

# Stable seasonal migration patterns in giant pandas

Meng Wang<sup>1,2</sup>, Yong-Gang Nie<sup>1</sup>, Ronald R. Swaisgood<sup>3</sup>, Wei Wei<sup>1</sup>, Wen-Liang Zhou<sup>1</sup>, Ze-Jun Zhang<sup>1</sup>, Gui-Ming Wang<sup>4</sup>, Fu-Wen Wei<sup>1,2,\*</sup>

<sup>1</sup> Key Laboratory of Animal Ecology and Conservation Biology, Institute of Zoology, Chinese Academy of Sciences, Beijing 100101, China

<sup>2</sup> University of Chinese Academy of Sciences, Beijing 100049, China

<sup>3</sup> Giant Panda Research, San Diego Zoo Institute for Conservation Research, Escondido, California 92027, USA

<sup>4</sup> Department of Wildlife, Fisheries and Aquaculture, Mississippi State University, Mississippi 39762, USA

## ABSTRACT

A critical function of animal movement is to maximize access to essential resources in temporally fluctuating and spatially heterogeneous environments. Seasonally mediated resource fluctuations may influence animal movements, enabling them to track changing resource distributions, resulting in annual migration patterns. The conservation-dependent giant panda (*Ailuropoda melanoleuca*) displays seasonal movement patterns; however, the key factor driving these seasonal migration patterns remains poorly understood. Here, we used GPS tracking collars to monitor the movements of six giant pandas over a 12-year period across different elevations, and performed statistical analysis of seasonal migration directions, routes, habitat revisitation, home range overlap, first arrival events, and stability. Our results revealed a compelling pattern of seasonal migrations that facilitated the ability of the pandas to forage at the appropriate time and place to maximize nutritional intake. Our results indicated that pandas utilize spatial memory to locate reliable food resources, as evidenced by their annual return to the same or similar winter and summer home ranges and the consistently maintained percentage of home range overlap. These novel insights into giant panda foraging and movement ecology not only enhance our understanding of its ability to adapt to nutritionally poor dietary resources but also provide important information for the development of resource utilization-based protection and management strategies.

**Keywords:** Giant panda; Seasonal migration; Home range; Foraging ecology; Spatial memory

## INTRODUCTION

Migration—or seasonal movement behavior—is an important

This is an open-access article distributed under the terms of the Creative Commons Attribution Non-Commercial License (<http://creativecommons.org/licenses/by-nc/4.0/>), which permits unrestricted non-commercial use, distribution, and reproduction in any medium, provided the original work is properly cited.

Copyright ©2023 Editorial Office of Zoological Research, Kunming Institute of Zoology, Chinese Academy of Sciences

ecological process (Fryxell & Sinclair, 1988) widely found in both terrestrial and marine systems (Avgar et al., 2014; Bailey et al., 2009). Spatially heterogeneous and temporally dynamic resource distribution is a critical driver of species movement patterns (Fagan et al., 2013), which serve to maximize resource acquisition (Albon & Langvatn, 1992; Deacy et al., 2018; Middleton et al., 2018). One of the key functions of seasonal migration is to facilitate access to optimal foraging habitats (Aikens et al., 2017; Avgar et al., 2015; Schindler et al., 2013), thus enabling the acquisition of energy and nutrients that are critical for survival, growth, and reproduction (Barboza & Parker, 2008; Ben-David, 1997; Monteith et al., 2014). For herbivores, plant phenology is a primary factor that shapes the resource landscape (Aikens et al., 2017). The Green Wave Hypothesis posits that animal migration is not confined to a dichotomous migration between two seasonal habitats, but rather is the result of tracking changing resources along a migratory path. When animals repeatedly return to the same foraging areas across years, they frequently employ spatial memory as a means of efficiently navigating the landscape (Abrahms et al., 2019; Bracis & Mueller, 2017; Merkle et al., 2019; Ranc et al., 2021). This movement pattern differs markedly from behavioral adjustment based on current conditions or environmental gradients (Betts et al., 2008; Singh et al., 2010). The role of memory is to forecast future conditions by invoking past experiences (Abrahms et al., 2019) and guide migration to temporally predictable resource-rich locations (Mueller et al., 2011; Mueller & Fagan, 2008). Spatial memory can facilitate navigation to high-quality foraging patches (Bracis et al., 2015; Merkle et al., 2014; Polansky et al., 2015) and stopover sites (Mettke-Hofmann & Gwinner, 2003). Given their high daily food intake requirements, herbivores tend to return to the same seasonal home range they have used in the past (Merkle et al., 2014), resulting in more efficient resource utilization (Van Moorter et al., 2009). Spatial memory serves to ensure reliable access to food resources, thereby maximizing nutritional gain while minimizing risk of food resource scarcity (Wolf et al., 2009). The concept of home range can be defined as a cognitive

Received: 02 December 2022; Accepted: 20 February 2023; Online: 20 February 2023

Foundation items: This work was supported by the National Natural Science Foundation of China (31821001) and Strategic Priority Research Program of the Chinese Academy of Sciences (XDB3100000)

\*Corresponding author, E-mail: [weifw@ioz.ac.cn](mailto:weifw@ioz.ac.cn)

map, encompassing the territory an animal has stored in its memory due its significance and relevance (Powell, 2000), with home-range fidelity considered to be a reflection of spatial memory (Sahanatien et al., 2015). Therefore, repeated movement patterns within a home range guided by spatial memory can increase foraging efficiency (Spencer, 2012).

Despite its recent downlisting from “Endangered” to “Vulnerable”, the survival of the giant panda (*Ailuropoda melanoleuca*) remains contingent upon conservation efforts in the foreseeable future (Swaigood et al., 2016). China has established many protective measures to support the ongoing recovery of the panda population, utilizing an increasingly comprehensive body of scientific knowledge to inform conservation policies and management decisions (Swaigood et al., 2018; Wang & Liu, 2017; Wei et al., 2015b). Key contributions from scientific study have centered around foraging behavior, habitat utilization, and movement patterns. Despite evolving an obligate herbivorous foraging strategy (Han et al., 2019), the digestive organs and protein demands of the giant panda remain similar to those of its carnivore ancestors (Nie et al., 2019). This disadvantage is partially mitigated by the presence of a specific gut microbiome that facilitates extraction of nutrients from bamboo (Wei et al., 2015c), including the facilitation of starch and sucrose metabolism and vitamin B12 biosynthesis (Huang et al., 2021). The giant panda predominately inhabits low-elevation habitats but migrates to high elevations each summer (Connor et al., 2016). Pandas acquire approximately half of their energy from protein sources, utilizing nitrogen-maximization foraging strategies by switching to different parts and species of bamboo at different times of the year (Nie et al., 2015, 2019). Due to the low nutritional content of bamboo and relatively inefficient digestion processes compared with other herbivores, pandas must consume large quantities of food each day to meet their energy and nutritional requirements (Wei et al., 2015d; Zhu et al., 2011a). Consequently, as a highly specialized and energy-constrained large herbivorous species, pandas must adopt conservative foraging strategies that ensure access to a stable and reliable food supply.

