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Seasonal changes in 3D space use and foraging strategies in the avivorous bat *Ia io*

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ABSTRACT

To cope with seasonal changes in food availability, animals need to optimize their behaviors, including shifts in temporal activity patterns and spatial use in habitats. Most studies focused on the temporal activity pattern or habitat use in two-dimensional (2D) space. However, studies on the simultaneous changes in temporal activity patterns and habitat use in three-dimensional (3D) space are limited. In this study, we used the great evening bat (*Ia io*) to investigate differences in the activity pattern and space use during the summer and autumn. We collected and analyzed the Global Positioning System (GPS) data and activity data obtained from accelerometers. The results showed that bats displayed seasonal variations in their movement patterns. Specifically, compared with summer, *I. io* individuals were found to extend their foraging duration and adopt a low-energy consumption pattern of activity in autumn. Furthermore, there was a notable increase in the vertical extent of the 3D habitat utilization range for these bats, although the 2D habitat size in autumn remained similar to that in summer. These changes manifested both temporally and spatially, potentially as a response to the reduced availability of insect resources from summer to autumn, and the arrival of migratory birds in autumn as an alternative food source. Our results suggest that *I. io* seasonally adjust their foraging strategies and spatial use from two to three dimensions. Our study provides important insights into the seasonal behaviour dynamics of bats during summer and autumn, which may contribute to understanding their ecological strategies and inform conservation efforts.

Keywords: Activity patterns; Bats; Seasonal change; Space use; Three-Dimensional habitat

INTRODUCTION

Animal movement is the result of both internal (e.g., energy needs) and external factors (e.g., safety and food or resource availability) affecting the studied organism (Dinsmore, 2007; Harel et al., 2016; Morellet et al., 2013; Nathan et al., 2008; Spiegel et al., 2013). To comprehensively understand animal behavior and ecology, determining how animals adjust their temporal (activity patterns) and spatial (habitat use) distribution in response to changing environments is essential (Bridge et al., 2011; Wong & Candolin, 2015).

To adapt to different environmental conditions, animals often change their activity patterns and habitat use to optimize their resource utilization and meet their energy needs. For example, animals might increase their activity level during colder and drier seasons to obtain more food and meet their energy demands or forage at greater distances to acquire more resources (Ariano-Sánchez et al., 2020; Morellet et al., 2013). The changes in animal activity patterns are likely to exhibit a consistent correlation with variations in spatial utilization. Specifically, animals adjust their activity durations across diverse habitats in response to ecological factors, including resource availability, predation risks. These adjustments, driven by the spatial and temporal distribution of resources, enable animals to optimize foraging efficiency and energy utilization (Chandler et al., 2020; Larrucea & Brussard, 2009).

The animal habitat use has historically investigated on two-dimensional (2D) spatial utilization, which captures only horizontal movements across latitude and longitude, but there is growing recognition of the need to incorporate the vertical dimension into ecological studies. The 2D approach

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represents space as a flat plane, emphasizing lateral range but neglecting elevation or depth. However, many species, particularly bats, alongside marine mammals, fish, birds, arboreal mammals, marsupials, amphibians, and insects, actively utilize the vertical axis, moving through height or depth in ways that a 2D model cannot account for (Aspillaga et al., 2019; Gámez & Harris, 2022; Jones & Barmuta, 2000; Mena et al., 2020; Schreier et al., 2009). Limiting analysis to 2D can distort our understanding of space use, resource utilization, and competition. For instance, a previous studies showed that 2D methods often overestimate spatial overlap, as animals may share horizontal positions but occupy distinct vertical levels, thereby avoiding direct interaction (Simpfendorfer et al., 2012). Thus, 3D spatial analysis provides a more precise and comprehensive framework, particularly in ecosystems with significant vertical complexity (Gámez & Harris, 2022). Exploring 3D space use is therefore critical to accurately assess how seasonal changes affect habitat utilization and to reveal the nuanced relationship between activity patterns and spatial dynamics in three dimensions.

Although bats are known to fly at high altitudes and efficiently utilize high-altitude ecological niches, this aspect of their behavior has been relatively less emphasized (McCracken et al., 2021; Voigt et al., 2018). Some bat species, such as the Mexican free-tailed bat (*Tadarida brasiliensis*), can fly at altitudes of 3 000 m above ground (McCracken et al., 2021; Williams et al., 1973), and the European free-tailed bat (*Tadarida teniotis*) reaches heights exceeding 1 600 m above ground (O’Mara et al., 2021). Increasingly, studies report on bats’ utilization of 3D space, including the North American Brazilian free-tailed bat (*Tadarida brasiliensis*) (Krauel et al., 2018; McCracken et al., 2016), the European common noctule (*Nyctalus noctula*) (O'Mara et al., 2019a, 2019b; Reusch et al., 2023; Roeleke et al., 2016), and the Asian wrinkle-lipped free-tailed bat (*Mops plicatus*) (Srilopan et al., 2025; Voigt et al., 2020). However, information on how bats respond to seasonal changes in 3D space use is limited.

However, few studies have integrated the temporal (activity patterns) and spatial (habitat use) dimensions of animal behavior and their relationships (Charnov, 1976; Halle & Stenseth, 2000). While the activity patterns of temperate-zone species have been well documented (Erkert, 1982; Feng et al., 2022; Jones & Rydell, 1994; Mariton et al., 2023), comparatively fewer studies have investigated how subtropical bats adjust their diel and seasonal behavior, particularly in three-dimensional space (Niga et al., 2023). One reason for the limited number of studies on bats is the difficulty in tracking bat activity patterns, although researchers have developed acoustic sampling methods for this purpose (Kingston, 2009; Runkel et al., 2021). Moreover, some studies on bat activity patterns are limited to specific geographical areas or neglect individual-level comparisons, hindering comprehensive population monitoring (Grimm et al., 2025). Thus, to better understand the daily activity patterns of bats, including resting, foraging, and active times, accelerometers might be used for accurately measuring the energy expenditure associated with animal movement and behavior over time (Egert-Berg et al., 2018; Hurme et al., 2025; Stidsholt et al., 2024). To better monitor the seasonal habitat use and activity patterns of bats, miniature GPS devices have been developed and might be used for studying their movement (Conenna et al., 2019; Cvikel & Yovel, 2014; Hall & Bennett, 2021; Tsoar et al., 2011).

