

Contrasting effects of wind farm disturbances on multi-dimensional competition and coexistence of sympatric mesocarnivores[☆]

Mingshuo Qin^{a,b,1}, Wenhong Xiao^{a,1}, Xinyue Xia^c, Kai Xu^{a,b}, Dazhao Song^c, Zhishu Xiao^{a,b,*}

^a State Key Laboratory of Integrated Management of Pest Insects and Rodents, Institute of Zoology, Chinese Academy of Sciences, Beijing, China

^b University of Chinese Academy of Sciences, Beijing, China

^c Chinese Felid Conservation Alliance, Chongqing, China

ARTICLE INFO

Keywords:

Competition
Mesocarnivores
Niche partitioning
Species coexistence
Wind farm development
Biodiversity conservation

ABSTRACT

Wind power generation is expanding rapidly as a sustainable energy development solution to mitigate climate change. However, a significant knowledge gap remains regarding the impacts of wind farm (WF) development on wildlife, particularly how different species respond to the disturbance from WFs. To address this, we used camera-trapping surveys and fecal-DNA metabarcoding data collected from both WF and non-WF areas. We aimed to investigate the multi-dimensional effects of WF disturbances on the competition and coexistence between two key mesocarnivores, red foxes (*Vulpes vulpes*) and Pallas's cats (*Otocolobus manul*) in the Hexi Corridor, Northwest China. Given their distinct ecological characteristics and responses to human disturbances, we hypothesized that WF disturbances would differentially affect both species across spatial, temporal and diet niche dimensions. As expected, WF disturbances diminished prey availability and increased trophic niche overlap. Temporal niches playing a crucial role in facilitating coexistence through Pallas's cats shifting their daily activity patterns to reduce overlap with human activity. Despite significant differences in habitat preferences, spatial niche overlap between the two species remained similar across WF and non-WF areas, likely due to prey availability and livestock distribution. Our results highlight the complex interplay of spatial, temporal, and trophic niche dimensions in mitigating competition and promoting coexistence among sympatric carnivore species. Our findings provide guidance for balancing renewable energy goals with biodiversity conservation, emphasizing the importance of habitat preservation, prey management, and WF placement strategies during WF development.

1. Introduction

The competitive exclusion principle predicts that species with overlapping requirements cannot coexist stably over long periods without partitioning resources across niche dimensions (Hardin, 1960). Particularly among carnivores, species avoid competitive exclusion by partitioning niches like space, time and diet, a critical mechanism for reducing interspecific competition and promoting coexistence (Schoener, 1974). Here, 'niche partitioning' is defined as the process by which species reduce competition by differentiating their use of resources in space, time, and diet, while 'niche overlap' refers to the degree to which species share these resources.

However, human-induced disturbances can disrupt this partitioning equilibrium by reshaping niche space across different dimensions (Manlick and Pauli, 2020; Smith et al., 2024). Such disturbances compress spatial and temporal niches, causing carnivores to avoid certain areas and times (Gaynor et al., 2018; Tucker et al., 2018). For instance, in West Africa, anthropogenic activities have led to increased spatial niche overlap between African lions (*Panthera leo*) and spotted hyenas (*Crocuta crocuta*) (Sogbohossou et al., 2018). The disruption of spatio-temporal niche partitioning is likely a common consequence of human disturbance, potentially limiting niche differentiation among carnivores and intensifying their competition. Similarly, these disturbances may also reduce prey accessibility and homogenize prey

[☆] This article is part of a Special issue entitled: 'Species interactions' published in Biological Conservation.

* Corresponding author at: Institute of Zoology, Chinese Academy of Sciences, 1 Beichen West Road, Chaoyang District, Beijing 100101, China.

E-mail address: xiaozs@ioz.ac.cn (Z. Xiao).

¹ These authors contributed equally to this work.

resources (Manlick and Pauli, 2020). For example, reduced prey populations in a Kenyan national park resulted in decreased dietary niche breadth and increased niche overlap among carnivores (Creel et al., 2018). The contraction of available trophic niches may further heighten competition among carnivore species. In the context of disturbance, understanding the potential linkages among spatial, temporal, and trophic niche dimensions is crucial. When disturbances constrain one dimension, carnivores may achieve coexistence through differentiation along other ecological dimensions (Manlick and Pauli, 2020; Smith et al., 2024).

Critically, interspecific variation in behavioral responses to human disturbance can buffer competition intensification, thereby facilitating carnivore coexistence (Lowry et al., 2013; Samia et al., 2015; Deuel et al., 2017). For instance, species with lower tolerance to human disturbance may change their spatiotemporal habitat use to minimize exposure to disturbances (Ferrão da Costa et al., 2018; Llaneza et al., 2018; Stillfried et al., 2015), while more tolerant species may prefer human-modified habitats (Deuel et al., 2017). This differential response facilitates niche segregation, may reduce competitive intensity among carnivores. For example, in North America, red foxes (*Vulpes vulpes*) can exploit more urbanized areas, while coyotes (*Canis latrans*) exhibit a strong preference for more natural habitats; this spatial segregation aids their coexistence (Mueller et al., 2018). However, current research on sympatric carnivore niche partitioning predominantly examines single niche dimensions, overlooking species-specific drivers (Bu et al., 2016; Shao et al., 2021; Tian et al., 2022). This limitation impedes holistic understanding of wildlife adaptations to anthropogenic environments and underscores the necessity for multidimensional assessments.

Wind farms (WFs) are rapidly expanding globally as a sustainable energy solution to mitigate climate change and reduce reliance on fossil fuels. Crucially differing from urbanization or industrial disturbances, WFs exhibit its unique attributes. The infrastructure within WFs features a spatially dispersed “point-line” configuration (wind turbines connected by roads), which retains larger areas of habitat. Beyond the direct habitat destruction caused by infrastructure, operational stressors such as chronic noise, vibration, and the increased presence of human activities may cause carnivores to modify habitat use and activity patterns, thereby further complicating niche partitioning among carnivore species (Łopucki and Perzanowski, 2018; Skarin et al., 2018). For instance, studies on American martens (*Martes americana*), red foxes, and wolves (*Canis lupus*) revealed that martens were most frequently documented along high-altitude hiking trails and were relatively scarce on WF access roads. In contrast, red foxes and wolves exhibited the opposite activity pattern (Skarin et al., 2018). These changes may cushion competition between martens and the other two carnivores while potentially increasing interspecific competition between red foxes and wolves within WF complexes, ultimately altering carnivore coexistence patterns. Therefore, understanding how WFs impact the coexistence patterns of carnivores is crucial for balancing sustainable renewable energy development and biodiversity conservation.

Human activities have profoundly transformed carnivore communities in many regions across China and around other parts of the world, leading to the decline or disappearance of large carnivores from most of their historical habitats (Moreira-Arce et al., 2015; Prugh et al., 2009). For example, in the Hexi Corridor, an ecologically significant region in Northwest China characterized by vast arid steppes and desert landscapes, large carnivores such as snow leopards (*Panthera uncia*) have experienced substantial population declines due to habitat destruction, poaching, and prey populations decrease (Schaller et al., 1988; Snow Leopard Network, 2014). This decline is part of a broader global trend of apex predator loss, resulting in mesocarnivores becoming the dominant predators in many ecosystems, filling the void left by large carnivores (Avrin et al., 2023; Roemer et al., 2009). The Hexi Corridor is also a typical site for renewable energy development, with many WFs being established (D. Wang et al., 2022; G. Wang et al., 2022; Zhang et al., 2015). This area provides crucial habitats for mesocarnivores such as red

foxes (*Vulpes vulpes*) and Pallas's cats (*Otocolobus manul*), which have similar habitat preferences and dietary requirements, potentially intensifying competition between them (Ma et al., 2024; D. Wang et al., 2022; G. Wang et al., 2022). However, these species exhibit significant differences in their ecological traits and responses to human disturbance. Red foxes are dietary generalists with higher behavioral plasticity that can adapt to various environmental conditions and often exploit human-provided food sources (D. Wang et al., 2022; G. Wang et al., 2022; Lin et al., 2010; Hoffmann and Sillero-Zubiri, 2021). In contrast, Pallas's cats maintain a specialized diet, primarily feeding on small mammals like plateau pikas (*Ochotona curzoniae*) and rely on sheltered habitats like rocky crevices or dense vegetation for stalking prey and breeding (Zhao et al., 2019). This specialization makes them especially vulnerable to habitat changes and human disturbances (Ross et al., 2010a; Zhao et al., 2019). Therefore, these interspecific differences between red foxes and Pallas's cats offer a unique opportunity to explore how WF disturbances influence the coexistence of sympatric mesocarnivores across multiple ecological niches dimensions.