To investigate the impact of spatial memory on the seasonal migration and habitat utilization of the wild giant panda, we conducted a comprehensive study using GPS-collar data collected from six individuals from 2007 to 2018 in a key nature reserve. We aimed to test the hypothesis that the migration patterns, routes, and home ranges of pandas are influenced by their spatial memory, demonstrating a strong tendency to repeatedly use the same routes to return to the same high and low elevation ranges each year to access stable and consistent food resources. The findings of this study provide valuable insights into the foraging and ranging strategies of pandas, which will help guide conservation efforts and improve the management of foraging resources to support the continued recovery of this species.

## MATERIALS AND METHODS

### Study area and GPS tracking of giant pandas

The study area is located in Foping National Nature Reserve on the southern slopes of the Qinling Mountains in southwestern China, covering an area of 292 km<sup>2</sup> and an altitudinal range of 980–2 904 m above sea level (a.s.l.) (Zhou et al., 2022a). The region features a stable temperate and moist habitat (Lai et al., 2020; Pan et al., 2001), thus providing

stable habitat selection for giant pandas (Li et al., 2022). Based on the recent fourth national survey of giant pandas, Foping Reserve is estimated to contain 70–80 wild individuals, with the largest known population density in China (mean density 0.13 capita/km<sup>2</sup>) (National Forestry and Grassland Administration, 2021). Giant pandas spend 13.5–15.2 hours a day eating (Schaller et al., 1985), primarily feeding on two bamboo species, i.e., *Bashania fargesii*, which grows at a mean altitude of 1 600 m a.s.l. and produces shoots in May, and *Fargesia qinlingensis*, which grows at a mean altitude of 2 400 m a.s.l. and produces shoots in early June (Nie et al., 2015). Data on local temperature were obtained from the Foping Meteorological Station (E107.59°, N33.31°; elevation: 827.2 m a.s.l.).

From 2007 to 2018, six giant pandas (one female and five males) were fitted with GPS collars (Lotek Engineering, Newmarket, Ontario, Canada) programmed to record location every three hours. The ages of the six pandas were determined based on the diameter of the fecal bolus, length of bamboo bite fragments in feces (Schaller et al., 1985; Zhou et al., 2022b), and morphological characteristics of animals during capture. Data from individuals monitored over 12 months, excluding the mating season due to the divergent movement patterns driven by reproductive needs, were selected (Zhang et al., 2014). “Weiwei” was not included in the overlap analysis because only one year of movement data was obtained. The ages of each individual with complete monitoring records are shown in Supplementary Table S1.

### Statistical analyses

To show seasonal migration patterns of each individual during the observation period, mean temperature data obtained from the Foping Meteorological Station were linked to the elevation of each panda based on timestamps. Fluctuations in temperature were used to reflect changing seasons. We determined the spatial range of winter and summer habitats based on utilization and elevational range of seasonal habitat. We then determined the first arrival time of each panda entering their winter and summer habitats during seasonal migrations and tested the correlation between the first arrival time and local mean temperature. We also recorded fine-scale patterns of panda activity within the winter and summer habitats, as well as the direction of movement and annual visits. Finally, we recorded the paths used by pandas to traverse between winter and summer habitats and the time taken for each panda to complete their migration.

We used second-generation kernel estimation “plug-in” methods (Jones et al., 1996; Wand & Jones, 1995) to estimate the 95% home ranges of giant pandas in their winter and summer habitats separately. This approach addresses the challenges associated with bandwidth selection for kernel density estimation (KDE) and autocorrelated GPS data and represents a significant improvement over “first generation” methods (Walter et al., 2011). We then calculated the overlap area (OA) and percentage of home range overlap (PO) of each individual. The method for quantifying static overlap considering the spatial domain of the individual home ranges followed Kernohan et al. (2001).

$$PO[i, i - 1] = OA[i, i - 1]/A[i - 1] \quad (1)$$

where,  $OA[i, i - 1]$  is the intersection area of the two 95% home ranges in year  $i$  and  $i - 1$  and  $A[i]$  is the 95% area of the home range in year  $i$ . We first conducted the Shapiro-Wilk test to



determine normality of the data, then used *t*-test or Wilcoxon test to compare differences in the overlap area and percentage of home range overlap between winter and summer habitats. We also compared differences in migration time within a year and differences in home range overlap area and percentage of home range overlap between males and females. Using the Generalized Additive Model (GAM) (Wood, 2017), we linked the 95% home range overlap area and 95% percentage of home range overlap with individual age to assess the stability of the home range over the life of each panda. Additionally, we used GAM to model the relationship between age and migration time.

Geographic analyses were conducted using ArcGIS v10.5 (Environmental Systems Research Institute Inc., Redlands, USA) and all statistical analyses and plots were generated using R v4.0.5.

## RESULTS

All six pandas showed clear patterns of seasonal habitat utilization (Figure 1). The pandas were tracked for a total of 6 393 monitoring days (51 150 locations) and the mean GPS fix rate was 75.2% ( $\pm 5.4\%$  SE, min=51.7%, max=80.9%) due to the dense bamboo and forest canopy. The amount of data collected varied among individuals: Xiyue, 2 771 days; Cancan, 1 023 days; Lili, 694 days; Niuniu, 1 020 days; and Weiwei, 327 days (due to collar damage). All pandas exhibited seasonal elevational migration (Figure 2A) and completed summer habitat migration within a short period, with first arrivals occurring between 20 May and 20 June during a period of stable ambient temperature ( $R^2=0.03$ ,  $P=0.51$ ;

Figure 2B). However, the return to winter habitats differed among the pandas, occurring between August and October when temperatures significantly declined ( $R^2=0.80$ ,  $P<0.001$ ; Figure 2C).