The great evening bat (*Ia io*), known for its bird-eating habits, adapts its hunting strategy seasonally: it preys on insects during summer and shifts to targeting migratory birds at night in autumn, especially when insect availability dwindles (Gong et al., 2023). Capable of swift flight at high altitudes, *I. io* presents an ideal subject for examining seasonal variations in activity patterns and three-dimensional (3D) space utilization(Gong et al., 2022). Our previous study has found no notable differences in two-dimensional (2D) spatial use between summer and autumn (Wang et al., 2023). In light of these findings, our study aims to delve deeper into the population activity patterns of *I. io* during these seasons, to explore the nuances of activity patterns and 3D spatial utilization.

Here we made two hypotheses. First, the distinct differences would be observed in the activity patterns of *I. io* between summer and autumn. We predicted that in autumn, when insect resources become scarce and migratory birds are available, *I. io* will alter their movement patterns, resulting in extended foraging durations and varied movement intensities. This prediction is based on the understanding that preying on nocturnally migrating birds requires bats to fly at higher altitudes and speeds, and to process more complex sensory information. Compared to insect foraging, these challenges necessitate greater time investment, making lower activity intensity more reasonable during this period (Gong et al., 2021). Second, there would be significant variations in the 3D spatial utilization of *I. io* across the two seasons. Specifically, we proposed that in autumn, *I. io* would expand their spatial range in the vertical dimension to prey on high-altitude migratory birds, adapting to the altered distribution of their food resources.

MATERIALS AND METHODS

Study site and species

All research activities involving bats were conducted under permits and approved by the Science and Technology Ethics Committee of Northeast Normal University (approval number: NENU-W-2020-1003), adhering to the guidelines of the use of animals in research (ASAB/ABS) and applicable governmental regulations. The study area was located in the mountainous region of southwest China (Xingyi City, Guizhou Province), has a subtropical monsoon climate, with hot, humid summers and mild, drier autumns. Spanning elevations from 700 to 2 200 m a.s.l., the topography is characterized by a karst landscape featuring rugged limestone formations, caves, sinkholes, and steep valleys. The area is located on one of the eight global migratory routes of birds in Central Asia (www.birdlife.org/worldwide/programme-additional-info/migratorybirds-and-flyways). There are many caves, among which the Feilong Cave (N24°58.41′, E104°52.79′) is inhabited by the largest population of *I. io* (about 80 bats) in this area. Most individuals of *I. io* in the Feilong Cave are males, and we found that *I. io* in this population mainly prey on insects in summer (June to August) and birds in autumn (September to November) (Gong et al., 2021). In this study, adult male *I. io* bats were captured at Feilong Cave using mist nets in November 2020 and June 2021, respectively.

Tag attachment

We captured bats that were returning to their roosts after foraging early morning (about an hour before sunrise) in summer and autumn. We tracked a total of 14 bats, with seven in summer and seven in autumn. First, we used medical glue (Compont Medical-Surgical Glue, China, https://www.compont.com/yyj) to stick the GPS tag (HQXS, HQBG0603) with a three-axis accelerometer, which could be operated by the GSM data transmission system (Global System for Mobile Communication, MC20, Quectel Wireless Solutions, China), on the back of the bat. After tagging each bat, they were individually placed in cloth bags for a 30-minute adaptation period to ensure the GPS logger was securely attached to their backs. Following this, they were promptly released back to their roosts. To minimize disturbance, the entire process of attaching GPS loggers and releasing the bats was completed within an hour. This allowed the bats approximately 12 hours in the roost to acclimate to the GPS loggers before embarking on their nocturnal foraging activities. The weight of the GPS tag was 3.5±0.2 g (Mean±SD), with dimensions of 20 mm long× 17 mm wide×9 mm high. This constituted 5.7%±0.6% (Mean±SD) of the bat's body mass (Supplementary Table S1). Previous studies indicated that tags constituting less than 10% of body weight may not have significant short-term effects on bats (Cvikel et al., 2015; Harten et al., 2020), though some research suggests limiting tags to below 5% for longer studies to minimize potential impacts (Kelling et al., 2024). Our previous study confirmed that GPS tags had no adverse effects on the body mass of *I. io* (Wang et al., 2023). In the present study, tags were designed to detach automatically within 7 to 10 days, limiting the duration of any potential impact.

The sampling period of the accelerometer was synchronized with that of the GPS, with both operating at 10-minute intervals, while the accelerometer frequency was set to 50 Hz to ensure high-resolution and accurate classification of bat activity and resting states (see Appendix A). This setup allowed for continuous sampling to accurately capture bat activity data. The total activity value was recorded throughout the study period. Our sampling periods for each season were 1900h to 0700h in summer and 1900h to 0800h (UTC+8 h) in autumn.

Kernel density estimation

We used kernel density estimation (KDE) to evaluate the utilization of space by the tagged bats. KDE estimates the probability density of animal locations by smoothing observed positional data points, thereby producing a continuous surface representing areas of higher and lower usage. We used the package "ks" (v.1.14.0) in the R v.4.1.1 (R Core Team, 2021) to construct 2D and 3D nuclear density distributions, respectively. Animal space utilization is usually quantified using the utilization distribution (UD), which represents the probability distribution of an animal's observed spatial locations. Specifically, a UD derived from kernel density estimation indicates areas actually used by individuals based on recorded positional data, with higher UD values signifying areas of more intensive use. We used 2D and 3D kernel density estimation to delineate the 95% isoline (UD95%, representing general activity space) and the 50% isoline (UD50%, representing core activity space) for each season. The volume of the respective utilization range was calculated using the "rgl" (v.1.0.1) and "mic3d" (v.0.9.1) packages.

Calculation of spatial overlaps

We compared the overlap ratio of UD between summer and autumn to estimate population space use overlap. This involved calculating the proportion of the summer range (2D-UD area or 3D-UD volume) that overlaps with the autumn range, and vice versa. We quantified spatial overlap using two indices: the Volume of Intersection (VI), which measures absolute shared volume (or area) for a straightforward assessment of overlap extent, and the Utilization Distribution Overlap Index (UDOI), which incorporates both overlap extent and similarity in space-use intensity for a more nuanced evaluation of utilization patterns (Cooper et al., 2014; Fieberg & Kochanny, 2005). Both indices provide complementary insights into habitat sharing, with VI emphasizing raw spatial congruence and UDOI highlighting behavioral similarity in space use. The VI calculations for 2D and 3D space are shown in Eq. 1 and Eq. 2, respectively:

$$\mathrm{VI}\,(2\mathrm{D}) = \iint_{-\infty-\infty}^{\infty\infty} \min(\mathrm{UD}_1\,(x,y)\,,\mathrm{UD}_2(x,y))dxdy \tag{1}$$

$$\mathrm{VI}\,(3D) = \iiint_{-\infty-\infty-\infty}^{\infty\infty\infty} \min(\mathrm{UD}_1(x,y,z),\mathrm{UD}_2(x,y,z))dxdydz \tag{2}$$

Here, UD1 and UD2 represent the summer and autumn utilization distributions, respectively, with the value of VI ranging from 0 (no overlap) to 1 (full overlap). When calculating the VI value of a 3D space, the vertical height (z) should be included in the formula.