To address the above questions, we used camera-trapping and fecal-DNA metabarcoding to investigate the competition and coexistence patterns between red foxes and Pallas's cats, across spatial, temporal and trophic niche dimensions in both WF areas and non-WF areas (as controls) in the northern desert of the Hexi Corridor. Considering their different ecological traits and varying responses to human disturbances (D. Wang et al., 2022; G. Wang et al., 2022; Yang et al., 2024; Zaman et al., 2020), we formulated three dimension-specific hypotheses: (1) In temporal niche, we predicted that red foxes exhibiting higher tolerance to human activity, would maintain their temporal patterns, whereas disturbance-sensitive Pallas's cats would shift activity toward late-night hours to avoid human activities, thereby reducing temporal overlap with red foxes. (2) In spatial niche, similar to temporal shifts, we expected Pallas's cats to avoid WF infrastructure and roads due to disturbance, while red foxes might utilize these areas. Consequently, spatial overlap between the species should decrease within WF areas. (3) In trophic niche dimension, despite red foxes potentially expanding their niche breadth through anthropogenic subsidies, diminished prey availability in WF areas would increase trophic niche overlap between the species. Collectively, we expected that WF areas would exhibit higher trophic niche overlap between Pallas's cats and red foxes compared to control sites, and thus may potentially intensify interspecific competition due to diminished prey resources. These reduced spatiotemporal niche overlaps would serve as the core mechanism enabling their coexistence in WF areas (Fig. 1).

2. Methods

2.1. Study area

The study was conducted in Zhangye City of Gansu Province, Northwest China, within a comprehensive energy base (110°32'53.15"E, 39°11'58.33"N), a region characterized by numerous wind and solar farms. The desert steppe in the study area features undulating topography, arid conditions, and a continental desert climate, with an annual average temperature of 5.7 °C and average precipitation of 130 mm. The area is home to diverse wildlife, including mesocarnivores such as red foxes and Pallas's cats, along with their primary prey like Chinese hamster (*Cricetulus barabensis*), Pallas's Sandgrouse (*Syrhaptes paradoxus*) and Midday jird (*Meriones meridianus*). Additionally, vulnerable species like goitered gazelle (*Gazella subgutturosa*) and Macqueen's Bustard (*Chlamydotis macqueeni*) also inhabit the region.

We selected four WF areas and their corresponding non-WF areas as study sites (Fig. 2). The non-WF areas, situated at least 3 km from the WFs, were chosen to minimize potential disturbance while maintaining similar abiotic and biotic conditions. The selected sites included the Pingshanhu WF (PSH), Jiecheng WF (JC), Mengtiokuang WF (MTK), and Banqiao WF (BQ), along with their respective non-WF areas. Human

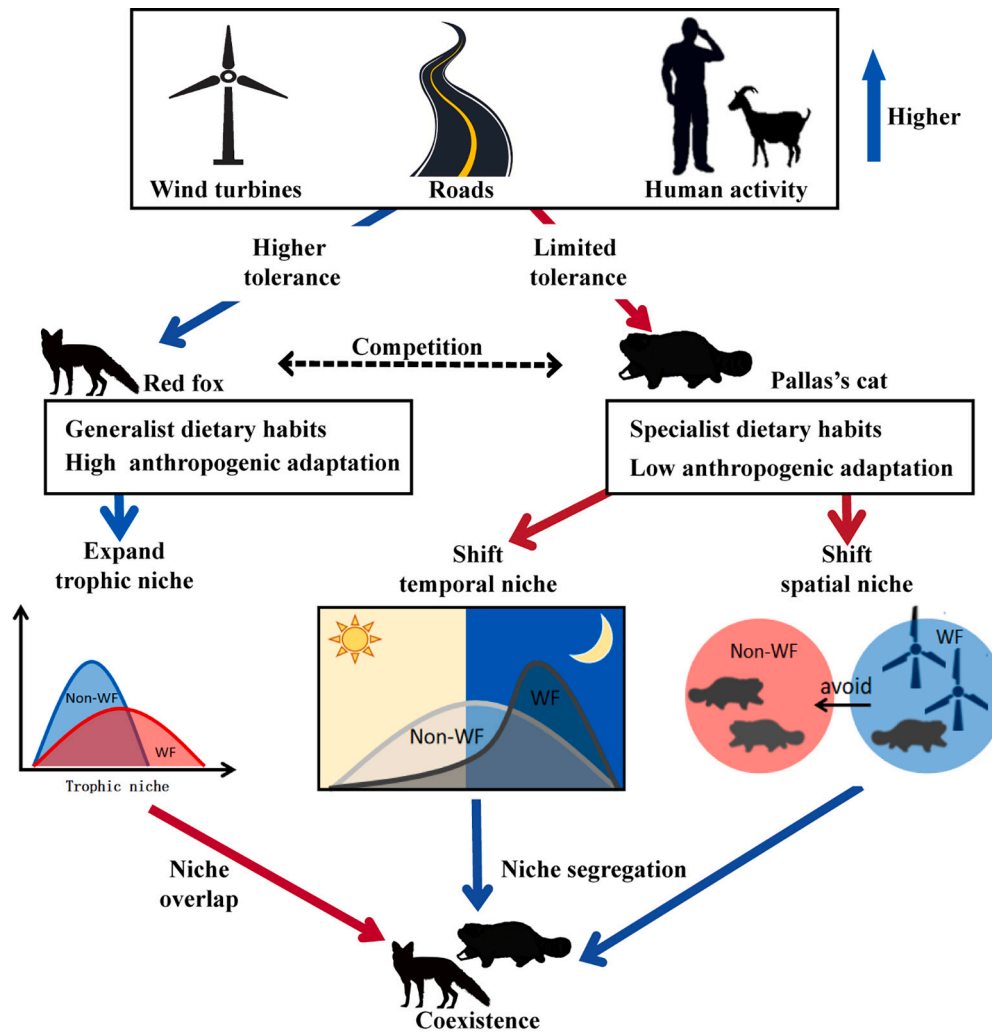


Fig. 1. Conceptual model of multi-dimensional (spatial, temporal and trophic) effects of WF disturbances on the competition and coexistence of sympatric carnivores, i.e. red foxes (*Vulpes vulpes*) and Pallas's cats (*Otocolobus manul*). Red foxes exhibited greater tolerance to WF-related disturbances by expanding their trophic niche. In contrast, Pallas's cats, being more sensitive to disturbances, primarily adjusted their temporal activity patterns to minimize exposure to WF impacts and competition. WF disturbances led to increased trophic niche overlap between the two species, while temporal niche segregation emerged as a critical factor promoting their coexistence in disturbed habitats.

disturbances in these areas were primarily caused by turbine operations, routine maintenance activities, and livestock grazing (from sheep, *Ovis aries*, donkeys, *Equus asinus* and camels, *Camelus bactrianus*).

2.2. Camera-trap monitoring and fecal sampling

We applied camera-trap monitoring and fecal DNA sampling because these methods provide detailed data on spatial, temporal and trophic niche partitioning, allowing us to comprehensively assess the impacts of WFs.

Camera-trap monitoring took place from March to October 2023 using a 1 km × 1 km grid system (Fig. 2, Table 1). One camera trap was placed at a trail, turnoff, or ridge near the center of each grid, targeting areas commonly used by predators patrolling their territories. This strategic placement minimized potential issues related to the detection radius and efficiency, such as the inability to identify animals at long distances during nighttime (Blašković et al., 2022; Palencia et al., 2021). The distance between camera traps ranged from 800 m to 1200 m. The traps were set to operate continuously for 24 h, and the data were managed through the China Biodiversity Monitoring and Research Network platform (Sino BON-Mammals, <https://www.gscloud.cn/ca meradata/>). Additional technical specifications, including camera

models, installation height, and parameter settings, are provided in the Supplementary Information.

Noninvasive fecal samples were conducted systematically along paths and ridges within the camera-trapping areas. Samples were collected and stored in ethanol before being transferred to sterile centrifuge tubes containing silica desiccant for −20 °C storage until DNA extraction. Detailed sampling protocols and DNA metabarcoding methods are described in the Supplementary Information.

2.3. Data analysis

To test our hypothesis and predictions, we used camera-trap data to assess spatial and temporal activity patterns and fecal DNA analysis to evaluate dietary composition. All data analyses were carried out in R statistical programming software (version 4.3.0, R Core Team, 2013), while GIS operations were performed in ArcGIS (ESRI Inc., Redlands, CA, USA).

For each camera-trapping site, a continuous 24-hour operational period was considered one effective camera day (Xiao et al., 2019). An independent event for each species was defined as all detections within a 30-minute interval at each camera-trapping site (O'Brien et al., 2003). Given limited information on types of human activities (such as herders,

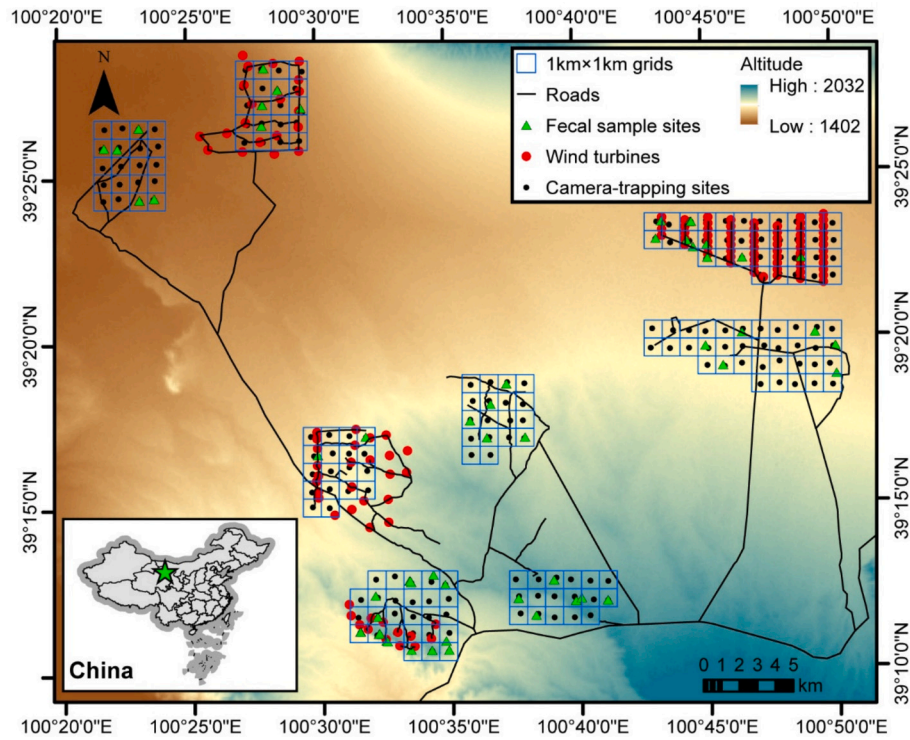


Fig. 2. Distribution of wind turbines, sampling grids (1 km × 1 km each grid), camera-trapping stations and fecal collection sites in this study.

