Article

DO NEST-DEPARTURE AND NEST-RETURN RHYTHMS OF BUMBLEBEES ALIGN WITH COMMUNITY-LEVEL FLOWER VISITATION PATTERNS?

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Abstract—Bumblebees (*Bombus* spp.) are key high-elevation pollinators, yet their nest-level activity patterns and their synchronization with community-level floral visitation remain poorly understood. In previous studies, bumblebees showed bimodal floral visitation patterns in wild high-elevation communities, with activity peaks in the morning and afternoon. However, it is unknown whether nest activity mirrors these patterns in the field. Understanding this relationship is important for linking colony-level behaviour with pollination dynamics in natural communities. In this study, we investigated the daily departure and return behaviour of a natural colony of *Bombus lepidus* in the Hengduan Mountains, southwestern China, and their coordination with floral visitation in the nearby communities during the 2019 flowering season. We also examined associations between environmental factors and nest activity across the day. During the observation period, overall activity declined over the season, whereas the proportion of returning bees carrying pollen increased. Daily nest departures and returns exhibited pronounced bimodal patterns that closely paralleled floral foraging activity, albeit with slight temporal offsets between the independently sampled activity distributions. Colony activity was associated with nest-entrance environmental conditions, showing unimodal (non-linear) responses: activity peaked at a nest entrance air temperature of approximately 24 °C and nest entrance relative humidity of 50–55%. Morning activity was relatively insensitive to environmental variation, whereas afternoon behaviour was more responsive to microclimatic fluctuations. Our results suggest that nest-entrance microclimate may be linked to daily activity patterns and their temporal alignment with floral resources at a local scale.

Keywords—Temporal niche, *Bombus lepidus*, bumblebee nest activity, foraging behaviour, environmental factors

INTRODUCTION

Temporal coordination and matching of plant-pollinator interactions can span a wide range of timescales, from seasonal rhythms across different periods of the year to fine-scale rhythms occurring over minutes or even seconds, ensuring that pollinators remain active during the flowering periods of plants, benefiting both interacting partners (Boisvert & Sherry 2006). Numerous studies have shown that both plant flowering and pollinator foraging behaviours are also influenced by endogenous circadian rhythms shaped by the Earth's daily rotation (Dunlap et al. 2004). Pollinator activity varies considerably among taxa. While most pollinating animals, such as butterflies, bees, and birds, are primarily diurnal, some moths and bats exhibit nocturnal activity patterns (Bloch 2010; Borges et al. 2016; Johnson et al. 2019).

The daily rhythms of pollinators (e.g., timing of departure from and return to the nest) and the flowering rhythms of plants both influence pollinator foraging and plant pollination. For example, a single successful pollination visit can markedly advance the timing of flower closure of some plants (Fründ et al. 2011). Flowers of some species within the subfamily Cichorioideae typically open in the early morning and close one to two hours after pollination (Bloch et al. 2017). Similarly, plants can influence and regulate the temporal activity of pollinators; studies have shown that a successful foraging event by *Melipona fasciata* (a stingless bee) may cause the bee to depart earlier from the nest on the following day, altering its foraging rhythm (Biesmeijer 1998). Furthermore, these rhythms are flexible and respond to resource availability and sensory constraints; for example, while bumblebees can exploit known food sources in low light, they tend to return to the nest with significantly smaller pollen loads as evening light fades, indicating a strategic trade-off between foraging gains and the sensory costs of navigation (Chapman et al. 2022; 2024). However, our understanding of the circadian organization underlying pollination-related traits remains largely based on studies of *Apis mellifera*, and much less is known about wild bees and their floral partners (Bloch et al. 2017). For most wild bees, it remains unclear to what extent daily rhythms are regulated by endogenous circadian clocks and external environmental cues, such as light and temperature cycles, and how these factors interact (Bloch et al. 2017).

A better understanding of pollinator daily rhythms requires considering activity patterns at the nest level. In social bees, nest-level activity patterns provide a direct connection between individual foraging decisions and colony-level activity dynamics. The nest entrance links colony activity with external microclimatic conditions and influences worker departure and return. However, little is known about how *Bombus* nest-level diurnal activity patterns (e.g., departure from and return to the nest) correspond to, or deviate from, community-level visitation patterns, and how these patterns are modulated by microclimatic factors. While previous studies have highlighted the importance of light as a cue for individual decision-making at the nest (Chapman et al. 2022; 2024), it remains unclear how these fine-scale behavioural responses manifest in high-altitude environments where solar radiation and temperature fluctuate drastically (Mani 1968). Therefore, understanding bumblebee nest activity cycles and their associations with nest-entrance microclimatic conditions is essential for revealing how colony-level activity is linked to foraging behaviour and plant–pollinator temporal matching in alpine ecosystems

Fine-scale daytime variation in pollinator visitation remains largely unexplored in the Hengduan Mountains region. Characterizing visitation patterns in relation to environmental conditions is important for revealing how pollination interactions are structured in alpine ecosystems. Visitation rates are influenced by weather conditions, which can affect bee flight performance and foraging behaviour (Vicens & Bosch 2000; Peat & Goulson 2005; Wratt 1968; Heinrich & Heinrich 1983; Corbet et al. 1993; Woods et al. 2005; Abou-Shaara 2014). A previous study showed that, on sunny days, diurnal pollinator visitation in the Hengduan alpine environment commonly followed a bimodal pattern, which is associated with diurnal variation in solar radiation (Xu et al. 2021). As large ectotherms, *Bombus* may reduce midday foraging activity when intense solar radiation elevates body temperature beyond optimal levels or increases evaporative water loss (Prendergast 2022), which may contribute to variation in daily activity patterns under high-altitude conditions. Such behavioural adjustments may reflect the constraints imposed by intense solar radiation in alpine environments, where excessive heating can reduce foraging performance and influence the timing of pollinator activity peaks (Xu et al. 2021).