All pandas used the same general winter habitat area but demonstrated a preference for distinct summer habitat patches (Figure 3A). Notably, summer habitat 1 (SH1) in the north was divided into two patches, and summer habitat 2 (SH2) in the east was divided into three patches, which were used to evaluate individual migration patterns across years. All tracked individuals exhibited consistent seasonal migration patterns from one year to the next. For instance, Cancan consistently selected patch SH1.1, while Xiyue migrated to all SH2 patches over the course of seven years but never to SH1. With only two years of data, Lili, Qiangqiang, and Niuniu did not show clear patterns of summer habitat use but did migrate to adjacent areas of summer habitat in both years. As seen in Figure 3A, the pandas showed strong tendencies to migrate in similar directions across years. Notably, all pandas exhibited individualistic, multiphasic movement paths during seasonal migration. (Figure 3B–F) and maintained a stable overlapping winter and summer home range core (Supplementary Figure S1).

The degree of home range overlap among individual pandas in summer and winter habitats was analyzed (Figure 4A, B). No differences were evident in area of home range overlap between winter (mean was  $3.26 \text{ km}^2 \pm 0.48 \text{ SE}$ , min=2.05  $\text{km}^2$ , max=4.15  $\text{km}^2$ ) (Shapiro-Wilk normality test,  $W=0.82$ ,  $P=0.09$ ) and summer habitats (mean was  $3.17 \text{ km}^2 \pm 0.89 \text{ SE}$ , min=0.49  $\text{km}^2$ , max=6.00  $\text{km}^2$ ) (Shapiro-Wilk

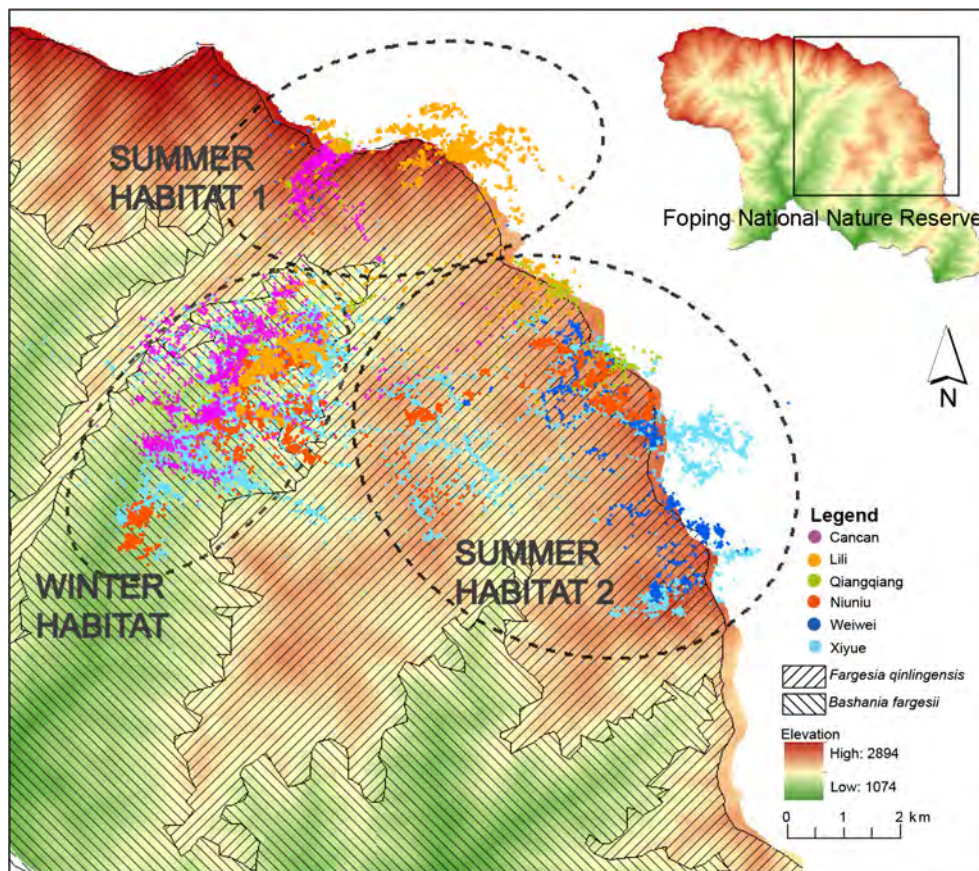
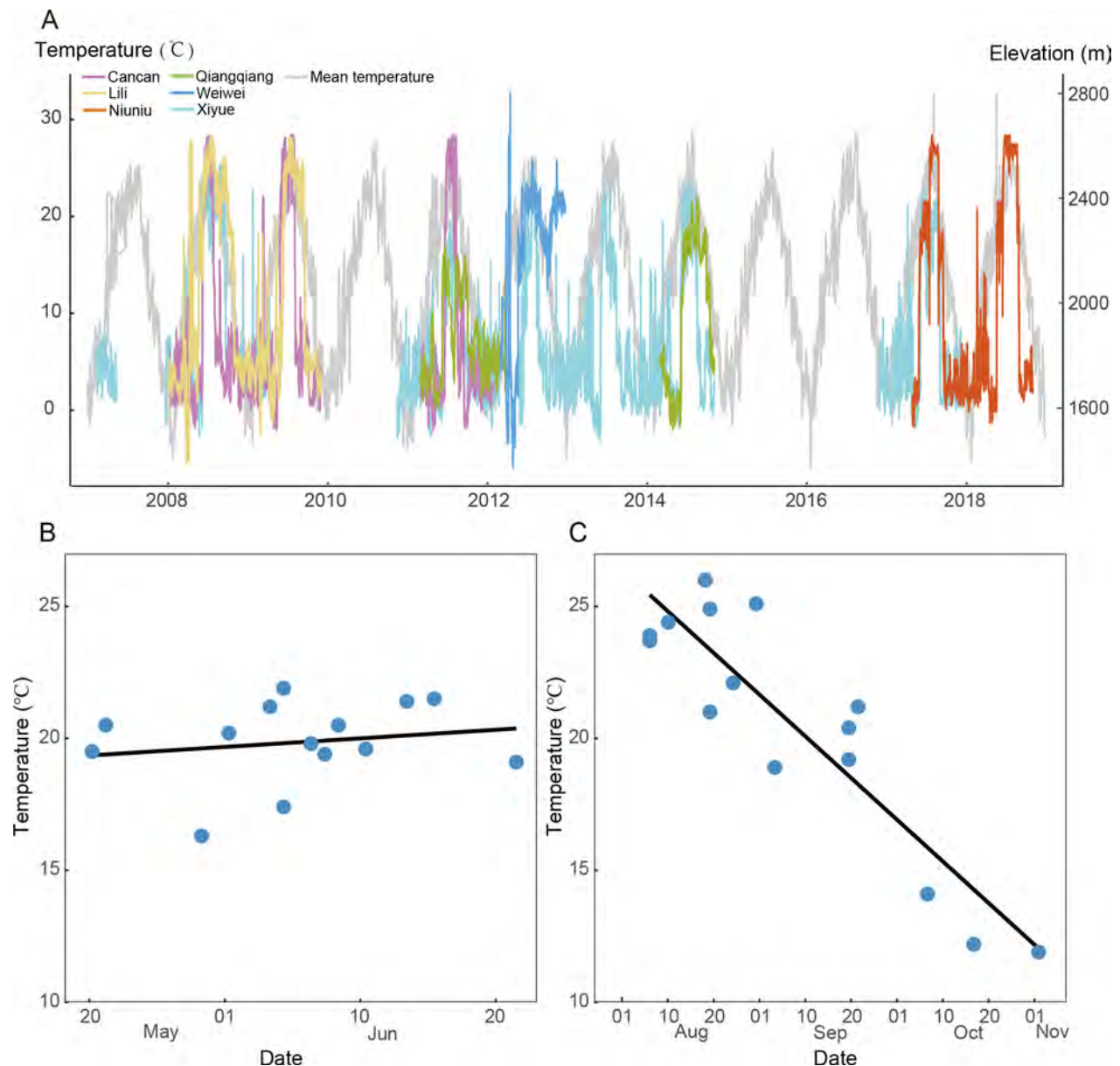