We used the Utilization Distribution Overlap Index (UDOI) to assess space-use overlap in 2D and 3D space (Eq. 3 and Eq. 4, respectively):

$$\mathrm{UDOI}\,(2\mathrm{D}) = \mathrm{A}_{1,2} \iint_{-\infty-\infty}^{\infty\infty} \mathrm{UD}_1\,(x,y) \times \mathrm{UD}_2\,(x,y)\,dxdy \tag{3}$$

$$\mathrm{UDOI}\,(3\mathrm{D}) = \mathrm{V}_{1,2} \iiint_{-\infty-\infty-\infty}^{\infty\infty\infty} \mathrm{UD}_1(x,y,z) \times \mathrm{UD}_2(x,y,z)dxdydz \tag{4}$$

Here, $\mathrm{A}_{1,2}$ refers to the overlapping area between the 2D utilization distributions (UDs) of summer and autumn, and $\mathrm{V}_{1,2}$ represents the overlapping volume between their 3D UDs. The UDOI value increases with both the degree of spatial overlap and the similarity of space-use intensity, with values near 0 indicating minimal overlap and values approaching 1 indicating substantial overlap with similar space-use intensity.

Analysis of the activity

We used activity data recorded as unitless activity counts (reflecting movement intensity) from a three-axis accelerometer (see Appendix A for details on data collection, limitations, and seasonal comparisons) to evaluate temporal differences in activity patterns at both individual and population levels. First, each 10-minute interval was classified as either "resting" or "active" based on an empirically determined activity threshold of 50 (see details in Appendix B). Values below this threshold represented resting or minimal movement (e.g., crawling, low-intensity movement), while values equal to or above 50 reflected active behaviors including flight. To ensure analytical consistency, only nights with complete activity records (i.e., covering the entire nocturnal period from emergence to return) were included, yielding 26 nights in summer and 13 in autumn, with 1–5 nights of data per individual. To further characterize activity, we applied k-means clustering to the active intervals and divided them into four activity intensity categories: low (50–217), medium (218–403), high (404–645), and very high (646–974) (see details in Appendix C). This enabled us to distinguish different behavioral states across a gradient of movement intensity. For each bat, we calculated several activity metrics including mean activity intensity, activity duration (total time spent active), and timing of activity onset, termination, and peak. These values were computed at the individual level and then averaged across individuals within each season to ensure equal weighting. The proportion of active intervals throughout the night was also examined to evaluate population-level nocturnal activity preferences. To extend GPS battery life, data collection began at 1900 h in both seasons. Since autumn sunset occurred around 1820 h, this design may slightly underestimate early activity. However, field observations found that *I. io* emerges later than other insectivorous bats, and most individuals had initiated activity by or shortly before 1900 h. We acknowledged this limitation and have discussed its implications in the Appendix D.

Statistical analysis

Activity data, recorded in 10-minute intervals for each individual, served as the basis for the analysis. When comparing overall activity intensity between seasons, data from all activity states (including resting) were included. For comparisons focusing solely on active states, data corresponding to resting (i.e., activity≤ 50) were excluded. To rigorously analyze the data while accounting for individual-level variability, two Generalized Linear Mixed Models (GLMMs) were implemented. "Hours since sunset" was calculated for each observation to explicitly account for temporal variation in bat activity. The response variable was activity intensity treated as count data and modeled with a Poisson error distribution and log-link function. Given the small sample size and the focus on detecting broad seasonal trends, models included only season and hours after sunset as fixed effect and individual ID as a random effect to account for repeated measures, thereby minimizing the risk of model overfitting. The first model evaluated seasonal differences in overall activity intensity across all states, including resting and active periods. The second model focused exclusively on active states, enabling a comparative analysis of activity intensity between seasons after excluding resting state data. These models provided a robust framework for quantifying seasonal effects on bat activity while addressing inter-individual variation and temporal dynamics. Additionally, we examined temporal autocorrelation by using the autocorrelation function (ACF) of the GLMM residuals. Results were reported as log-transformed estimates alongside their corresponding standard errors, *Z*-values, and *P*-values. To enhance the analysis of population-level activity rhythms and address potential biases from repeated measures, generalized additive mixed models (GAMMs) were fitted with a binomial family distribution using the "mgcv" package. Activity status (active vs. resting) served as the response variable, with a smooth term for time since sunset (binned in 10-minute intervals) and individual ID as a random effect to account for individual variability across nights. Separate GAMMs were fitted for summer and autumn to allow season-specific patterns. Additionally, to assess seasonal differences in the distribution of activity intensity categories, a chi-square test of independence was performed. This test compared frequency counts across four categories derived from k-means clustering of active intervals. Averages, such as mean activity intensity and duration, were first calculated at the individual level by aggregating data across all tracked nights per bat, then averaged across all bats. All analysis were conducted in R v.4.1.1. (R Core Team, 2021).

RESULTS

Activity intensity

Our analysis revealed no significant seasonal differences in overall activity intensity when considering both resting and active states (z=–0.54, *P*=0.59; Table 1). In contrast, when focusing exclusively on active states (excluding the resting state, defined as activity≤50), there was a positive but non-significant trend toward higher activity intensity during summer compared to autumn (z=1.68, *P*=0.094; Table 1; Figure 1B). Importantly, in both analyses, "hours since sunset" showed a highly significant negative association with activity (all data: Estimate=–0.072, z=–222.2, *P*< 0.001; active intervals only: Estimate=–0.026, z=–76.8, *P*<0.001), indicating that activity declined over the course of the night. Residual autocorrelation analyses indicated moderate short-term autocorrelation at short time lags, which declined rapidly to near zero with increasing lag (Supplementary Figure S3). The distribution of activity intensity across seasons is illustrated in Figure 1. Further analysis of activity intensity states revealed significant seasonal differences in the distribution of activity levels (χ^2=224.76, df=4, *P*<0.001). Notably, the proportion of time intervals classified as resting was significantly higher in summer (44.2%) compared to autumn (26.2%). Autumn showed a higher prevalence of high-intensity activity (12.1%) compared to summer (9.1%), whereas very high-intensity activities were notably more frequent in summer (11.5%) than in autumn (2.6%) (Figure 2A). These findings indicated that while overall activity intensity remains relatively stable across seasons, the distribution of activity types differs markedly, with summer characterized by increased resting and autumn by a