Table 1

Summary of camera-trapping surveys and fecal sampling in four wind farms (including Pingshanhu, PSH, Jiecheng, JC, Mengtiekuan, MTK, and Banqiao, BQ) and their corresponding non-WF areas.

Statistics	PSH		JC		BQ		MTK		Total
	WF	Non-WF	WF	Non-WF	WF	Non-WF	WF	Non-WF	
No. grids (1 km × 1 km)	32	32	25	17	16	18	15	9	164
No. camera-trapping stations	32	32	25	17	16	18	15	9	164
Trap effort (camera days)	4604	3591	4588	2326	2024	2460	2357	904	22,854
Independent events	1861	3151	1370	1491	1634	2057	945	647	13,156
Mammal richness	11	11	9	7	8	5	9	6	12
Red fox independent events	132	372	35	45	61	158	24	13	840
Red fox RAI	2.87	10.36	0.76	1.93	3.01	6.42	1.02	1.44	3.68
Pallas's cat independent events	8	19	17	9	3	0	6	0	62
Pallas's cat RAI	0.17	0.53	0.37	0.39	0.15	0	0.25	0	0.27
Human RAI	0.80	0.36	0.19	1.16	3.41	1.99	2.04	0.22	1.09
Livestock RAI	17.79	20.94	0.28	4.34	39.67	57.89	18.84	30.97	20.17
Prey RAI	2.41	7.05	2.77	2.19	2.52	2.28	1.19	13.05	3.48
No. Red fox fecal samples	7	3	6	2	4	4	1	5	32
No. Pallas's cat fecal samples	2	10	6	8	1	2	1	0	30

WF workers, vehicles), all human activity encounters were categorized as general “human” events, indicating human presence. We then calculated the relative abundance index (RAI) for prey, humans, and livestock at each site based on independent events per 100 camera days (O'Brien, 2011). These indices were used as explanatory variables representing human disturbance and biological variables in our modeling.

2.3.1. Spatial analysis

We used a single-species, single-season occupancy model to evaluate the spatial distribution of red fox and Pallas's cat, as well as the effects of WF and natural factors on their occupancy rates. This model accounts for species false absences, addressing the issue of incomplete detection. By constructing a detection history (detected/undetected) for the target species through repeated detection, the model infers the effects of environmental factors on species occupancy (ψ) and detection (p) rate (MacKenzie et al., 2002). Given that the home range sizes of red foxes and Pallas's cats might span multiple camera-trapping grids (Ross et al.,

2010a, 2010b; Munkhzul et al., 2012), there we used ‘occupancy rate’ to characterize habitat use intensity for both carnivores (Xiao et al., 2018; Li et al., 2019).

To assess the factors influencing the detection and occupancy of red foxes and Pallas's cats, we selected anthropogenic, natural, and biological factors. All anthropogenic, natural, and biological factors were incorporated into both the detection and occupancy sub-models. In the detection sub-model, these covariates explain potential influences on animal detectability near sampling sites. In the occupancy sub-model, they explain potential impacts on animal habitat use (Xiao et al., 2018; Li et al., 2019). Anthropogenic disturbance factors included wind turbine kernel densities “TKD”, road kernel densities “RKD”, human RIA “Human”, and livestock RAI “Livestock”. Natural factors included vegetation cover (NDVI) and roughness index (Roughness) (Ross et al., 2010a, 2012; Steinmetz et al., 2021), while prey abundance (RAI of rat and Pallas's Sandgrouse, primary prey based on dietary analysis) was included as a biological factor. Kernel density analysis function in

ArcMap 10.4 (ESRI Inc, redlands, CA, USA) was used to estimate the spatial distribution of wind turbines and roads by calculating their densities at each grid pixel. The roughness index and NDVI were derived from 30-meter resolution ASTER Global Digital Elevation Model (GDEM) data and Landsat 5 data, respectively. Except for all RAI values, all variables were calculated within a 30 m radius buffer around the camera-trapping sites. We assessed multicollinearity among all covariates using Pearson correlation tests, confirming that all correlation coefficients were less than 0.6. All data were standardized to have a mean of 0 and standard deviation of 1.

We constructed a detection matrix using independent events for each species, with 27 columns representing 7-day sampling periods, and 164 rows representing camera-trapping sites. The matrix recorded whether each carnivore species was detected (1) or not (0) across multiple 7-day intervals, to decrease the bias due to any potential unmodeled spatial autocorrelation (Goldstein et al., 2024). Using the “unmarked” package in R (Fiske and Chandler, 2011), we constructed single-species, single-season occupancy models and evaluated all possible covariate combinations. Models with $\Delta AIC \leq 2$ were selected as optimal based on Akaike’s Information Criterion (AIC). When multiple optimal models were identified, we averaged these models with equal weights to obtain covariate estimates. Model fit and overdispersion parameters were assessed using 1000 bootstrap samples with p-values > 0.05 indicating an adequate fit and $\hat{c}$ -hat values close to 1 indicating satisfactory convergence. Based on the optimal model, we calculated the occupancy rates of red fox and Pallas’s cat at each camera-trapping site. We performed Wilcoxon rank-sum tests to compare red fox and Pallas’s cat occupancy differences between WF and non-WF areas, based on the occupancy rates of camera-trap sites. The Wilcoxon rank-sum tests using the *wilcoxTest* function from the “car” package (Fox and Weisberg, 2018).

Finally, we assessed the spatial overlap between red fox and Pallas’s cat using Pianka’s O index (O_{jk}) in WF and non-WF areas. The index was calculated for WF and non-WF groups separately, using red fox and Pallas’s cat occupancy rates from all camera-trapping sites within each group as input vectors (Pianka, 1973; Xu et al., 2024). We estimated the 95 % confidence intervals using 1000 bootstrap replicates of niche overlap between the two species. The analysis was conducted using the “spaa” package in R version 4.0.3 (Zhang, 2016; Gotelli, 2000).

2.3.2. Temporal analysis

To analyze the daily activity patterns of red foxes and Pallas’s cats, we generated activity density curves for both species in WF and non-WF areas to visualize and compare their daily activities. And used $\Delta 4$ to describe temporal overlap coefficients between red foxes and Pallas’s cats, which calculated using the overlap area based on the kernel density curves of two species density functions (Ridout and Linkie, 2009). We used the timestamps from independent events and transformed them into “solar time” in radians to account for seasonal variations in day length (Vazquez et al., 2019). The conversion to solar time was calculated using the *sunTime* function from the “overlap” package (Ridout and Linkie, 2009), and activity curves were calculated using the *fitact* function from the “activity” package (Rowcliffe et al., 2014). We then used the *compareCkern* function from the “overlap” package to compute the temporal overlap coefficients $\Delta 4$ between red fox and Pallas’s cat separately of WF and non-WF areas. We estimated the 95 % confidence intervals using 1000 bootstrap samples (Ridout and Linkie, 2009). Finally, we compared the percentage change in overlap coefficients between WF and non-WF areas, with values ranging from 0 (no overlap) to 1 (complete overlap). To further explore the potential reasons for the differences in activity patterns between red fox and Pallas’s cat in WF and non-WF areas, we analyzed the activity curves of their main prey (rat and Pallas’s Sandgrouse), as well as those of humans and livestock in both areas. We also computed the overlap between carnivores and these groups to identify potential drivers of the observed differences.

To further evaluate the differences in diurnal, nocturnal, and

crepuscular activity probabilities for red fox and Pallas’s cat in WF and non-WF areas, we calculated the activity probabilities using the Bayesian probabilistic multinomial modeling approach developed by Gerber et al. (2024) and implemented in the “Diel.Niche” package. We defined these periods based on available light at each camera trap location (Ensing et al., 2014; Hut et al., 2013). Specifically, daytime was classified as the period between the end of the morning astronomical dawn and the beginning of the astronomical dusk, while nighttime was defined as the interval from the end of the astronomical dusk to the start of the astronomical dawn. The remaining periods were categorized as dawn and dusk. We used the “Suncalc” package to calculate the solar angle, and categorize each independent event as daytime, nighttime, or twilight (Smith et al., 2024; Thieumel et al., 2019). The diel niche model was fitted using three Markov chains with 5000 iterations each, discarding the first 1000 as burn-in.