Figure 1 Seasonal migration and habitat-use patterns of six GPS-collared giant pandas in winter and summer habitats illustrating dominant bamboo species distribution



**Figure 2** Stability analysis of seasonal migration time of six GPS-collared giant pandas

A: Migration patterns in elevation and temperature across 12 years. B, C: Varied time and temperature and their correlation of first arrival event in summer habitat (B) and winter habitat (C). Blue dots indicate temperature and date that pandas first arrive at winter or summer habitat.

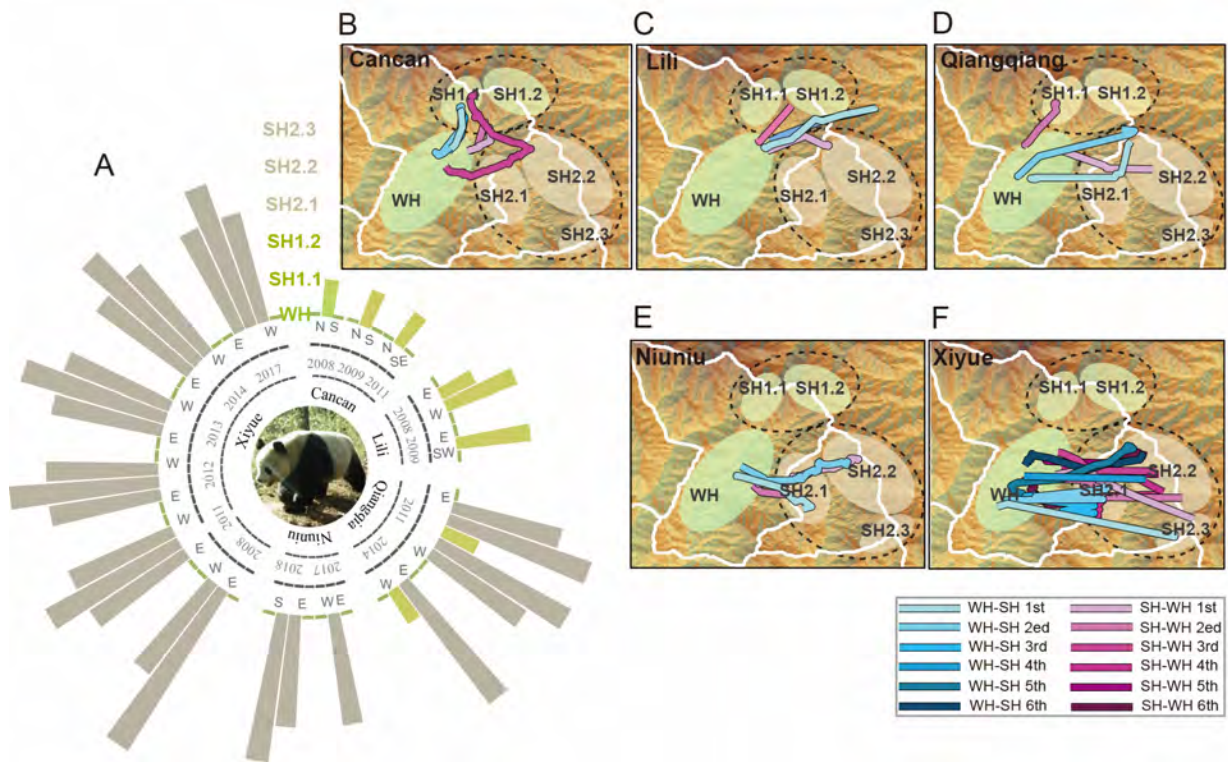
normality test,  $W=0.95$ ,  $P=0.71$ ) ( $t$ -test,  $t=-0.11$ ,  $df=7.64$ ,  $P=0.92$ ). No significance differences were observed in the percentage of home range overlap between winter (mean=50.00%±6% SE, min=28%, max=64%) (Shapiro-Wilk normality test,  $W=0.87$ ,  $P=0.22$ ) and summer habitats (mean=36.14%±10.13%, min=7.2%, max=63.17%) (Shapiro-Wilk normality test,  $W=0.98$ ,  $P=0.69$ ) ( $t$ -test,  $t=-1.43$ ,  $df=8.15$ ,  $P=0.19$ ). No differences were detected in time spent during the two seasonal migrations of the year (WH-SH: Shapiro-Wilk normality test,  $W=0.61$ ,  $P<0.01$ ; SH-WH: Shapiro-Wilk normality test,  $W=0.62$ ,  $P<0.01$ ) (Wilcoxon test,  $W=100.50$ ,  $P=0.26$ ; Figure 4C). Further analysis indicated that the female had a smaller home range overlap area than the males (female: Shapiro-Wilk normality test,  $W=0.97$ ,  $P=0.66$ ; male: Shapiro-Wilk normality test,  $W=0.93$ ,  $P=0.11$ ) ( $t=3.09$ ,  $df=5.94$ ,  $P<0.05$ ; Supplementary Figure S2A), but no difference was detected in the percentage of home range overlap (female: Shapiro-Wilk normality test,  $W=0.99$ ,  $P=0.84$ ; male: Shapiro-Wilk normality test,  $W=0.97$ ,  $P=0.53$ ) ( $t=2.19$ ,  $df=2.96$ ,  $P=0.12$ ;

Supplementary Figure S2B). GAM analysis revealed that home range overlap area initially increased with increasing age, reaching a peak at 10 years before declining ( $R^2=0.52$ , 67.1% deviance explained; Figure 4D). However, the percentage of home range overlap remained stable throughout the entire tracking period ( $R^2=0.02$ , 1.79% deviance explained; Figure 4E). Furthermore, the pandas spent more time migrating as they aged ( $R^2=0.22$ , 27% deviance explained; Figure 4F).