Table 1 Generalized Linear Mixed Model (GLMM) results for effects on bat activity, incorporating season and hours since sunset

All states (Including resting)				
Factors	Estimate	Std. Error	*Z*-value	*P*-value
Intercept	5.895	0.106	55.715	***P*<0.001**
Season (Summer)	–0.081	0.15	–0.539	0.59
Hours since sunset	–0.072	0.0003	–222.199	***P*<0.001**
Only active states (Excluding resting)				
Factors	Estimate	Std. Error	*Z*-value	*P*-value
Intercept	5.873	0.078	75.184	***P*<0.001**
Season (Summer)	0.185	0.11	1.677	0.094
Hours since sunset	–0.026	0.0003	–76.805	***P*<0.001**

The "All states" model includes resting and active states. The "Only active states" model covers active behaviors only. Fixed effects are log-transformed estimates with standard errors (Std. Error), *Z*-values, and *P*-values. Significant results (*P*<0.05) are in bold.

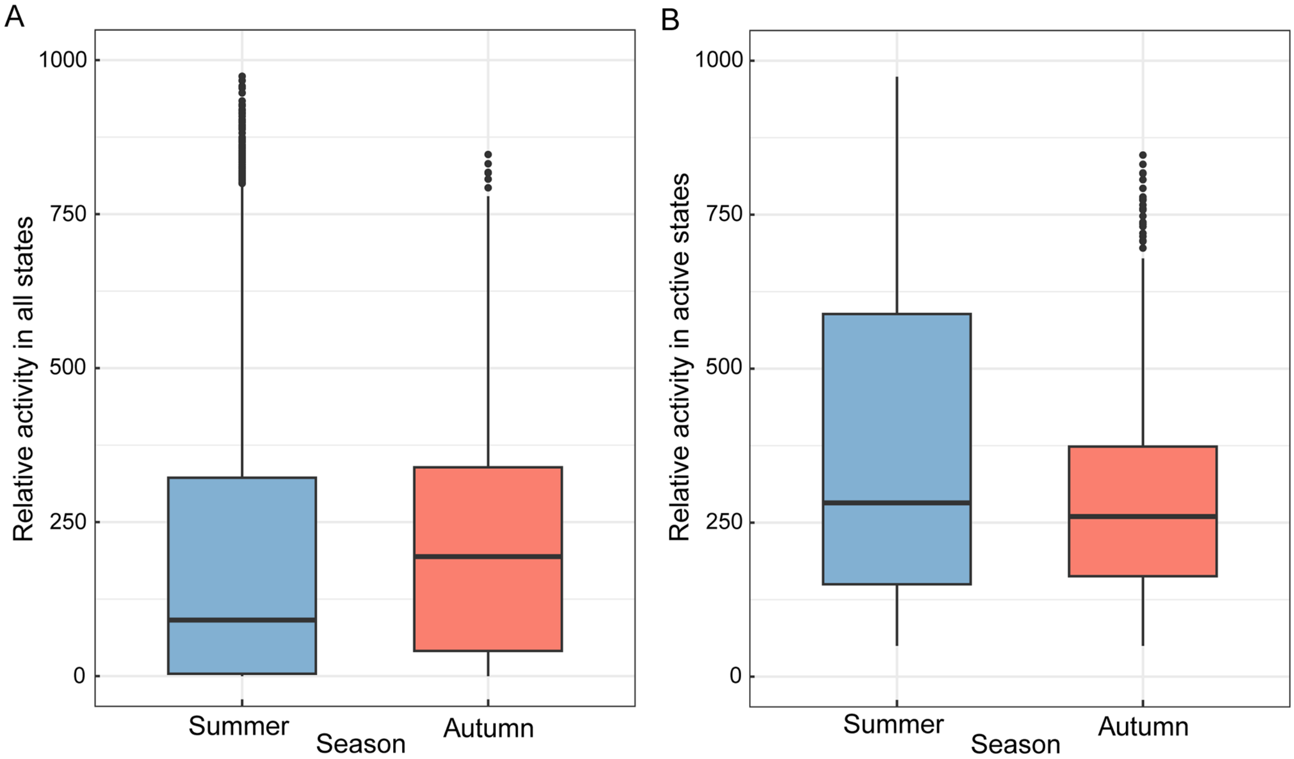

Figure 1 Activity intensity of *Ia io* in summer and autumn

A: All states (activity and resting). B: Active state only.

greater prevalence of high-intensity activity.

Activity times

The differences in the activity times between summer and autumn included two aspects. First, bats in autumn exhibited an earlier onset and a later termination of activities compared to those in summer (Figure 2B, C). In summer, bats generally initiated activity approximately 90–120 minutes after sunset, whereas in autumn, more than half of the bats showed activity in the first recorded interval (40–50 minutes post-sunset), suggesting onset within the preceding 30–60 minutes based on emergence observations (Figure 3A). Moreover, in summer, bats typically ceased activity before sunrise, while in autumn, bats often remained active up to 60 minutes after sunrise (Figure 3A). Second, the active periods in summer were shorter than those in autumn, while the resting periods and the longest periods of rest in summer were longer than those in autumn (Supplementary Table S2).

Activity peak

In autumn, bats showed relatively consistent activity throughout the night, with the GAMM indicating a sustained proportion of active individuals (F=3.5, P<0.05) (Figure 3B). In contrast, in summer, bats exhibited higher activity at specific times, with three distinct peaks (approximately 60–70, 240, and 560 minutes post-sunset) as identified by the GAMM-smoothed curve (F=5.0, P<0.01) (Figure 3B). This resulted in a more variable activity pattern in summer compared to autumn. We quantified activity preferences by comparing the percentage of nights in which each 10-minute interval was categorized as active. In autumn, only 7 time periods (70 minutes) exhibited≤50% activity rates, whereas in summer, 36 time periods (360 minutes) had≤50% activity (Figure 3A). Activity preference was generally higher in autumn during most periods of the night, except for periods corresponding to 90–150 minutes after sunset and 90–60 minutes before sunrise, when summer showed higher activity levels (Figure 3A).