2.3.3. Dietary analysis

To evaluate the trophic niche partitioning of red fox and Pallas’s cat in WF and non-WF areas, we constructed a food web network using the “bipartite” R package (Dormann et al., 2008) and quantified dietary niche overlap using Pianka’s O index (O_{jk}). We determined the food composition by calculating the relative read abundance (RRA) (Shao et al., 2021). Food niche width was calculated using Levin’s index, and interspecific diel activity overlap was evaluated using O_{jk} . We analyzed the differences in RRA-based dietary composition between red fox and Pallas’s cat using permutational multivariate analysis of variance (perMANOVA) with 9999 permutations (implemented in the *adonis* function) and visualized the results using non-metric multidimensional scaling (NMDS) based on Bray-Curtis dissimilarity (Oksanen et al., 2013).

3. Results

Across 164 camera-trapping sites (excluding 17 sites due to equipment loss or damage), we recorded 13,156 independent events over 22,854 effective camera days. We documented 62 independent events of Pallas’s cats, 840 events of red foxes, 327 events of humans, 795 events of prey (777 events of rats and 18 events of Pallas’s sandgrouse) and 4609 events of livestock (Table 1). From 96 suspected carnivorous fecal samples, fecal DNA analysis yielded 62 usable samples (excluding 6 *Buteo lagopus*, 5 *Felis silvestris*, 8 uncertain samples and 15 samples with insufficient quantities for sequencing). These samples included 32 from red foxes and 30 from Pallas’s cats (Table 1).

3.1. Spatial niche partitioning

We evaluated spatial niche partitioning by comparing occupancy rates between WF and non-WF areas. Spatial analysis showed that red foxes and Pallas’s cats had distinct habitat preferences (Table S1). Results from single-species, single-season occupancy models indicated that red fox exhibited a significantly higher overall occupancy probability (estimated at 0.829 ± 0.10) compared to the Pallas’s cat (estimated occupancy probability of 0.414 ± 0.271). Based on the optimal model ($\Delta AIC \leq 2$), it was found that the occupancy rate of the red fox was influenced by vegetation cover and livestock encounter rate (Fig. 3, Table S2). Specifically, the occupancy rate decreased with an increase in the NDVI and was positively correlated with the livestock RAI (Fig. 3, Table S2). The Pallas’s cat occupancy rate was influenced by livestock encounter rate, wind turbine density, road density, and prey availability. For the Pallas’s cat, the occupancy rate decreased with increases in livestock RAI, RKD, and TKD but increased with higher prey RAI (Fig. 3, Table S2). The Wilcoxon rank-sum test revealed no significant difference in the occupancy rate between the red fox and Pallas’s cat in both the WF and non-WF regions (Fig. S1). Spatial overlap indices (Pianka’s index) were similar between WF (0.833, 95 % CI: 0.798–0.869) and non-WF areas (0.859, 95 % CI: 0.827–0.891), with no statistically significant

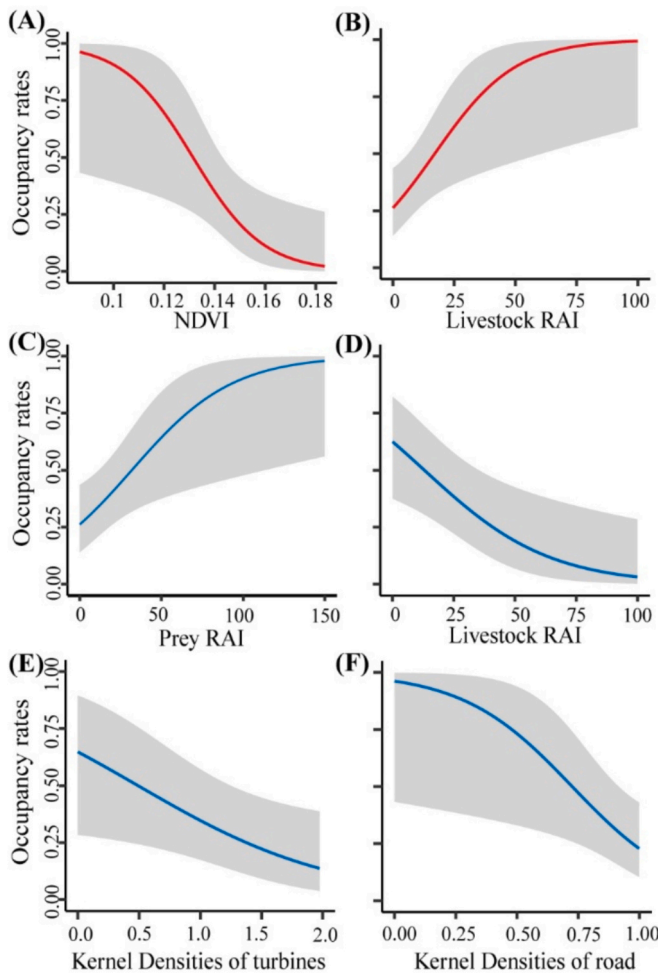


Fig. 3. The curve illustrates the relationship between the species occupancy rates and covariates derived from the optimal model ($\Delta AIC \leq 2$). The red curves depict the associations between red fox occupancy and covariates (A–B), while the blue curves represent the relationships between Pallas's cat occupancy and covariates (C–F). The solid line denotes the fitted polynomial regression, and the grey region represents the 95 % confidence interval. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

difference (Fig. 4).

3.2. Temporal niche partitioning

We assessed temporal niche partitioning through activity pattern analysis. There were some differences in activity patterns between red foxes and Pallas's cats under WF disturbances. In non-WF areas, both species exhibited similar activity patterns with a high overlap coefficient ($\Delta 4 = 0.81$, 95 % CI: 0.79–0.95, $p = 0.82$) and peak activity occurring at dawn and dusk (Figs. 4, 5). In contrast, within WF areas ($\Delta 4 = 0.76$, 95 % CI: 0.64–0.88, $p = 0.06$), Pallas's cats shifted their activity peak to the midnight (22:00–24:00), reducing dawn activity, while red fox activity patterns remained largely unchanged (Figs. 4, 5).

Further analysis using diel niche models revealed that both red foxes and Pallas's cats exhibited cathemeral activity patterns (active at multiple times of the day) in WF and non-WF areas (Fig. S2). The red fox showed the highest nocturnal activity levels in both WF and non-WF areas, with activity probabilities of 0.482 (95 % CI = 0.421–0.543) in WF areas and 0.408 (95 % CI = 0.369–0.447) in non-WF areas (Fig. 6). In contrast, Pallas's cats were more crepuscular in non-WF regions, with a twilight activity probability of 0.416 (95 % CI = 0.253–0.588), while

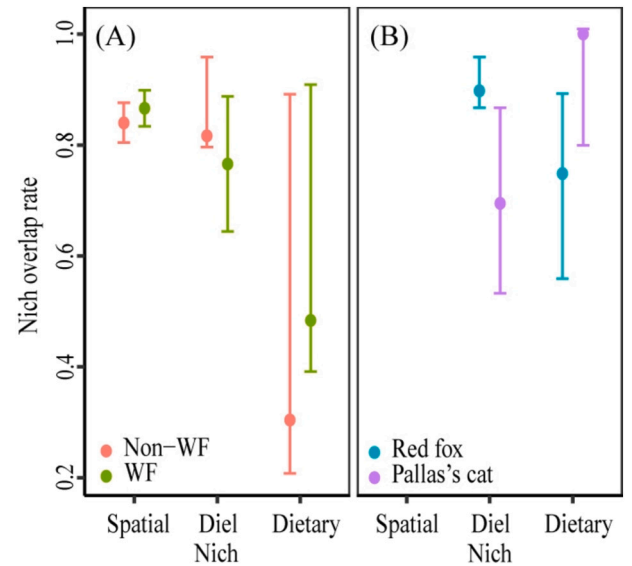


Fig. 4. The intraspecific and interspecific spatial overlap (Pianka's index), temporal activity overlap ($\Delta 4$ overlap coefficient), dietary overlap (Pianka's index) and confidence intervals of red foxes and Pallas's cats in wind farm (WF) and non-wind farm (non-WF) areas. (A) Interspecific niche overlap between red foxes and Pallas's cats in WF and non-WF areas; (B) Intraspecific niche overlap between WF and non-WF areas for each species.

their nocturnal activity increased in WF areas, reaching a probability of 0.513 (95 % CI = 0.354–0.669) (Fig. S3, Table 2). Compared to non-WF, prey and livestock grazing activity patterns in WF showed less temporal variation with prey being predominantly nocturnal and grazing activities occurring more frequently during the day, from sunrise to sunset. Human activity density was higher during daytime in WF areas.