## DISCUSSION

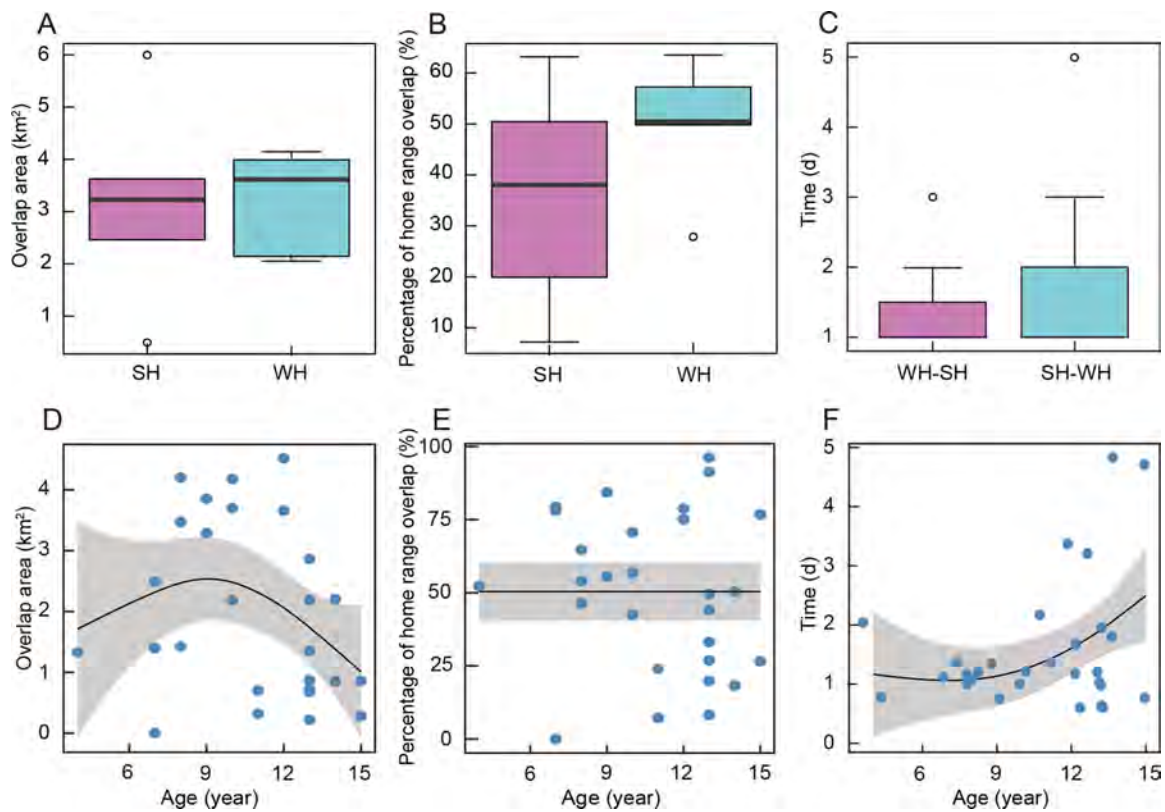
Our study revealed that giant pandas use spatial memory to revisit reliable foraging sites during seasonal migrations. These seasonal migration patterns and stable home ranges contribute to the acquisition of food resources in a spatially and temporally heterogeneous foodscape. While previous studies have demonstrated that the foraging strategies of giant pandas are driven by energy acquisition (Nie et al., 2015,





**Figure 3 Seasonal migration patterns across summer and winter habitats and movement paths of five GPS-collared giant pandas**

A: Migration movement directions (N: North; S: South; E: East; W: West) for individual pandas across winter and summer habitat. Specific bars represent revisited habitat patches for each migration event. B–F: Movement paths for each seasonal migration event for five individuals. SH: Summer habitat; WH: Winter habitat; numerals indicate different habitat patches and sub-patches; WH-SH 1st: Migration route from winter to summer habitat in first observation year; SH-WH 1st: Migration route from summer to winter habitat in first observation year.



**Figure 4 Stability analysis of home range and migration of six GPS-collared giant pandas**

A, B: Home range overlap area and percentage of home range overlap of seasonal habitats. C: Time spent during migration to summer and winter habitat. D–F: Relationships between age and home range overlap area, percentage of home range overlap and migration time. SH: Summer habitat; WH: Winter habitat; WH-SH: Migrate from winter habitat to summer habitat; SH-WH: Migrate from summer habitat to winter habitat.

2019) and a preference for high-protein diets (Schaller et al., 1985; Wei et al., 2015d), our study is the first to report that seasonal movements in pandas may be shaped by spatial memory.

The Green Wave Hypothesis posits that migratory movements are guided by closely tracking the dynamics of spring green up, sometimes referred to as “green wave surfing” (Van Der Graaf et al., 2006). However, our migration pattern results combined with previous nutritional evidence indicate that pandas do not align their movements with improving nutritional quality along their elevational migratory path, but rather move directly and rapidly from low-elevation habitat patches containing one bamboo species to high-elevation patches containing a different species with a temporally delayed phenology (Nie et al., 2015, 2019). This suggests that pandas are not surfing a single, continuous resource wave, but rather capitalizing on multiple, smaller waves (Nie et al., 2019). As one wave declines in nutritional value, pandas move to another wave, which may necessitate migration, but may also involve a dietary switch between bamboo shoots and leaves (Nie et al., 2015). Dietary switching between two discontinuously distributed bamboo species effectively excludes the utilization of a single green wave as a foraging strategy, i.e., the wave is not “surfable” (Aikens et al., 2020).