Space use between two seasons

In the two-dimension space, the size of the active area and the core active area used by the entire population of *I. io* was similar (Table 2; Figure 4A). But in the three-dimension space, the active area and the core active area were larger in autumn than in summer, and the active area used in autumn was 2.1 times larger than that in summer. The core activity area in autumn had a greater volume (2.6 times) than that in summer (Table 2; Figure 4B, C). Furthermore, when accounting for altitude above ground level, the same seasonal trend in spatial use was observed (Supplementary Figure S2).

Overlap between two seasons

Our analysis reveals that while there is a substantial overlap in the two-dimensional (2D) activity areas between summer and autumn (59.48% in summer and 60.35% in autumn, with overlap indices of 0.38 and 0.48, respectively), the overlap in three-dimensional (3D) space is markedly lower. Specifically, the overlapping volume of the overall activity regions accounts for only 26.86% in summer and 12.85% in autumn (VI and UDOI indices of 0.11 and 0.05, respectively). Moreover, the core activity regions (50% UD) show even lower overlap, with 21.35% in summer and 8.21% in autumn, and corresponding indices of 0.06 and 0.01.

DISCUSSION

In this study, our results showed that *I. io* adjusted their activity patterns and expanded their utilization of three-dimensional (3D) spatial habitats in response to seasonal variations, which are likely related to changes in food availability confirmed by our previous study (Wang et al., 2023). These results supported our two hypotheses. These

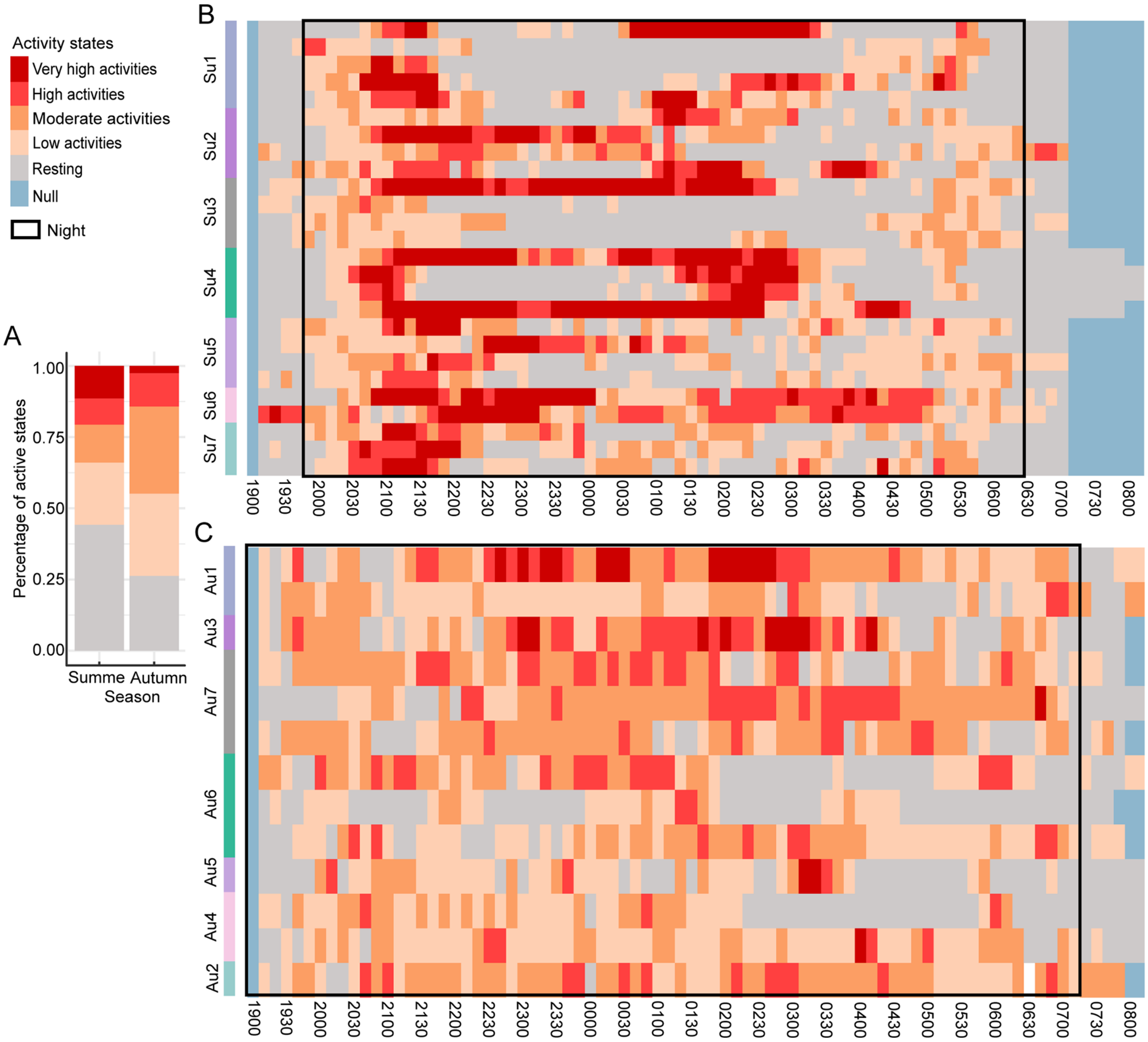

Figure 2 Activity patterns and states of seven bats in summer and autumn

A: Proportion of activity and resting states in the two seasons (excluding null values). B, C: Daily activity is represented by color-coded bars (low, medium, high, and very high), with resting states shown in gray and missing values in blue. Data were sampled for 26 nights in summer (B) and 13 nights in autumn (C). The X-axis represents time, with each bar corresponding to one day. The black box indicates the period from sunset to sunrise.

findings suggest that bats may adjust their temporal and spatial behaviors across seasons, and longer activity patterns may be associated with larger spatial utilization ranges. The increase in the spatial habitat occurs not only in the horizontal dimension but also in the 3D space, including the vertical dimension. Overall, our studies provided new insights into how animals adjust their activity patterns and space use patterns in response to environmental changes.

The potential causes for the differences in daily activity patterns among seasons

Animals often adjust their activity patterns to address seasonal changes in food resource availability (Fryxell et al., 2008; Owen-Smith, 1994). Previous studies on temperate bats have shown that foraging behaviors shift in response to seasonal factors, such as breeding cycles (Heim et al., 2016; Mackie & Racey, 2007). These changes in activity patterns might involve spending more time foraging in seasons with limited food resources. In this study, we observed that bats exhibit dynamic changes in their activity patterns. Although overall activity intensity did not differ significantly between seasons, our results tentatively suggest that bats may engage in longer-duration, lower-intensity activities during autumn foraging. Additionally, we also noticed a shift in the peak of nocturnal activity in *I. io* between autumn and summer. Notably, summer activity in *I. io* is characterized by both a higher proportion of resting and very high-intensity intervals, suggesting a strategy of intense, short-duration foraging bouts followed by extended rest, likely driven by the abundance of insect prey.