3.3. Trophic niche partitioning

We identified 17 prey taxa from 62 samples, representing 8 taxonomic orders of vertebrates, with 15 identified at the species level, one at the genus level, and one at the family level. These included 10 mammal species, two bird species, two reptile species, and three livestock species. In both WF and non-WF areas, Pallas's cats primarily consumed Cricetidae species (56.19 % in WF and 59.47 % in non-WF areas), followed by livestock (13.33 % in WF areas and 16.75 % in non-WF areas) and Middy jirds (13.91 % in WF areas and 12.91 % in non-WF areas) (Fig. 7). Red foxes, on the other hand, primarily consumed livestock (38.38 %) and Pallas's Sandgrouse (29.07 %) in non-WF areas. In WF areas, their diet shifted to include more Middy jirds (17.93 %), livestock (14.2 %), and Pallas's Sandgrouse (13.0 %) (Fig. 7). Among these, livestock detected in both WF and non-WF areas exclusively comprised sheep and Bactrian camels. In WF areas, sheep accounted for 73.17 % of Pallas's cats livestock consumed versus 26.83 % for Bactrian camels. This proportion was 74.00 % versus 26.00 % in non-WF areas. For red foxes in WF areas, the ratio was 70.60 % versus 29.40 %, and 53.21 % versus 46.79 % in non-WF areas.

Trophic niche overlap between red foxes and Pallas's cats was higher in WF areas ($Ojk = 0.482$, 95 % CI: 0.391–0.901) compared to non-WF areas ($Ojk = 0.305$, 95 % CI: 0.21–0.884) (Fig. 4). Dietary differences were more pronounced in non-WF areas, as shown by perMANOVA and NMDS analyses (Fig. 7). The Levin index revealed that red foxes had a narrower trophic niche width in WF areas (2.64 ± 1.66) compared to non-WF areas (3.57 ± 1.62), while Pallas's cats exhibited a slightly narrower niche width in WF areas (1.53 ± 0.45) compared to non-WF areas (1.84 ± 0.62).

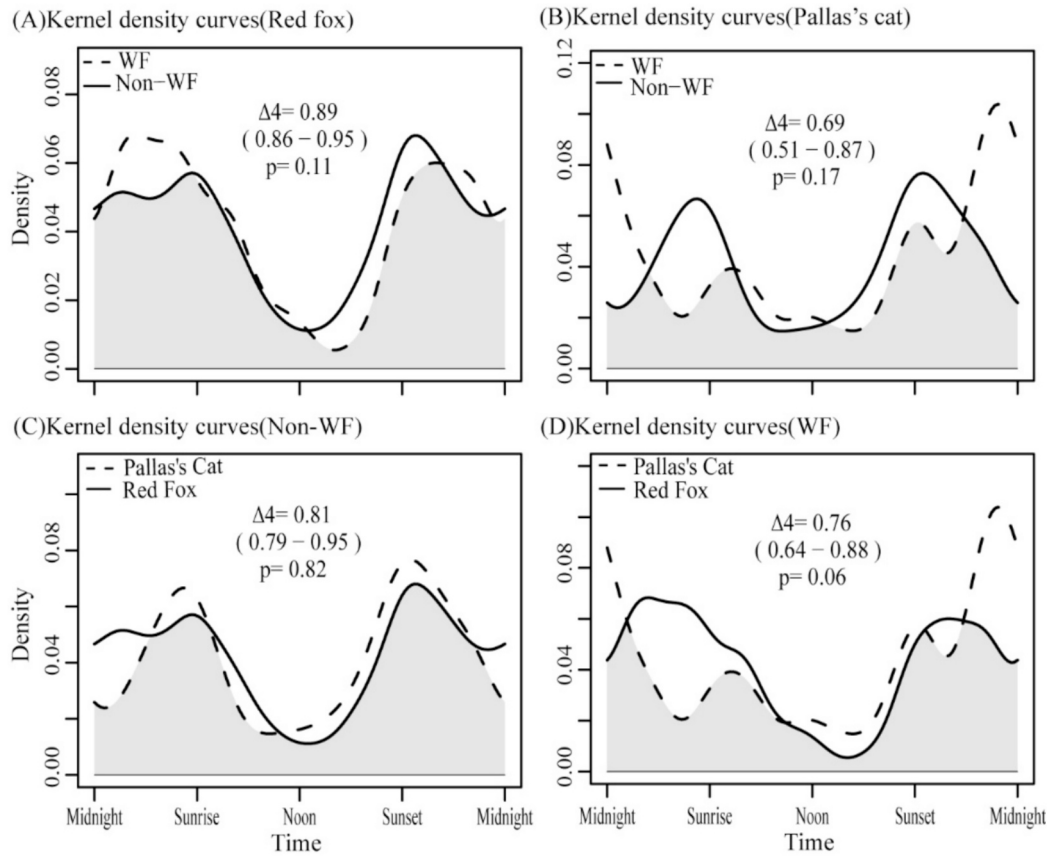


Fig. 5. Kernel density curves depicting the daily activity patterns of red foxes and Pallas's cats in wind farm (WF) and non-wind farm (non-WF) areas. The shaded represents the temporal overlap between the two distributions, and the area represents the overlap coefficient ($\Delta 4$). The P-value was obtained from the Wald test.

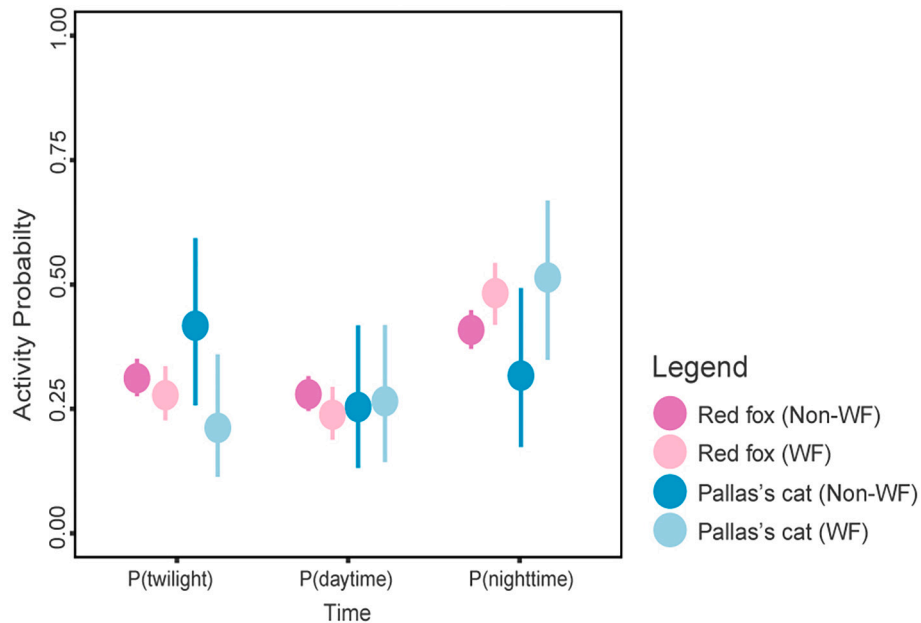


Fig. 6. Estimated activity probabilities from diel niche model of red foxes and Pallas's cats.

4. Discussion

Our study demonstrates that multidimensional niche partitioning may be essential for understanding the competition and coexistence between red foxes and Pallas's cats in response to WF disturbances. As

expected, our results support the hypothesis that trophic niche overlap between these carnivores is higher in WF areas than in non-WF areas. Concurrently, Pallas's cats exhibited a temporal shift toward deeper nocturnal activity to avoid human presence. This behavioral adjustment reduced temporal niche overlap with red foxes, likely constituting the

Table 2
Temporal activity overlap ($\Delta 4$ overlap coefficient) and confidence intervals of red foxes and Pallas's cats with prey, human and livestock in wind farm (WF) and non-wind farm (non-WF) areas.

	Red fox		Pallas's cat	
	Non-WF	WF	Non-WF	WF
Prey	0.61 (0.54–0.64)	0.65 (0.56–0.69)	0.54 (0.37–0.68)	0.63 (0.43–0.71)
Human	0.43 (0.31–0.46)	0.55 (0.45–0.59)	0.44 (0.25–0.53)	0.56 (0.40–0.70)
Livestock	0.49 (0.45–0.52)	0.46 (0.39–0.50)	0.52 (0.35–0.67)	0.46 (0.32–0.62)

