. To interpolate the 23 values of the average NDVI time series for display purposes, as well as to diminish noise caused mainly by remnant of clouds in the data, the TIMESAT software package and an adaptive Savitzky-Golay smoothing filter were used (Jönsson and Eklundh, 2004). The interpolated NDVI trajectory of each pixel was normalized to cover the range of 0 percent to 100 percent, indicating the minimum and maximum NDVI for a given pixel, respectively, and producing the Relative Phenological Development (RPD) metric.
where \( \text{NDVI}_{\text{min}} \) and \( \text{NDVI}_{\text{max}} \) are the minimum and maximum NDVI for the pixel, respectively, and \( \text{NDVI} \) is the NDVI at time \( t \). Thus, when viewing the RPD of two pixels at a given time \( t \), one can compare the state of greenness of the two pixels irrespective of their absolute NDVI values. Annual RPD trajectories were plotted along axes of time and altitude (Beck et al., 2008).

Compatibility of the NDVI and Animal Movement Data

The MODIS sensor was launched in 1999, whereas the datasets on the movement of the radio-collared giant pandas and golden takin were from 1992 to 1996. To test whether the phenological trends of 2001 to 2005 are considered to be representative of the period of 1992 to 1996, we first compared temperature and precipitation of the study area in the two periods, as these two factors are the main drivers of plant phenology (Cleland et al., 2007). In general, the 1992 to 1996 period is comparable to the 2001 to 2005 period, although the mean monthly temperature was slightly higher than the 2001 to 2005 maximum in August, November, and December (Figure 2). The difference was greatest in November, where the 1992 to 1996 mean was 0.65°C warmer than the 2001 to 2005 maximum. The mean monthly precipitation in the 1992 to 1996 period was 4 mm lower than the 2001 to 2005 minimum in September, and 32 mm higher than the 2001 to 2005 maximum in November. Overall, the climate in the period with NDVI image observations was slightly colder in summer and autumn than in the period with animals, and also slightly wetter. The year 2002 was unusual as it saw 210 mm of rainfall on 09 June (Hou et al., 2006). However, when excluding the year 2002 from the NDVI data composition as described in Figure 2, the average NDVI values for the 23 images did not change by more than 0.03. Hence, the phenological trend in 2001 to 2005 is generally representative of the years with animal observations.

To further test whether the phenological trends of 2001 to 2005 may be considered to be similar to the period 1992 to 1996, we compared the global inventory monitoring and modeling study (GIMMS) NDVI dataset of the two periods. The GIMMS-NDVI dataset is derived from satellite imagery obtained from the advanced very high resolution radiometer (AVHRR) instrument onboard the NOAA satellite series. The dataset has been corrected for calibration, view geometry, volcanic aerosols, and other effects not related to vegetation change (Tucker et al., 2004). The GIMMS-NDVI dataset is available on a bimonthly basis from July 1981 to present with a spatial resolution of 8 km (http://www.landcover.org/data/gimms/).

Foping Nature Reserve is covered by three GIMMS pixels, which were averaged and concatenated into two datasets covering 1992 to 1996 and 2001 to 2005. To diminish noise caused mainly by remnants of clouds, these datasets were then processed using TIMESAT software and an adaptive Savitzky-Golay smoothing filter (Jönsson and Eklundh, 2004), as described above for the MODIS-NDVI from 2001 to 2005. The average GIMMS-NDVI values for the two periods are shown in Figure 3, and their similarities were tested using a paired design equivalence testing in EquivTest™ 2.0 (Statistical Solutions, Ltd., 2006). The result shows that the mean NDVI values between the 24 images of GIMMS 1992 to 1996 and those of GIMMS 2001 to 2005 are equivalent (two one-sided tests, 95 percent CI, \( p = 0.00 \)) within the equivalence bounds of \((-0.11, 0.11)\) at \( \alpha = 0.05 \). We therefore concluded that the phenological conditions between 2001 and 2005 are representative of the 1992 to 1996 period.

Figure 2. Range of (a) monthly temperatures, and (b) cumulative precipitation in Foping from 1992 to 1996, when giant panda and golden takin location data were collected (lines), and from 2001 to 2005, when MODIS NDVI data were collected (shaded area, excluding 2002). The year 2002 (dashed line) was unusual, because it saw very high rainfall (210 mm) on 09 June.