Our prior study supports these observations, revealing that insect abundance and diversity drop significantly in autumn compared to summer (see details in Wang et al., 2023), while the proportion of *I. io* preying on migratory birds rises sharply (78% in autumn vs. 6% in summer) (Gong et al., 2021, 2022). These behavioral shifts may reflect a strategic adjustment to seasonal variations in food type and availability, in line with

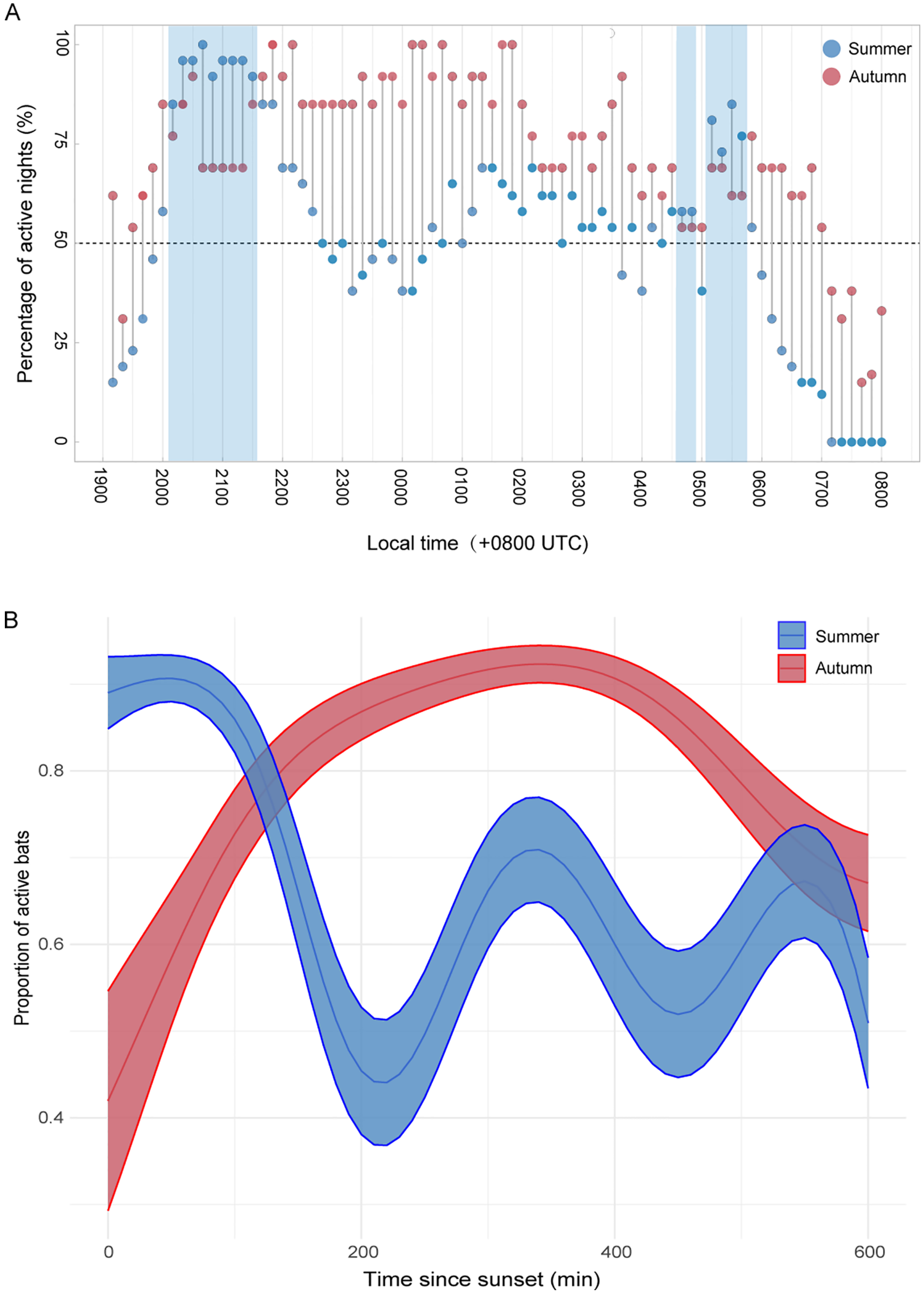

Figure 3 Night activity fluctuates in summer and autumn

A: Proportion of active nights per period. Each point represents the percentage of nights during which the corresponding 10-minute interval was categorized as active. The dashed line marks 50% active nights. Blue areas indicate higher active night proportions in summer. B: Activity variation, depicted as a continuous curve representing the time trend of the whole seasonal population, fitted using GAMMs with individual as a random effect, and the grey area indicates the 95% confidence interval. Blue represents summer, red represents autumn.

Table 2 Comparison of overlap percentages and index values (VI, UDOI) in 2D and 3D space for active and core active areas (95% and 50% density distributions)

		2D				3D			
Season	Kernel Density (%)	Area (km^2)	% Overlap	VI	UDOI	Volume (km^3)	% overlap	VI	UDOI
Summer	95	416	59.48	0.38	0.48	4647	26.86	0.11	0.06
	50	82	27.02	0.11	0.02	512	21.35	0.05	0.01
Autumn	95	409	60.35	0.38	0.48	9711	12.85	0.11	0.06
	50	82	27.46	0.11	0.02	1331	8.21	0.05	0.01

VI: Volume of intersection, UDOI: Utilization distribution overlap index.

optimal foraging theory, which posits that animals adjust prey selection and foraging effort to maximize net energy gain (Charnov, 1976; Owen-Smith, 1994; Schoener, 1971). The activity peaks at the beginning and end of the night in summer, consistent with patterns observed in other insectivorous bats, may be linked to peaks in insect activity (Heim et al., 2016). In contrast, the absence of clear peaks in autumn could result from the dietary shift to migratory birds, whose nocturnal activity is more constant than that of insects. In autumn, the apparent extension of foraging duration and lower-intensity activity in *I. io* might be linked to the need to pursue migratory birds as an alternative prey source when insect abundance declines. This behavioral pattern could reflect a flexible strategy to maintain foraging success under changing resource conditions. The prolonged, low-intensity foraging may enable individuals to search continuously for food or efficiently exploit concentrated prey patches. Our statistical models further supported these observations, demonstrating that activity intensity significantly declined over the course of the night and exhibited moderate short-term temporal autocorrelation typical of animal behavioral rhythms. However, such a strategy may be species-specific and tied to the unique seasonal shift of *I. io* toward bird predation and may not generalize to other insectivorous bats that do not exhibit similar dietary transitions. Thus, seasonal differences necessitate distinct foraging strategies: a short, rapid approach in summer versus a longer, slower one in autumn.