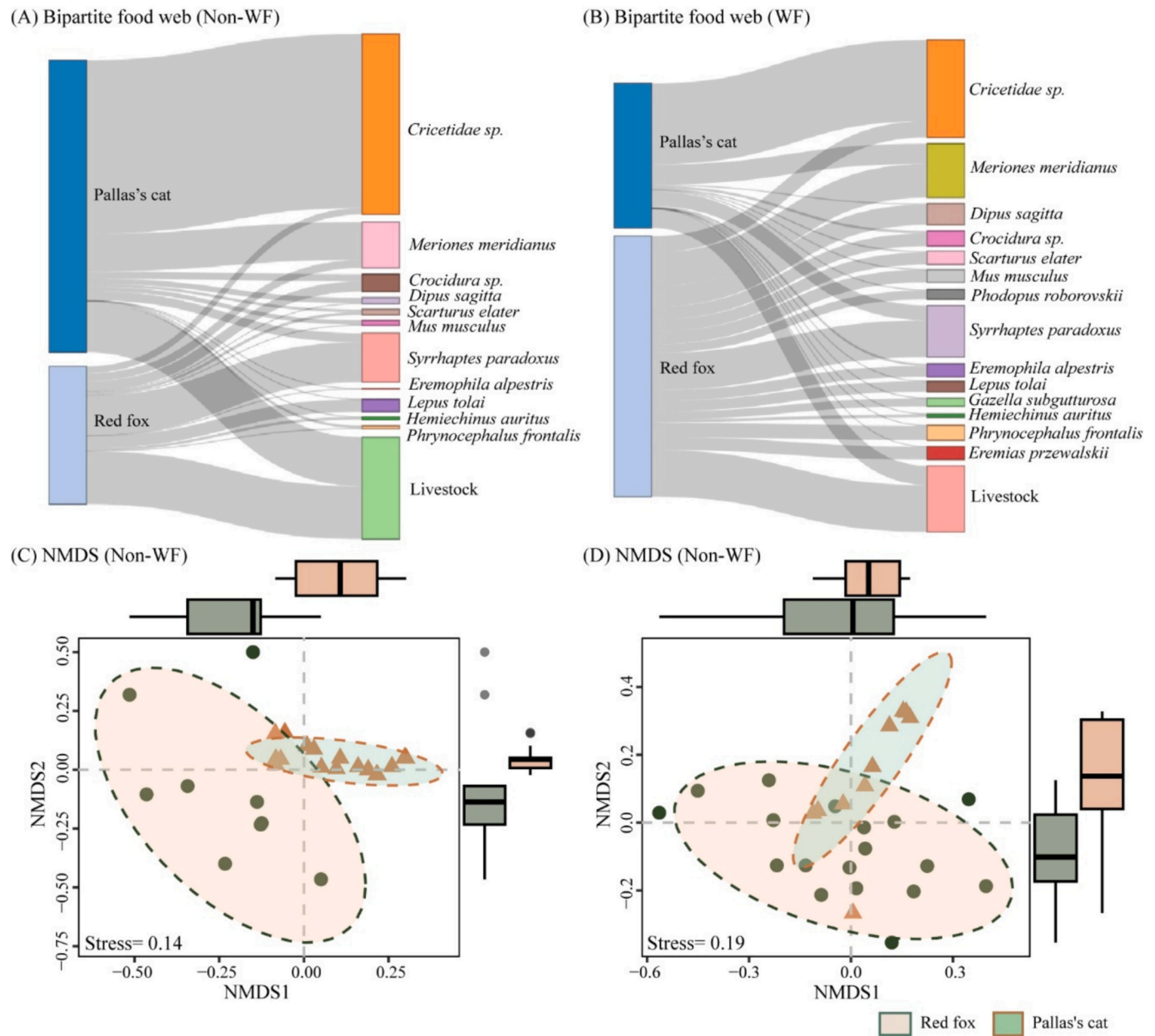


Fig. 7. Dietary niche partitioning among red foxes and Pallas's cats in wind farm (WF) and non-wind farm (non-WF) areas. At the top, bipartite food webs are depicted for both WF and non-WF areas (A–B). Below is the NMDS of RRA-based Bray-Curtis dissimilarity between red foxes and Pallas's cats in both areas (C–D).

core mechanism enabling their coexistence in WF areas. This result highlights the need for conservation strategies that consider both spatial, temporal and trophic niche dynamics, and strategic placement of WFs and management of prey resources may help mitigate these impacts and promote coexistence.

WF disturbances had distinct spatial effects on red foxes and Pallas's cats, driven by the differences in their ecological traits and responses to

human activities. Red foxes preferred areas with higher livestock encounter rates, demonstrating their adaptability to anthropogenic environments, potentially mediated by exploitation of anthropogenic food subsidies associated with grazing practices. In contrast, Pallas's cats preferred habitats rich in prey and low in human disturbance, avoiding areas with high road and turbine densities. These findings align with previous research highlighting the sensitivity of Pallas's cats to habitat

fragmentation and human activity (Ross et al., 2010a, 2020). Nevertheless, spatial overlap analysis revealed no significant difference in the overlap between WF and non-WF areas. This may be due to WF management practices, such as fencing and road maintenance, which reduce livestock abundance in the area, while red foxes are more likely to occupy the regions with livestock grazing. The prey distribution may be crucial in shaping the spatial patterns of both species. This suggests that while WF disturbances influence habitat preferences, spatial niche differentiation is minimized by factors such as prey availability, livestock distribution, and habitat conditions in both WF and non-WF areas. Conservation strategies should prioritize the management of prey resources to reduce competition and promote coexistence in WF areas. Ensuring sufficient prey availability is essential for maintaining stable populations and reducing human-wildlife conflict.

Besides the spatial niche dynamics, temporal niche adjustments also emerged as a critical adaptive strategy for Pallas's cats under WF disturbances, where daytime human activity has significantly increased because of turbine maintenance and improved road accessibility. Their increased midnight activity reduces the temporal overlap with red foxes and better aligns with the activity patterns of their prey. In contrast, red foxes maintained their mainly nocturnal activity patterns in both WF and non-WF areas, demonstrating higher tolerance to human disturbances. These results support previous research suggesting that mammals often become more nocturnal in response to human activity (Gaynor et al., 2018). These results support our hypothesis that WF disturbances drive temporal niche segregation, allowing Pallas's cats to reduce direct competition with red foxes. This suggests that temporal niche shifts may be a critical adaptive mechanism for Pallas's cats to coexist with red foxes under WF disturbances. However, the increased temporal overlap between carnivores and humans in WF areas may intensify stress and degrade habitat quality for sensitive species like Pallas's cats. Future management should strive to minimize human activity during the key periods of carnivore activity to maintain temporal niche dynamics.

In the trophic niche, our results revealed higher niche overlap between red foxes and Pallas's cats in WF areas compared to non-WF areas. This pattern likely stems from prey community disruption caused by WF disturbances. Supporting this, two of the four WF sites exhibited lower prey RAI than paired non-WF sites. Furthermore, grazing restrictions within WFs limited red foxes' access to anthropogenic food subsidies, forcing both species to rely on depauperate prey communities in WF areas. Consequently, the increased trophic niche overlap indicates heightened resource competition potential. Notably, red foxes consumed more livestock in non-WF areas with higher livestock RAI, highlighting their generalist foraging strategy and adaptability to human-modified landscapes (Hoffmann and Sillero-Zubiri, 2021). Conversely, Pallas's cats maintained a specialized diet mainly consisting of Cricetidae species, consistent with their ecological traits as dietary specialists (Ross et al., 2010b). Such dietary specialization is known to make species more vulnerable to environmental changes (Boyles et al., 2007). Livestocks like sheep and Bactrian camels, constituted 13.33–16.75 % of Pallas's cat diets. We hypothesize that this derives from scavenging on carcasses from geographically induced mortality (e.g., falls/injuries), a behavior potentially shared by foxes. Our trophic analysis underscores that prey resource management may be imperative for balancing WF development with carnivore conservation.

As discussed above, the niche partitioning mechanisms between red foxes and Pallas's cats under WF disturbance exhibit complex interdependencies across temporal, spatial, and trophic dimensions. Our results demonstrate that when WF disturbances constrain trophic niche availability through prey resource reduction, these carnivores alleviate competitive pressure by temporal niche differentiation. Consistent with existing frameworks, anthropogenic disturbances that limit one niche dimension often trigger compensatory shifts in other dimensions to facilitate coexistence among competing carnivores (Manlick and Pauli, 2020; Smith et al., 2024). This restructuring of interspecific niche

partitioning is mediated by disturbance intensity, species-specific behavioral adaptations, and prey supply dynamics (Chen et al., 2023; Penjor et al., 2022; Smith et al., 2024). However, these different strategies reduce the competition between the two mesocarnivore species and highlight potential vulnerabilities, especially for species with specialized diets. As global energy transition accelerates, these multidimensional insights become critically important for balancing climate solutions with biodiversity conservation imperatives.

Grassland and desert ecosystems, with their high wind potential and low human population density, are increasingly being targeted for wind energy development. Concurrently, in our study, the Pallas's cat is endemic to the grasslands and deserts of Central Asia (Ross et al., 2020), and exhibits greater vulnerability to WF impacts than red fox which more tolerant to human disturbance. Although widely distributed across Central Asia, the overall population density of Pallas's cats remains low (Ross et al., 2020). Studies utilizing radio collars and camera traps have reported densities ranging from 4 to 15 per 100 km² (Ross et al., 2010a; Anile et al., 2021). This species is particularly sensitive to habitat fragmentation and anthropogenic disturbance (Ross et al., 2019), relying critically on intact habitat structure and stable prey availability. To mitigate extinction risks, we propose strategic WF siting that avoids core habitats of viable Pallas's cat populations during planning phases. Concurrently, implement ecological restoration through revegetation of temporarily disturbed zones and comprehensive construction waste removal, ensuring prey population recovery. Finally, enforce strict access control via road surveillance systems to restrict non-essential personnel entry within WF perimeters.

5. Conclusion

This study highlights the multifaceted effects of WF disturbances on niche partitioning among sympatric carnivore species, revealing distinct yet interconnected adaptive strategies. While our study highlights the impact of WFs, other factors such as climate change and disease prevalence could also influence these patterns. However, given the spatial and temporal consistency of our findings, we believe that WF disturbances are the primary driver. Under the disturbance, the reduction of potential prey resources may increase trophic niche overlap between Pallas's cats and red foxes. However, the temporal avoidance of human activities by Pallas's cats has reduced the temporal niche overlap with red foxes, thereby facilitating coexistence between these species within WF areas. These results highlight the complex balance between competition and coexistence in human-altered landscapes. Moreover, they also emphasize the importance of considering multidimensional niche dynamics in conservation planning and WF management. By integrating habitat preservation, prey management, and strategic WF placement, this study offers a novel approach to balancing renewable energy development with biodiversity conservation, providing actionable insights for future conservation efforts. Future research should focus on long-term monitoring of WF impacts on wildlife communities. Conservation strategies should prioritize habitat preservation and prey management to mitigate the effects of renewable energy development.