Our findings provide insights into how pandas accomplish seasonal migration. As reported in Nie et al. (2019), dietary shifts and seasonal migration appear to be driven by declining resource quality and the availability of superior resources elsewhere. Our study showed that pandas rapidly arrived at their summer habitats but exhibited variations in their return patterns (Figure 2B, C). These variations are likely a consequence of the need to exploit nutritional opportunities associated with the bamboo shooting period. However, the pandas do not appear to follow a “green wave” trajectory in their migratory movements between summer and winter habitats, relying instead on spatial memory. Furthermore, the dietary transition from arrow-bamboo leaves to wood-bamboo leaves does not induce a significant nutritional difference as compared to the consumption of bamboo shoots (Nie et al., 2015). This hypothesis is supported by the observation that individual pandas exhibited a strong tendency to return to the same foraging area year after year, and that movement between habitats was highly directional, without any circuitous foraging paths (Zhang et al., 2014). Our results suggest that, similar to the migratory behavior of zebras (*Equus burchelli*) where memory plays a greater role than perception in the selection of migratory routes (Bracis & Mueller, 2017), pandas navigate to foraging areas that extend beyond their perceptual range. Although our data are unable to elucidate the underlying mechanisms, it appears that pandas integrate memories of past information regarding foraging habitat with spatial knowledge, thereby efficiently guiding navigation between seasonal foraging grounds. This was demonstrated by the consistent directional navigation observed over a six-year period for Xiyue, who moved east when leaving for summer habitat and west upon return (Figure 3A, F). Similar consistency in directional navigation was observed in the other four pandas, leading to the frequent use of the same or adjacent habitats in their summer and winter ranges each year. These results suggest that memory plays a crucial role in interannual consistency in migratory routes, allowing pandas to locate familiar foraging locations with greater

efficiency and replenish the energy expended by migration (Merkle et al., 2014; Powell, 2000). This efficiency is of vital importance, especially following the period of relatively poor foraging conditions from September to April, which is likely to compromise body condition and survival (Li et al., 2017; Nie et al., 2015). The repeated return of pandas to the same sites each year likely enhances foraging and navigational efficiency, as site familiarity can have a substantial impact on these variables and contribute to fitness in a variety of taxa, and are important drivers of population performance, site fidelity, and win-stay/lose-shift foraging strategies (Piper, 2011; Stamps, 1995). This adaptive memory strategy, finely tuned to optimize resource acquisition, is expected to confer fitness benefits to pandas. The green wave surfing strategy improves body condition and fitness in other migratory herbivores (Middleton et al., 2018), while memory-based migration confers fitness benefits that support larger populations due to more efficient resource extraction (Fryxell et al., 1988; Riotte-Lambert et al., 2017; Rolandsen et al., 2017), which may help sustain the high panda population density found in the Qinling Mountains (National Forestry and Grassland Administration, 2021). The nutritional strategy of pandas supports vital life processes such as mating, gestation, parturition, and lactation (Nie et al., 2015), and our findings provide insight into how pandas time their seasonal movements and dietary shifts to optimize nutritional gain.

In addition to filling knowledge gaps regarding panda movement ecology, our findings also have compelling implications for conservation. The memory-based migratory patterns between seasonal habitats identified in our study may play an important role in determining the population dynamics and survival of pandas in the landscape. The availability of bamboo shoots, serving as “keystone resources” (Terborgh, 1986) that offer nutrition during periods of resource scarcity, may increase the carrying capacity of panda populations. The seasonal migratory patterns of pandas are essential for exploiting these highly seasonal resources. However, anthropogenic disruption of migratory routes is a growing global conservation challenge, potentially leading to population collapse (Bolger et al., 2008; Tucker et al., 2018). Although panda migration is relatively truncated compared to that of large herbivores and bird species, anthropogenic disturbance or habitat loss can disrupt their movements, with detrimental consequences for individuals and populations. Road construction and other barriers to movement can impact habitat use and genetic connectivity in pandas (Xu et al., 2017; Zhu et al., 2011b). Thus, we recommend judicious management decisions regarding the placement of roads and other infrastructure that may interrupt migratory routes. To ensure the effectiveness of protected areas, it is essential that they encompass both summer and winter habitats, enabling pandas to access critical foraging resources throughout the year. Additionally, the insights gained from our study have important implications for the use of translocations as a recovery tool in increasingly fragmented panda landscapes (He et al., 2019; Yang et al., 2018). Given the pronounced seasonal variation in resource availability, translocations need to be carefully timed to coincide with abundant bamboo shoot growth. Furthermore, to the extent that panda migrations are guided by memory or cultural transmission, the relocation of naïve individuals may pose challenges as it can take multiple generations for a translocated population to re-establish migratory patterns and efficiently exploit and become familiar

with seasonally available resources (Jesmer et al., 2018). To mitigate these challenges, translocation programs for pandas should consider implementing training programs or other strategies aimed at expediting acquisition of knowledge (e.g., through cultural transmission) regarding seasonally and geographically varying distribution of bamboo resources, as well as the migratory routes that connect disparate foraging habitats. Ultimately, a deeper understanding of the interplay among learning, habitat familiarity, and animal migrations will be instrumental in developing more effective conservation strategies for this important ecological phenomenon (Bracis & Mueller, 2017; Jesmer et al., 2018; Merkle et al., 2019).

The depiction presented herein of a highly adaptive species capable of avoiding extinction in the absence of anthropogenic disturbance strengthens support for additional investment in its continued recovery. Accumulating evidence refutes the premature claims that giant pandas are too highly specialized and are pre-destined for extinction; the panda is not at an evolutionary dead end (Wei et al., 2015a). Given its recent downlisting to “Vulnerable” (Swaigood et al., 2016), the giant panda has shown a strong biological capacity for recovery. Ecological investigations of movement patterns, such as our own, will continue to provide a scientific foundation for informed management of the giant panda.

#### SCIENTIFIC FIELD SURVEY PERMISSION INFORMATION

Permission for field surveys in Foping National Nature Reserve was granted by the National Forestry and Grassland Administration and the Foping National Nature Reserve.

#### SUPPLEMENTARY DATA

Supplementary data to this article can be found online.

#### COMPETING INTERESTS

The authors declare that they have no competing interests.

#### AUTHORS' CONTRIBUTIONS

M.W., F.W.W., and Y.G.N. conceived and designed the study. Y.G.N., W.W., W.L.Z., and Z.J.Z. conducted the surveys. M.W. and Y.G.N. prepared the data. M.W. and G.M.W. analyzed the data. M.W. and R.R.S. wrote the paper. All authors read and approved the final version of the manuscript.

#### ACKNOWLEDGMENTS

We gratefully acknowledge the support of the San Diego Zoo Global Wildlife Conservancy, Foping National Nature Reserve, and field staff.

#### REFERENCES

Abrahms B, Hazen EL, Aikens EO, et al. 2019. Memory and resource tracking drive blue whale migrations. *Proceedings of the National Academy of Sciences of the United States of America*, **116**(12): 5582–5587.

Aikens EO, Kauffman MJ, Merkle JA, et al. 2017. The greenscape shapes surfing of resource waves in a large migratory herbivore. *Ecology Letters*, **20**(6): 741–750.