Figure 3. Comparison of annual NDVI trajectories over the Foping Nature Reserve during two periods using GIMMS-NDVI datasets. The x-axis represents NDVI images, two per month, starting on 01 January. Each point in the figure represents a five-year mean NDVI value with the standard deviation shown as a vertical bar.
Estimation of Seasonal Activity Ranges of the Two Species

Based on the elevation data for the six giant pandas and three golden takin (Figure 4), as well as previous studies (Liu et al., 2002; Zeng et al., 2008), we partitioned the radio-telemetry locations of giant pandas and golden takin into four seasonal activity ranges, being a winter non-migration range, a spring migration range, a summer non-migration range, and an autumn migration range (Table 1).

We then generated 95 percent space-use contours for the four seasonal activity ranges for each species with the Hawths Analysis Tools for ArcGIS© software (Beyer, 2004), that uses an extension of the fixed kernel density estimator (KDE). Fixed KDE is one of the most commonly applied space-use estimators in wildlife studies and has been used to estimate animal home ranges (Worton, 1989), interactions (Millspaugh et al., 2004), and resource selection (Marzluff et al., 2004), among others.

Classification of Bamboo Abundance from Remote Sensing Images

Remote sensing can be used to map the distribution of land-cover over large areas. However, most attempts to map the density of understory vegetation such as bamboo have not been successful (Morain, 1986; De Wulf et al., 1988). In the Foping Nature Reserve, the overstory is composed of varying degrees of deciduous and coniferous cover. These typically limit spectral information from the understory bamboo reaching a spaceborne or airborne sensor, thus restricting traditional remote sensing classification approaches. However, recently Wang et al. (2009a and 2009b) successfully classified three density classes of understory bamboo (i.e., dense, sparse, and non-bamboo) in the Foping Nature Reserve using medium resolution (30 m × 30 m) satellite images. In these two studies, the authors firstly examined the mapping accuracies of understory bamboo, based on four seasons Landsat TM/ETM+ images and ground-surveyed bamboo cover data, using four classifiers (i.e., decision tree, Mahalanobis distance, maximum likelihood, and artificial neural networks). The results suggested that winter is the optimal season for quantifying the coverage of evergreen understory bamboos in a mixed forest area, regardless of the classification methods used (Wang et al., 2009a). To further improve the bamboo mapping accuracy, a new method combining an artificial neural networks and a GIS expert system was applied on leaf-off ASTER image. The resulting maps of understory bamboo density had an overall accuracy of 73 percent (Wang et al., 2009b). To examine the difference in the proportion of dense bamboo forest between the seasonal activity ranges of the two species, a z-test for two proportions was applied (Kirk, 2007).

Results

Altitudinal Migration and Plant Phenology

At the lowest altitudes, the dormancy period continues until April, but lasts until May at the highest altitudes (Plate 1). After dormancy, the vegetation reaches near-maximum greenness in the course of about one and one-half months at the lowest altitudes, while on the mountain peaks maximum greenness occurs about two months after winter dormancy. The length of near-maximum greenness lasts for more than four months at lower elevations, but for only two months on the mountain plateaus and tops at higher elevations.

Altitudinal migration of giant pandas and golden takin in response to plant phenology (i.e., RPD) were different (Plate 1). Between ten-day period 11 and 13, golden takin descended from the intermediate elevations to the lowest elevations, coinciding with an increase in RPD from 28 percent to 83 percent. In the same period, giant pandas showed a slight downhill-movement while RPD in their habitat increases from 20 percent to 76 percent. Comparison of the mean RPD showed that the golden takin migrated to the areas with advanced plant phenology earlier than giant pandas.

Table 1. Elevations and Times for Determining the Four Seasonal Activity Ranges of Giant Panda and Golden Takin (TD is Ten-Day Interval)