CRedit authorship contribution statement

Mingshuo Qin: Writing – review & editing, Writing – original draft, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Wenhong Xiao:** Writing – review & editing, Project administration, Methodology, Formal analysis, Conceptualization. **Xinyue Xia:** Methodology, Investigation, Data curation, Conceptualization. **Kai Xu:** Writing – review & editing, Writing – original draft, Methodology, Formal analysis. **Dazhao Song:** Methodology, Investigation, Conceptualization. **Zhishu Xiao:** Writing – review & editing, Project administration, Methodology, Funding acquisition, Conceptualization.

Declaration of competing interest

The authors declare that they have no competing interests.

Acknowledgments

We appreciate the support from the National Key Research and Development Program of China (2022YFF1301401), Initiative Scientific Research Program, Institute of Zoology, CAS (2024IOZ0105), and the China Biodiversity Monitoring and Research Network (Sino BON-Mammals). We would like to thank Mr. Qi Li, Xin Zhen and other colleagues of Chinese Felid Conservation Alliance for their generous assistance in the field surveys.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.biocon.2025.111458>.

Data availability

Data will be made available on request.

References

- Anile, S., Augugliaro, C., Munkhtsog, B., et al., 2021. Density and activity patterns of Pallas's cats, *Otocolobus manul*, in central Mongolia. *Wildl. Res.* 48, 264–272.
- Avrin, A.C., Pekins, C.E., Wilmers, C.C., Sperry, J.H., Allen, M.L., 2023. Can a mesocarnivore fill the functional role of an apex predator? *Ecosphere* 14. <https://doi.org/10.1002/ecs2.4383>.
- Blasković, S., Gomercić, T., Topličanec, I., Sindićić, M., 2022. Temporal overlap of human and apex predator activity on wildlife trails and forest roads. *J. Vertebr. Biol.* 71, 22029.22021-22029.
- Boyles, J.G., Storm, J.J., Will, C., 2007. The perils of picky eating: dietary breadth is related to extinction risk in insectivorous bats. *PLoS ONE* 2, e672.
- Bu, H., Wang, F., McShea, W.J., Lu, Z., Wang, D., Li, S., 2016. Spatial co-occurrence and activity patterns of mesocarnivores in the temperate forests of Southwest China. *PLoS One* 11, e0164271. <https://doi.org/10.1371/journal.pone.0164271>.
- Chen, Y., Liu, B., Fan, D., Li, S., 2023. Temporal response of mesocarnivores to human activity and infrastructure in Taihang Mountains, Central North China: shifts in activity patterns and their overlap. *Animals* 13. <https://doi.org/10.3390/ani13040688>.
- Creel, S., Matandiko, W., Schuette, P., et al., 2018. Changes in African large carnivore diets over the past half-century reveal the loss of large prey. *J. Appl. Ecol.* 55, 2908–2916.
- Deuel, N.R., Conner, L.M., Miller, K.V., Chamberlain, M.J., Cherry, M.J., Tannenbaum, L. V., 2017. Habitat selection and diurnal refugia of gray foxes in Southwestern Georgia, USA. *PLoS One* 12, e0186402. <https://doi.org/10.1371/journal.pone.0186402>.
- Dormann, C.F., Gruber, B., Fründ, J., 2008. Introducing the bipartite package: analysing ecological networks. *Interaction* 1 (0.2413793), 8–11.
- Ensing, E.P., Ciuti, S., de Wijs, F.A., et al., 2014. GPS based daily activity patterns in European red deer and North American elk (*Cervus elaphus*): indication for a weak circadian clock in ungulates. *PLoS ONE* 9, e106997. <https://doi.org/10.1371/journal.pone.0106997>.
- Ferrão da Costa, G., Paula, J., Petrucci-Fonseca, F., Álvares, F., 2018. The indirect impacts of wind farms on terrestrial mammals: insights from the disturbance and exclusion effects on wolves (*Canis lupus*). In: *Biodiversity and Wind Farms in Portugal*, pp. 111–134.
- Fiske, I., Chandler, R., 2011. Unmarked: an R package for fitting hierarchical models of wildlife occurrence and abundance. *J. Stat. Softw.* 43, 1–23.
- Fox, J., Weisberg, S., 2018. *An R Companion to Applied Regression*: Sage Publications. Sage publications.
- Gaynor, K.M., Hohnowski, C.E., Carter, N.H., Brashares, J.S., 2018. The influence of human disturbance on wildlife nocturnality. *Science* 360, 1232–1235. <https://doi.org/10.1126/science.aar7121>.
- Gerber, B.D., Devarajan, K., Farris, Z.J., Fidino, M., 2024. A model-based hypothesis framework to define and estimate the diel niche via the “Diel.Niche” R package. *J. Anim. Ecol.* 93, 132–146. <https://doi.org/10.1111/1365-2656.14035>.
- Goldstein, B.R., Jensen, A.J., Kays, R., et al., 2024. Guidelines for estimating occupancy from autocorrelated camera trap detections. *Methods Ecol. Evol.* 5 (7), 1177–1191.
- Gotelli, N.J., 2000. Null model analysis of species co-occurrence patterns. *Ecology* 81, 2606–2621.
- Hardin, G., 1960. The competitive exclusion principle: an idea that took a century to be born has implications in ecology, economics, and genetics. *Science* 131, 1292–1297.
- Hoffmann, M., Sillero-Zubiri, C., 2021. *Vulpes vulpes* (Amended Version of 2016 Assessment). The IUCN Red List of Threatened Species, 2021, e. T23062A193903628.