Aikens EO, Myrsetrud A, Merkle JA, et al. 2020. Wave-like patterns of plant phenology determine ungulate movement tactics. *Current Biology*, **30**(17): 3444–3449.e4.

Albon SD, Langvatn R. 1992. Plant phenology and the benefits of migration in a temperate ungulate. *Oikos*, **65**(3): 502–513.

Avgar T, Baker JA, Brown GS, et al. 2015. Space-use behaviour of woodland caribou based on a cognitive movement model. *Journal of Animal Ecology*, **84**(4): 1059–1070.

Avgar T, Street G, Fryxell JM. 2014. On the adaptive benefits of mammal migration. *Canadian Journal of Zoology*, **92**(6): 481–490.

Bailey H, Mate BR, Palacios DM, et al. 2009. Behavioural estimation of blue whale movements in the Northeast Pacific from state-space model analysis of satellite tracks. *Endangered Species Research*, **10**: 93–106.

Barboza PS, Parker KL. 2008. Allocating protein to reproduction in Arctic reindeer and caribou. *Physiological and Biochemical Zoology*, **81**(6): 835–855.

Ben-David M. 1997. Timing of reproduction in wild mink: the influence of spawning Pacific salmon. *Canadian Journal of Zoology*, **75**(3): 376–382.

Betts MG, Rodenhouse NL, Sillett TS, et al. 2008. Dynamic occupancy models reveal within-breeding season movement up a habitat quality gradient by a migratory songbird. *Ecography*, **31**(5): 592–600.

Bolger DT, Newmark WD, Morrison TA, et al. 2008. The need for integrative approaches to understand and conserve migratory ungulates. *Ecology Letters*, **11**(1): 63–77.

Bracis C, Gurarie E, Van Moorter B, et al. 2015. Memory effects on movement behavior in animal foraging. *PLoS One*, **10**(8): e0136057.

Bracis C, Mueller T. 2017. Memory, not just perception, plays an important role in terrestrial mammalian migration. *Proceedings of the Royal Society B: Biological Sciences*, **284**(1855): 20170449.

Connor T, Hull V, Liu JG. 2016. Telemetry research on elusive wildlife: a synthesis of studies on giant pandas. *Integrative Zoology*, **11**(4): 295–307.

Deacy WW, Erlenbach JA, Leacock WB, et al. 2018. Phenological tracking associated with increased salmon consumption by brown bears. *Scientific Reports*, **8**(1): 11008.

Fagan WF, Lewis MA, Auger-Méthé M, et al. 2013. Spatial memory and animal movement. *Ecology Letters*, **16**(10): 1316–1329.

Fryxell JM, Greever J, Sinclair ARE. 1988. Why are migratory ungulates so abundant?. *The American Naturalist*, **131**(6): 781–798.

Fryxell JM, Sinclair ARE. 1988. Causes and consequences of migration by large herbivores. *Trends in Ecology & Evolution*, **3**(9): 237–241.

Han H, Wei W, Hu YB, et al. 2019. Diet evolution and habitat contraction of giant pandas via stable isotope analysis. *Current Biology*, **29**(4): 664–669.e2.

He K, Dai Q, Foss-Grant A, et al. 2019. Movement and activity of reintroduced giant pandas. *Ursus*, **29**(2): 163–174.

Huang GP, Wang X, Hu YB, et al. 2021. Diet drives convergent evolution of gut microbiomes in bamboo-eating species. *Science China Life Sciences*, **64**(1): 88–95.

Jesmer BR, Merkle JA, Goheen JR, et al. 2018. Is ungulate migration culturally transmitted? Evidence of social learning from translocated animals. *Science*, **361**(6406): 1023–1025.

Jones MC, Marron JS, Sheather SJ. 1996. A brief survey of bandwidth selection for density estimation. *Journal of the American Statistical Association*, **91**(433): 401–407.

Kernohan BJ, Gitzen RA, Millspaugh JJ. 2001. Chapter 5 - Analysis of animal space use and movements. In: Millspaugh JJ, Marzluff JM. Radio Tracking and Animal Populations. San Diego: Academic Press, 125–166.

Lai XL, Zhou WL, Gao HL, et al. 2020. Impact of sympatric carnivores on den selection of wild giant pandas. *Zoological Research*, **41**(3): 273–280.

Li C, Bao ZQ, Luo XR, et al. 2022. Does high vegetation coverage equal high giant panda density?. *Zoological Research*, **43**(4): 608–611.

Li YX, Swaisgood RR, Wei W, et al. 2017. Withered on the stem: is bamboo a seasonally limiting resource for giant pandas?. *Environmental Science and Pollution Research*, **24**(11): 10537–10546.

Merkle JA, Fortin D, Morales JM. 2014. A memory-based foraging tactic reveals an adaptive mechanism for restricted space use. *Ecology Letters*, **17**(8): 924–931.

Merkle JA, Sawyer H, Monteith KL, et al. 2019. Spatial memory shapes migration and its benefits: evidence from a large herbivore. *Ecology Letters*, **22**(11): 1797–1805.