<table>
<thead>
<tr>
<th>Seasonal activity ranges</th>
<th>Winter non-migration</th>
<th>Spring migration</th>
<th>Summer non-migration</th>
<th>Autumn migration</th>
</tr>
</thead>
<tbody>
<tr>
<td>Giant Panda Elevation (m)</td>
<td>&lt;2,000</td>
<td>2,000–2,300</td>
<td>&gt;2,300</td>
<td>2,000–2,300</td>
</tr>
<tr>
<td>Time (TD)</td>
<td>28–16</td>
<td>17</td>
<td>18–24</td>
<td>25–27</td>
</tr>
<tr>
<td>Golden Takin Elevation (m)</td>
<td>2,000–2,300</td>
<td>1,400–2,300</td>
<td>&gt;2,300</td>
<td>1,600–2,300</td>
</tr>
<tr>
<td>Time (TD)</td>
<td>34–9</td>
<td>10–16</td>
<td>17–25</td>
<td>26–33</td>
</tr>
</tbody>
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pandas during their early-spring migration ($t = 2.86$, d.f. = 182, $p = 0.005$). From ten-day periods 14 to 17, the golden takin gradually ascended to high elevations followed a practically constant RPD gradient (RPD = ± 90 percent). In contrast to golden takin, the giant pandas stayed at low elevations until the start of the peak growing season around ten-day period 15 and then took only a week to move up to high elevations. Comparison of the mean RPD showed that the golden takin migrated upwards while the vegetation was in earlier phenological stages than giant pandas ($t = -10.00$, d.f. = 134, $p = 0.000$). During early-autumn migration, when golden takin started to leave their summer habitat, around ten-day period 26, the RPD at high elevation was about 76 percent. The golden takin gradually descended to the lowest elevation, where the RPD has decreased to 34 percent by ten-day period 31. The giant pandas only spent about four weeks (ten-day periods 25 to 28) descending from their high-elevation summer habitat to their low-elevation winter habitat where the RPD were 89 percent and 79 percent, respectively. Based on the mean RPD during autumn (ten-day periods 25 to 30), the golden takin followed later phenological stages of the vegetation, compared to the giant pandas ($t = -2.57$, d.f. = 175, $p = 0.0111$). During the late-autumn migration, the golden takin reached low elevations where the RPD values were close to 30 percent around ten-day period 32, about a month later than the pandas did. After a week at the lowest elevations, the takin ascended to intermediate elevations for overwintering.

### Seasonal Activity Ranges and Bamboo Abundance

The seasonal space-use of giant pandas and golden takin is different, based on the distribution of their seasonal activity ranges (Figure 5): in winter and spring their activity ranges are distinct, whereas in summer and autumn they overlap. Throughout the year, however, the takin are more dispersed than the pandas.

On average, the proportion of dense bamboo forest in the four seasonal activity ranges of giant pandas is higher than in that of golden takin (Figure 6; 36 ± 3.4 SD versus 23 ± 7.9 SD, z-value = 49.64, $\alpha = 0.05$). The difference is great in winter and summer (Figure 6a and 6c), which are the non-migration seasons, than in spring and autumn, which are the migration seasons (Figure 6b and 6d). The proportions of dense bamboo forest are lower in the two migration ranges than in the two non-migration ranges, and the difference is largest among the giant panda ranges (27 ± 2.4 SD versus 45 ± 4.5 SD, z-value = 33.35, $\alpha = 0.05$ for giant pandas; 20 ± 5.0 SD versus 27 ± 10.9 SD, z-value = 25.36, $\alpha = 0.05$ for golden takin). In the golden takin ranges, the difference was due to the higher proportion of the dense bamboo forest in the summer range (31 ± 14.7 SD), which overlaps with the giant panda summer range, compared to the autumn, spring and winter ranges (21 ± 5.6 SD).