While some temperate bats enter torpor in autumn and winter to conserve energy during food shortages (Barratt et al., 2023; Bondarenco et al., 2013; Fjelldal et al., 2022). *I. io* in our study area did not exhibit this behavior. Instead, they showed shorter inactivity periods in autumn than in summer. This discrepancy may be attributed, in part, to the subtropical climate of the region, where bats may not necessarily require prolonged hibernation. This species showed a shorter duration of inactivity in autumn than in summer, which might be explained by energy trade-offs. Animals need to find the optimal balance between gaining more energy and reducing their energy consumption to maximize net energy intake and survive in challenging environments (Castellano, 2019; Krebs & Davies, 2009). Our previous work indicates that preying on migratory birds compensates for reduced insect availability in autumn, providing substantial energy gains that support fat reserves for hibernation or migration (Gong et al., 2021). This may reflect an energy trade-off where actively foraging for high-energy prey like birds outweighs the benefits of torpor. Therefore, using strategies such as torpor to reduce energy consumption may be less effective than investing more time and energy into foraging to obtain higher quality food resources from the environment. Alternatively, the lack of torpor observed in our study may be due to favorable weather conditions during the autumn nights, which reduced the necessity for such energy-conserving behavior. More broadly, seasonal differences in weather conditions, such as variations in temperature, humidity, or wind patterns in subtropical regions, could also significantly affect bat activity rhythms and habitat use by influencing prey availability, flight energetics, and overall behavioral performances. Although our sunset-standardized results confirmed that the earlier autumn onset was not attributable to earlier sunset times, the longer nocturnal period in autumn may introduce a potential bias in activity duration estimates, warranting further scrutiny with photoperiod-matched comparisons.

The potential causes of changes in space utilization among seasons

Past studies using acoustic surveys, VHF, GPS, and radar tracking have demonstrated that bats, including diverse species such as *Tadarida brasiliensis* and *Nyctalus noctula*, utilize 3D space for foraging and other activities, extending their spatial behavior to include the vertical dimension (McCracken et al., 2016; Roeleke et al., 2018; Voigt et al., 2020). Our findings suggest that while bats largely share similar horizontal activity zones across seasons, the vertical dimension exhibits more pronounced seasonal differentiation. We observed partial spatial overlap of habitat use in *I. io* between summer and autumn in both 2D and 3D contexts, likely driven by seasonal shifts in food preferences and availability. Our data show a significant expansion of 3D space use in autumn, particularly in the vertical dimension, with active area volume increasing 2.1-fold and core active area volume 2.6-fold compared to summer, while 2D ranges remained stable.

Several factors may explain these patterns. First, the spatial distribution of food resources varies due to differing habitat preferences of insects and migratory birds, yet *I. io*'s year-round residence in the same area results in some overlap. Second, migratory birds occupy higher altitudes than insects (Bruderer et al., 2018; Kerlinger & Moore, 1989), driving the vertical expansion in autumn as bats pursue this prey. Although insectivorous bats can hunt migratory insects at high altitudes (McCracken et al., 2008; O'Mara et al., 2021), we found no sustained high-altitude flight in *I. io* during summer (Gong et al., 2022). Moreover, 3D overlap between seasons was lower than in 2D (e.g., 12.85% in autumn vs. 60.35% in 2D), suggesting that 3D analysis better distinguishes seasonal space use, especially for volant species. These results underscore the importance of incorporating vertical dimensions into ecological studies to capture the full scope of spatial behavior.

The relationships between temporal and spatial variation in movement patterns

For *I. io*, the shift to preying on migratory birds in autumn (Gong et al., 2021, 2022), likely drives vertical habitat expansion rather than horizontal spread, with increased 3D