- Hut, R.A., Paolucci, S., Dor, R., Kyriacou, C.P., Daan, S., 2013. Latitudinal clines: an evolutionary view on biological rhythms. *Proc. R. Soc. B Biol. Sci.* 280, 20130433. <https://doi.org/10.1098/rspb.2013.0433>.
- Li, Z., Wang, T., Smith, J.L.D., et al., 2019. Coexistence of two sympatric flagship carnivores in the human-dominated forest landscapes of Northeast Asia. *Landsc. Ecol.* 34, 291–305.
- Lin, X., Wu, K., Shi, L., 2010. Food habitats of the red fox (*Vulpes vulpes*) in the Junggar Basin Desert [in Chinese]. *Acta Theriol. Sin.* 30, 346.
- Llaneza, L., Szatarnil, V., López-Bao, J.V., 2018. The importance of fine-scale breeding site selection patterns under a landscape-sharing approach for wolf conservation. *Biodivers. Conserv.* 27, 1239–1256.
- Lopucki, R., Perzanowski, K., 2018. Effects of wind turbines on spatial distribution of the European hamster. *Ecol. Indic.* 84, 433–436.
- Lowry, H., Lill, A., Wong, B.B., 2013. Behavioural responses of wildlife to urban environments. *Biol. Rev.* 88, 537–549. <https://doi.org/10.1111/brv.12012>.
- Ma, Y., Chu, B., Ye, G., et al., 2024. Spatio-temporal overlap of dominant rodents and their predators in desert steppe of Qilian Mountains [in Chinese]. *Chin. J. Grassl. Turf* 44. <https://doi.org/10.13817/j.cnki.cyyyp.2024.06.008>.
- MacKenzie, D.I., Nichols, J.D., Lachman, G.B., Droege, S., Andrew Royle, J., Langtimm, C.A., 2002. Estimating site occupancy rates when detection probabilities are less than one. *Ecology* 83, 2248–2255.
- Manlick, P.J., Pauli, J.N., 2020. Human disturbance increases trophic niche overlap in terrestrial carnivore communities. *Proc. Natl. Acad. Sci.* 117, 26842–26848. <https://doi.org/10.1073/pnas.2012774117>.
- Moreira-Arce, D., Vergara, P.M., Boutin, S., Simonetti, J.A., Briceño, C., Acosta-Jamett, G., 2015. Native forest replacement by exotic plantations triggers changes in prey selection of mesocarnivores. *Biol. Conserv.* 192, 258–267. <https://doi.org/10.1016/j.biocon.2015.09.015>.
- Mueller, M.A., Drake, D., Allen, M.L., 2018. Coexistence of coyotes (*Canis latrans*) and red foxes (*Vulpes vulpes*) in an urban landscape. *PLoS One* 13, e0190971.
- Munkhzul, T., Murdoch, J.D., Samjaa, R., Reading, R.P., 2012. Home range characteristics of corsac and red foxes in Mongolia. *Erforschung Biologischer Ressourcen Mongolei (Halle/Saale)* 12, 93–104.
- O'Brien, T.G., 2011. Abundance, density and relative abundance: a conceptual framework. In: O'Connell, A.F., Nichols, J.D., Karanth, K.U. (Eds.), *Camera Traps in Animal Ecology: Methods and Analyses*. Springer Japan, Tokyo, pp. 71–96.
- O'Brien, T.G., Kinnaird, M.F., Wibisono, H.T., 2003. Crouching tigers, hidden prey: Sumatran tiger and prey populations in a tropical forest landscape. *Anim. Conserv.* 6, 131–139.
- Oksanen, J., Blanchet, F.G., Kindt, R., et al., 2013. Package “Vegan”. *Community Ecology Package, Version*, vol. 2, pp. 1–295.
- Palencia, P., Vicente, J., Soriguer, R.C., Acevedo, P., 2021. Towards a best-practices guide for camera trapping: assessing differences among camera trap models and settings under field conditions. *J. Zool.* 316, 197–208. <https://doi.org/10.1111/jzo.12945>.
- Penjor, U., Astaras, C., Cushman, S.A., Kaszta, Z., Macdonald, D.W., 2022. Contrasting effects of human settlement on the interaction among sympatric apex carnivores. *Proc. R. Soc. B* 289, 20212681. <https://doi.org/10.1098/rspb.2021.2681>.
- Pianka, E.R., 1973. The structure of lizard communities. *Annu. Rev. Ecol. Syst.* 53–74.
- Prugh, L.R., Stoner, C.J., Epps, C.W., Bean, W.T., Ripple, W.J., Laliberte, A.S., Brashares, J.S., 2009. The rise of the mesopredator. *Bioscience* 59, 779–791. <https://doi.org/10.1525/bio.2009.59.9.9>.
- R Core Team, R., 2013. *R: A Language and Environment for Statistical Computing*. Ridout, M.S., Linkie, M., 2009. Estimating overlap of daily activity patterns from camera trap data. *J. Agric. Biol. Environ. Stat.* 14, 322–337.
- Roemer, G.W., Gompper, M.E., Van Valkenburgh, B., 2009. The ecological role of the mammalian mesocarnivore. *Bioscience* 59, 165–173. <https://doi.org/10.1525/bio.2009.59.2.9>.
- Ross, S., Kamnitzer, R., Munkhtsog, B., Harris, S., 2010a. Den-site selection is critical for Pallas's cats (*Otocolobus manul*). *Can. J. Zool.* 88, 905–913. <https://doi.org/10.1139/z10-056>.
- Ross, S., Munkhtsog, B., Harris, S., 2010b. Dietary composition, plasticity, and prey selection of Pallas's cats. *J. Mammal.* 91, 811–817. <https://doi.org/10.1644/09-mamm-a-342.1>.
- Ross, S., Munkhtsog, B., Harris, S., 2012. Determinants of mesocarnivore range use: relative effects of prey and habitat properties on Pallas's cat home-range size. *J. Mammal.* 93, 1292–1300. <https://doi.org/10.1644/11-mamm-a-060.1>.
- Ross, S., Barashkova, A., Kirilyuk, V., Naidenko, S., 2019. The behaviour and ecology of the manul. *Cat News* 9–13.
- Ross, S., Barashkova, A., Dhendup, T., Munkhtsog, Moqanaki, E., 2020. *Otocolobus manul* (errata version published in 2020). In: *The IUCN Red List of Threatened Species*.
- Rowcliffe, J.M., Kays, R., Kranstauber, B., Carbone, C., Jansen, P.A., Fisher, D., 2014. Quantifying levels of animal activity using camera trap data. *Methods Ecol. Evol.* 5, 1170–1179. <https://doi.org/10.1111/2041-210x.12278>.
- Samia, D.S., Nakagawa, S., Nomura, F., Rangel, T.F., Blumstein, D.T., 2015. Increased tolerance to humans among disturbed wildlife. *Nat. Commun.* 6, 8877. <https://doi.org/10.1038/ncomms9877>.
- Schaller, G.B., Junrang, R., Mingjiang, Q., 1988. Status of the snow leopard *Panthera uncia* in Qinghai and Gansu Provinces, China. *Biol. Conserv.* 45, 179–194.
- Schoener, T.W., 1974. Resource partitioning in ecological communities: research on how similar species divide resources helps reveal the natural regulation of species diversity. *Science* 185, 27–39.
- Shao, X., Lu, Q., Xiong, M., et al., 2021. Prey partitioning and livestock consumption in the world's richest large carnivore assemblage. *Curr. Biol.* 31 (4887–4897), e4885. <https://doi.org/10.1016/j.cub.2021.08.067>.

- Skarin, A., Sandstrom, P., Alam, M., 2018. Out of sight of wind turbines-reindeer response to wind farms in operation. *Ecol. Evol.* 8, 9906–9919.
- Smith, A.F., Kasper, K., Lazzeri, L., et al., 2024. Reduced human disturbance increases diurnal activity in wolves, but not Eurasian lynx. *Glob. Ecol. Conserv.* 53. <https://doi.org/10.1016/j.gecco.2024.e02985>.
- Snow Leopard Network, 2014. Snow Leopard Survival Strategy. Seattle, Washington, USA, vol. 1, p. 145.
- Sogbohossou, E.A., Kassa, B.D., Waltert, M., Khorozyan, I., 2018. Spatiotemporal niche partitioning between the African lion (*Panthera leo leo*) and spotted hyena (*Crocuta crocuta*) in western African savannas. *Eur. J. Wildl. Res.* 64 (1).
- Steinmetz, R., Seuaturien, N., Intanajitjuy, P., Inrueang, P., Prempre, K., 2021. The effects of prey depletion on dietary niches of sympatric apex predators in Southeast Asia. *Integr. Zool.* 16, 19–32. <https://doi.org/10.1111/1749-4877.12461>.
- Stillfried, M., Belant, J.L., Svoboda, N.J., Beyer, D.E., Kramer-Schadt, S., 2015. When top predators become prey: black bears alter movement behaviour in response to hunting pressure. *Behav. Process.* 120, 30–39.
- Thieurmel, B., Elmarhraoui, A., Thieurmel, M.B., 2019. Package “Suncalc”. R Package Version 0.5.
- Tian, J., Zou, Q., Zhang, M., Hu, C., Khattak, R.H., Su, H., 2022. Spatial and temporal differentiation are not distinct but are covariant for facilitating coexistence of small and medium-sized carnivores in Southwestern China. *Glob. Ecol. Conserv.* 34. <https://doi.org/10.1016/j.gecco.2022.e02017>.
- Tucker, M.A., Böhning-Gaese, K., Fagan, W.F., et al., 2018. Moving in the Anthropocene: global reductions in terrestrial mammalian movements. *Science* 359 (6374), 466–469.
- Vazquez, C., Rowcliffe, J.M., Spoelstra, K., Jansen, P.A., Ellison, A., 2019. Comparing diel activity patterns of wildlife across latitudes and seasons: time transformations using day length. *Methods Ecol. Evol.* 10, 2057–2066. <https://doi.org/10.1111/2041-210x.13290>.
- Wang, D., Sai, Q., Wang, Z., Zhao, H., Lian, X., 2022. Spatiotemporal overlap among sympatric Pallas’s cat (*Otocolobus manul*), Tibetan fox (*Vulpes ferrilata*) and red fox (*V. vulpes*) in the source region of the Yangtze River [in Chinese]. *Biodivers. Sci.* 30, 21365.
- Wang, G., Zhao, Z., Tong, W., 2022. Construction and application of decision support indicator system for new energy development in Hexi Corridor. *Energy Rep.* 8, 187–193.
- Xiao, W., Hebblewhite, M., Robinson, H., et al., 2018. Relationships between humans and ungulate prey shape Amur tiger occurrence in a core protected area along the Sino-Russian border. *Ecol. Evol.* 8, 11677–11693.
- Xiao, Z., Chen, L., Song, X., Shu, Z., Xiao, R., Huang, X., 2019. Species inventory and assessment of large- and medium-size mammals and pheasants using camera trapping in the chebaling national nature reserve, Guangdong province [in Chinese]. *Biodivers. Sci.* 27, 237–242.
- Xu, K., Xiao, W., Hu, D., et al., 2024. Effects of livestock grazing on spatiotemporal interactions between snow leopards and ungulate prey. *Integr. Zool.* <https://doi.org/10.1111/1749-4877.12935>.
- Yang, X., Li, Z., Hong, W., Madexi, B., Sha, D., 2024. Diversity and spatial and temporal distribution pattern of large and medium-sized mammals in the eastern Qinghai-Tibet Plateau. *J. Sichuan For. Sci. Technol.* 45, 48–62.
- Zaman, M., Tolhurst, B.A., Zhu, M., Jiang, G., 2020. Den-site selection at multiple scales by the red fox (*Vulpes vulpes subsp. montana*) in a patchy human-dominated landscape. *Glob. Ecol. Conserv.* 23, e01136.
- Zhang, J., 2016. Spaa: species association analysis. R Package Version 0.2.2. <https://CRAN.R-project.org/package=spaa>.
- Zhang, Y.Z., Zhang, B., Liu, Y.Y., 2015. Wind speed change and influence on wind energy in recent 50 years over Hexi Corridor. *Adv. Mater. Res.* 1070, 284–290.
- Zhao, D., Yang, C., He, M., Chen, L., He, X., Ran, J., 2019. Habitat suitability assessment and daily activity patterns of *Otocolobus manul* in the Gongga Mountain National Nature Reserve [in Chinese]. *Sichuan J. Zool.* 38, 320–327.