### Discussion

Both giant pandas and golden takin respond to the “green wave” of vegetation phenology during their altitudinal migration, but in distinct ways. The migration of the golden takin is linked to the early spring and late autumn phenological stages (i.e., early-spring green-up and late-autumn senescence), whereas the migration pattern of the giant panda, is related to the late-spring and early-autumn phenological stages (i.e., late-spring green-up and early-autumn senescence). This migratory behavior of the golden takin is consistent with the hypothesis that the altitudinal
migration of most generalist herbivores is in response to the first greening of vegetation in spring and follows late senescence in autumn (Albon and Langvatn, 1992; Nicholson et al., 1997; Mysterud, 1999). The contrasting result for the giant panda seems to be a consequence of its particular foraging behavior, focused uniquely on the bamboo resource. Unlike golden takin, giant pandas are specialists, they eat bamboo almost exclusively. Giant pandas show marked seasonal preferences for certain parts of the bamboo plants (Schaller et al., 1985). They prefer leaves over stems during most of the year but favor bamboo shoots when available. Nutrient analysis shows that the shoot is the most digestible part of bamboo (Schaller et al., 1985), as well as offering the highest calorific intake at 34,020 KJ/day (Pan et al., 1988). In the Foping Nature Reserve, the two bamboo species (B. fargesii and F. qinlingensis) differ from the general vegetation in their annual cycle of shoot production. Their peak shooting periods occur three weeks later than the overall greening of the landscape. The shooting season of B. fargesii occurs from mid-April to the beginning of June, and peaks in May (Tian, 1989), and the shooting season of F. qinlingensis, which only grows above 2,000 m, occurs from the beginning of June to the end of July, and peaks from mid-June to mid-July (Pan et al., 1988; Tian, 1989). The shoots of F. qinlingensis are becoming available when the panda arrives at its high-elevation summer habitat in the middle of June. Our field observations also confirmed that giant pandas mainly consume the shoots of F. qinlingensis from the middle of June to the end of July (Yong et al., 1994). As the shoots of F. qinlingensis lignify in August, the giant pandas switch to eating leaves, and gradually descend to their winter habitats. The timing of the giant panda’s spring and autumn migrations corresponds closely the start and end of maximum availability of bamboo shoots at high elevations in our study area. We therefore suggest that the sprouting and aging of palatable and digestible bamboo shoots appear to be a driving force behind the migration of giant pandas.

Because golden takin are generalists, the phenological change of their forage is better represented by

Figure 5. Seasonal activity ranges of giant pandas and golden takin: (a) in winter, (b) during spring migration, (c) in summer, and (d) during autumn migration. The ranges were estimated by applying a fixed kernel density estimator on radio-telemetry data. The background map shows the bamboo abundance in the study area.
Satellite analysis of plant phenology is fundamentally different from traditional ground-based observations. The capacity of satellite sensors to detect important phenological events such as budding, flowering, and fruiting is limited by the ground resolution of the sensors and the effects of other vegetation and soil background characteristics (Reed et al., 1994). Satellite sensors measure broad-scale changes in the landscape, that may not be associated with phenological events of specific plants, especially when they occur in the understory (e.g., bamboo shooting), but can be descriptive of general vegetation phenological changes. Therefore, the altitudinal migration of golden takin may have a more explicit relationship with the NDVI-derived change in vegetation phenology than the migration of giant pandas has.

The cover of dense bamboo forest is consistently higher in the giant panda activity range than in the golden takin activity range. Bamboo cover in the giant panda’s migration ranges is lower than in its summer or winter activity ranges, but still higher than in the golden takin migration ranges. Because bamboo is poor in nutrients, strong preference for habitats with a high-bamboo density is vital to pandas, as it reduces the pandas’ energy expenditure while foraging (Reid and Hu, 1991). The migration pattern of giant pandas in the present study indicates that the animals avoid areas of low-bamboo density. Collared giant pandas only took one to three weeks to pass through sparse bamboo habitats during their spring and autumn migration, but spent about eight and three months, respectively, in their bamboo-rich winter and summer habitats. By contrast, golden takin are not as reliant on bamboo as giant pandas are. Besides bamboo, the golden takin usually feeds on herbs, shrubs, and young trees. It therefore prefers habitats with a greater proportion of open-land and with a lower bamboo density (Zeng et al., 2001). This was demonstrated again in the present study, where the golden takin occupied a habitat with less dense bamboo forest than the giant pandas did, especially in their spring and autumn migration ranges. Moreover, the golden takin spends more time migrating than the giant panda does, which presumably is linked to prolonged access to abundant and high quality food.

In summary, the relatively fast uphill and downhill movement of the giant panda may be attributed to the sparseness of the bamboo forest at intermediate elevations in the study area, and the consequent lack of forage for the giant panda. At these elevations, the diversity and density of plant species is high, providing varied forage for the golden takin, and therefore encouraging their relatively slow ascent and descent in spring and autumn, respectively. Our results suggest that the altitudinal migration patterns of both the giant panda and the golden takin follow the phenological development, and thus quality of their forage plants, and that the differences in migration are attributable to the differences in phenology and abundance of bamboo and non-bamboo plants. To our knowledge, this is the first report of the mechanism of altitudinal migration of sympatric species that has been tested successfully based on spatially-continuous variables derived from remote sensing.

Figure 6. Proportion of dense bamboo forest in four seasonal activity ranges: (a) winter range, (b) spring migration range, (c) summer range, and (d) autumn migration range, shown as mean ± 1SE for six giant pandas and three golden takin groups.
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