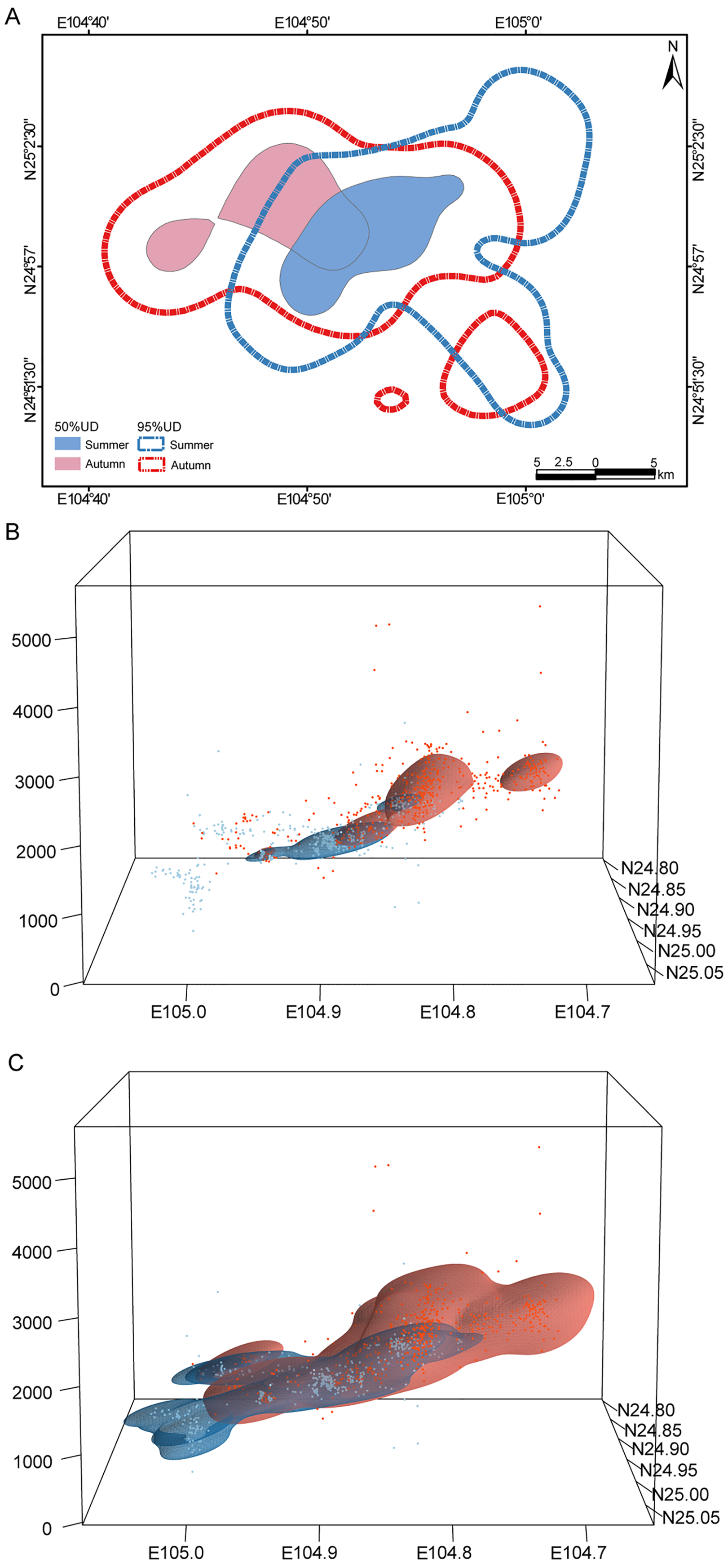

Figure 4 Space utilization and overlap in summer and autumn

A: Represents two-dimensional (2D) kernel density distributions of bat spatial use areas (95% and 50% isolines); B, C: Represent three-dimensional (3D) kernel density utilization distributions for 95% and 50% isolines, respectively; with altitude measured in meters above sea level (ASL); blue represents summer, and red represents autumn.

space use but stable 2D ranges. This finding was interesting, considering that most studies have primarily focused on changes in animal space utilization in the horizontal dimension, often neglecting or underestimating the characteristics and patterns of population space utilization (Gámez & Harris, 2022; Hutchinson, 1957). Although changes in 3D space use has been extensive studied in other highly mobile species like birds (Cooper et al., 2014; Khosravifard et al., 2020), marine mammals (Mcintyre et al., 2017), and amphibians (Ousterhout & Burkhart, 2017), research on bats' 3D space utilization has been gaining traction, though not as extensive. Our work focused on the 3D spatial niches of bats, which contributes to this emerging body of knowledge (Gámez & Harris, 2022; Oliveira & Scheffers, 2019).

Linking activity patterns to changes in space use can help to better understand how animals adjust their behavioral response to environmental changes. In the case of bats, we found that longer activity patterns correspond to larger spatial utilization ranges. Our results suggest that bats may expand their habitat range to accommodate their longer activity periods during certain seasons. Therefore, although the relationship between activity patterns and space use is intricate, changes in the activity patterns of *I. io* might directly affect their space use due to factors such as seasonal shifts in food availability and prey distribution. This integrated approach enhances our understanding of behavioral responses across dimensions.

Extending 3D spatial studies to other animals

The significance of 3D spatial analysis extends beyond *I. io* to other species with vertical movement, enhancing the generality of our findings. For volant animals like *I. io*, the vertical dimension is critical, as they exploit three-dimensional airspace to access resources such as high-altitude migratory birds. This behavior, less evident in 2D studies, highlights the necessity of 3D approaches for species with extensive vertical ranges. Similarly, arboreal animals (e.g., primates, marsupials) and birds navigating stratified habitats benefit from 3D analysis, which reveals niche separation and resource use more accurately than 2D methods (Gámez & Harris, 2022). For terrestrial species, such as pandas in montane habitats with variable elevations, incorporating the vertical axis could elucidate how altitude influences foraging and habitat selection, offering greater ecological insight than horizontal metrics alone (Tracey et al., 2014). Likewise, in marine environments, species like northern elephant seals (*Mirounga angustirostris*) utilize the vertical dimension of the ocean to forage, demonstrating spatial patterns that 2D analyses might misrepresent (Kienle et al., 2022). Unlike 2D analyses, which may overestimate spatial overlap by ignoring vertical separation, 3D frameworks provide a more precise understanding of space use and competition. Advances in GPS and accelerometer technology make such studies feasible across taxa, emphasizing their importance for unraveling ecological dynamics and informing conservation strategies (Nathan et al., 2022).

Study limitations and future directions

First, the sample size was limited to seven male *I. io* individuals per season, which may not fully capture the behavioral variability within the population, particularly among females, whose foraging behaviors may differ due to reproductive demands (Mackie & Racey, 2007). Second, different individuals were tracked across seasons, and the data were collected in different years (autumn 2020 and summer 2021). This introduces potential confounding effects of inter-individual and inter-annual variability. Although such effects cannot be entirely ruled out, the seasonal patterns we observed were consistent across multiple individuals within each season and aligned with known ecological shifts, suggesting that the main findings are robust. Third, the use of low-frequency GPS loggers may have led to inaccuracies in altitude estimation, potentially inflating the variance in 3D space-use metrics and affecting the precision of vertical space-use comparisons (Péron et al., 2020; Schaub et al., 2023). Furthermore, our GLMM analyses were limited by the small sample size and the inclusion of only season as an explanatory variable. Although our parsimonious model structure can minimize the risk of overfitting, it may have prevented the models from fully capturing other potential environmental influences on bat activity. Thus, the future studies should address these problems by increasing sample sizes, tracking the same individuals across seasons within the same year, monitoring environmental variables concurrently, and utilizing high-resolution tracking systems such as the Advanced Tracking and Localization of Animals in real-life Systems (ATLAS), a ground-based system optimized for small animals including bats (Toledo et al., 2020; Weiser et al., 2016).

CONCLUSIONS

To summarize, our results suggested that bats may adjust their movement strategies in temporal and spatial dimensions to cope with different environmental conditions across seasons. Temporally, bats may respond to seasonal changes in food resources by increasing their foraging time and adopting lower energy expenditure activity patterns. The observed trend toward longer activity patterns may be associated with larger spatial utilization ranges, including an expansion in the vertical dimension (3D space use), which could help ensure sufficient food acquisition.

DATA AVAILABILITY

Data are available from Figshare at https://doi.org/10.6084/m9.figshare.28845701.v1

SUPPLEMENTARY DATA

Supplementary data to this article can be found online.

COMPETING INTERESTS

The authors declare that they have no competing interests.

AUTHORS’ CONTRIBUTIONS

Z.W. and T.J. conceived and designed the study. Z.W., Z.H., and M.S. carried out field experiments. Z.W., L.G. and H.W. analyzed the data and wrote the manuscript, and H.W., T.J. and J.F. revised the manuscript. All authors read and approved the final version of the manuscript.

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