Mettker-Hofmann C, Gwinner E. 2003. Long-term memory for a life on the



- move. *Proceedings of the National Academy of Sciences of the United States of America*, **100**(10): 5863–5866.
- Middleton AD, Merkle JA, McWhirter DE, et al. 2018. Green-wave surfing increases fat gain in a migratory ungulate. *Oikos*, **127**(7): 1060–1068.
- Monteith KL, Bleich VC, Stephenson TR, et al. 2014. Life-history characteristics of mule deer: effects of nutrition in a variable environment. *Wildlife Monographs*, **186**(1): 1–62.
- Mueller T, Fagan WF. 2008. Search and navigation in dynamic environments: from individual behaviors to population distributions. *Oikos*, **117**(5): 654–664.
- Mueller T, Fagan WF, Grimm V. 2011. Integrating individual search and navigation behaviors in mechanistic movement models. *Theoretical Ecology*, **4**(3): 341–355.
- National Forestry and Grassland Administration. 2021. 4th National Survey Report on Giant Panda in China. Beijing: Science Press. (in Chinese)
- Nie YG, Wei FW, Zhou WL, et al. 2019. Giant pandas are macronutritional carnivores. *Current Biology*, **29**(10): 1677–1682.e2.
- Nie YG, Zhang ZJ, Raubenheimer D, et al. 2015. Obligate herbivory in an ancestrally carnivorous lineage: the giant panda and bamboo from the perspective of nutritional geometry. *Functional Ecology*, **29**(1): 26–34.
- Pan WS, Lv Z, Zhu XJ, et al. 2001. A Chance for Lasting Survival. Beijing: Peking University Press. (in Chinese)
- Piper WH. 2011. Making habitat selection more “familiar”: a review. *Behavioral Ecology and Sociobiology*, **65**(7): 1329–1351.
- Polansky L, Kilian W, Wittermyer G. 2015. Elucidating the significance of spatial memory on movement decisions by African savannah elephants using state–space models. *Proceedings of the Royal Society B: Biological Sciences*, **282**(1805): 20143042.
- Powell RA. 2000. Animal home ranges and territories and home range estimators. In: Boitani L, Fuller T. *Research Techniques in Animal Ecology: Controversies and Consequences*. New York: Columbia University Press, 65–110.
- Ranc N, Moorcroft PR, Ossi F, et al. 2021. Experimental evidence of memory-based foraging decisions in a large wild mammal. *Proceedings of the National Academy of Sciences of the United States of America*, **118**(15): e2014856118.
- Riotte-Lambert L, Benhamou S, Bonenfant C, et al. 2017. Spatial memory shapes density dependence in population dynamics. *Proceedings of the Royal Society B: Biological Sciences*, **284**(1867): 20171411.
- Rolandsen CM, Solberg EJ, Saether BE, et al. 2017. On fitness and partial migration in a large herbivore - migratory moose have higher reproductive performance than residents. *Oikos*, **126**(4): 547–555.
- Sahanatien V, Peacock E, Derocher AE. 2015. Population substructure and space use of Foxe Basin polar bears. *Ecology and Evolution*, **5**(14): 2851–2864.
- Schaller GB, Hu JC, Pan WS, et al. 1985. *The Giant Pandas of Wolong*. Chicago: University of Chicago Press.
- Schindler DE, Armstrong JB, Bentley KT, et al. 2013. Riding the crimson tide: mobile terrestrial consumers track phenological variation in spawning of an anadromous fish. *Biology Letters*, **9**(3): 20130048.
- Singh NJ, Grachev IA, Bekenov AB, et al. 2010. Tracking greenery across a latitudinal gradient in central Asia - the migration of the saiga antelope. *Diversity and Distributions*, **16**(4): 663–675.
- Spencer WD. 2012. Home ranges and the value of spatial information. *Journal of Mammalogy*, **93**(4): 929–947.
- Stamps J. 1995. Motor learning and the value of familiar space. *The American Naturalist*, **146**(1): 41–58.
- Swaigood RR, Wang DJ, Wei FW. 2016 (2016-10-12). *Ailuropoda melanoleuca*. IUCN Red List of Threatened Species, <http://hubaogy.cn/index/news/show/id/107.html>.
- Swaigood RR, Wang DJ, Wei FW. 2018. Panda downlisted but not out of the woods. *Conservation Letters*, **11**(1): e12355.
- Terborgh J. 1986. Keystone plant resources in the tropical forest. In: Soulé M. *Conservation Biology - the Science of Scarcity and Diversity*. Sunderland: Sinauer Associates, Inc.
- Tucker MA, Böhning-Gaese K, Fagan WF, et al. 2018. Moving in the Anthropocene: global reductions in terrestrial mammalian movements. *Science*, **359**(6374): 466–469.
- Van Der Graaf AJ, Stahl J, Klimkowska A, et al. 2006. Surfing on a green wave - how plant growth drives spring migration in the barnacle goose *Branta leucopsis*. *Ardea*, **94**(3): 567–577.
- Van Moorter B, Visscher D, Benhamou S, et al. 2009. Memory keeps you at home: a mechanistic model for home range emergence. *Oikos*, **118**(5): 641–652.
- Walter WD, Fischer JW, Baruch-Mordo S, et al. 2011. What is the proper method to delineate home range of an animal using today's advanced GPS telemetry systems: the initial step. USDA Wildlife Services-Staff Publications, 1375.
- Wand MP, Jones MC. 1995. *Kernel Smoothing*. London: Chapman & Hall.
- Wang F, Liu JG. 2017. Conservation planning beyond giant pandas: the need for an innovative telecoupling framework. *Science China Life Sciences*, **60**(5): 551–554.
- Wei FW, Hu YB, Yan L, et al. 2015a. Giant pandas are not an evolutionary cul-de-sac: evidence from multidisciplinary research. *Molecular Biology and Evolution*, **32**(1): 4–12.
- Wei FW, Swaigood R, Hu YB, et al. 2015b. Progress in the ecology and conservation of giant pandas. *Conservation Biology*, **29**(6): 1497–1507.
- Wei FW, Wang X, Wu Q. 2015c. The giant panda gut microbiome. *Trends in Microbiology*, **23**(8): 450–452.
- Wei W, Nie YG, Zhang ZJ, et al. 2015d. Hunting bamboo: foraging patch selection and utilization by giant pandas and implications for conservation. *Biological Conservation*, **186**: 260–267.
- Wolf M, Frair J, Merrill E, et al. 2009. The attraction of the known: the importance of spatial familiarity in habitat selection in wapiti *Cervus elaphus*. *Ecography*, **32**(3): 401–410.
- Wood SN. 2017. *Generalized Additive Models: An Introduction with R*. 2<sup>nd</sup> ed. New York: Chapman and Hall/CRC.
- Xu WH, Viña A, Kong LQ, et al. 2017. Reassessing the conservation status of the giant panda using remote sensing. *Nature Ecology & Evolution*, **1**(11): 1635–1638.
- Yang ZS, Gu XD, Nie YG, et al. 2018. Reintroduction of the giant panda into the wild: A good start suggests a bright future. *Biological Conservation*, **217**: 181–186.
- Zhang ZJ, Sheppard JK, Swaigood RR, et al. 2014. Ecological scale and seasonal heterogeneity in the spatial behaviors of giant pandas. *Integrative Zoology*, **9**(1): 46–60.
- Zhou WL, Wang M, Gao K, et al. 2022a. Behavioural thermoregulation by montane ungulates under climate warming. *Diversity and Distributions*, **28**(10): 2229–2238.
- Zhou WL, Wang M, Ma YJ, et al. 2022b. Community structure of the solitary giant pandas is maintained by indirect social connections. *Movement Ecology*, **10**(1): 53.
- Zhu LF, Wu Q, Dai JY, et al. 2011a. Evidence of cellulose metabolism by the giant panda gut microbiome. *Proceedings of the National Academy of Sciences of the United States of America*, **108**(43): 17714–17719.
- Zhu LF, Zhang SN, Gu XD, et al. 2011b. Significant genetic boundaries and spatial dynamics of giant pandas occupying fragmented habitat across southwest China. *Molecular Ecology*, **20**(6): 1122–1132.