Among alpine pollinators, bumblebees (*Bombus* spp.) are a key taxonomic group within the family Apidae, comprising 15 subgenera (Williams et al. 2008). Compared with honey bees (*Apis* spp.), bumblebees have several advantages in high-altitude and cold environments, including longer proboscises, larger body size, dense hair coverage, tolerance to low temperatures, and buzz pollination behaviour, making them especially important in these environments (Heinrich 1979; Goulson 2010). Despite their ecological importance, detailed data on bumblebee natural history and biological traits remain concentrated

on a few model species, leaving many taxa poorly studied (Hines 2025). These knowledge gaps highlight the need for detailed studies on the natural history and ecological traits of alpine bumblebees to understand better their role in alpine ecosystems.

Bombus (*Pyrobombus*) *lepidus* is widely distributed in the subalpine regions of the Hengduan Mountains. Beyond basic taxonomic and geographic information, quantitative data on its colony characteristics, phenology, nesting ecology, individual size, and foraging are almost entirely lacking (Hines 2025). Based on this research gap, the present study focuses on a single naturally occurring nest of *B. lepidus* to provide rare quantitative observations of nest-level activity in this poorly studied species. We also investigate whether nest departure and return behaviours correspond with community-level visitation patterns and are associated with local environmental conditions. Our study integrates nest-level activity observations, community-level floral visitation, and local microclimatic measurements to examine the links between bumblebee nest activity and flower-visitation patterns (Fig. 1). Specifically, we aim to address two key questions: 1) How do nest departure and return rhythms correspond with community-level floral visitation patterns, and are there temporal lags among these behaviours? 2) How are nest departure and return activities associated with nest-entrance microclimatic conditions, including temperature, humidity, wind velocity, and solar radiation? By integrating nest behaviour with community-level pollination dynamics and local microclimatic conditions, this study contributes to understanding the temporal structuring of pollination interactions in alpine systems.

MATERIALS AND METHODS

STUDY LOCATIONS AND SAMPLING OF INTERACTION DATA

This study was conducted at Yulong Snow Mountain near the city of Lijiang, Northwestern Yunnan, China (27°00′N, 100°10′E) at about 3200 m a.s.l. During the 2019 flowering season, we unexpectedly discovered only one natural nest of *B. lepidus* in the ecotone between a meadow and a forest transect, representing one colony that was

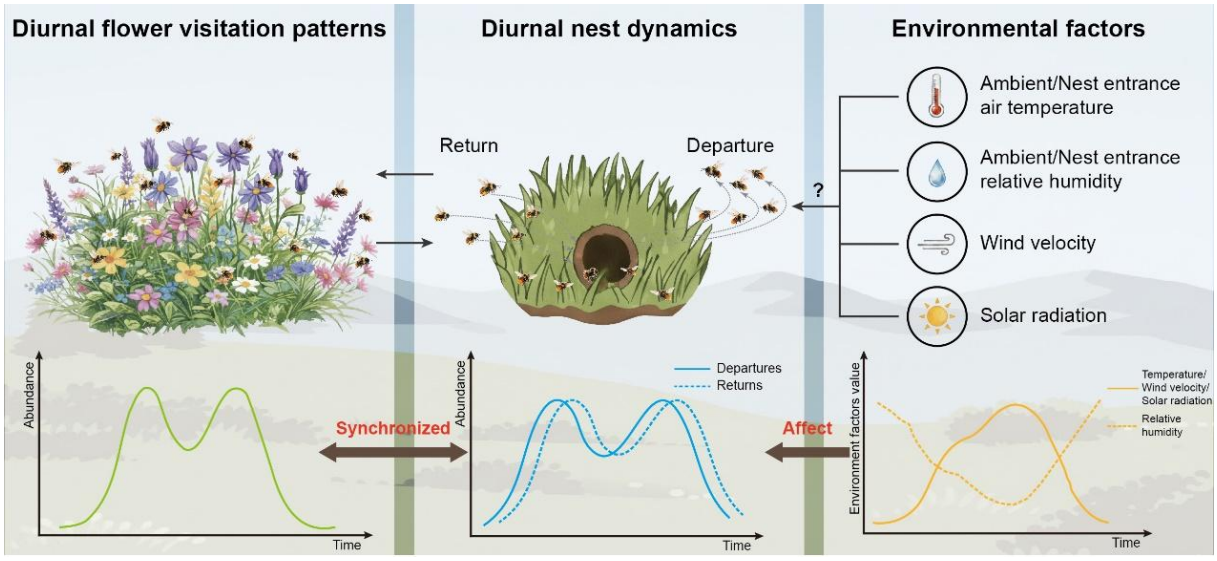


Figure 1. Conceptual framework illustrating the relationships among nest activity patterns, flower visitation, and environmental conditions in *Bombus lepidus* at Yulong Snow Mountain. The curves in the three boxes represent the diurnal patterns of community-level flower visitation (green), nest departure and return activity (blue solid and dashed lines), and the daily variation in different environmental factors (orange solid and dashed lines), respectively. Illustrations of the flower visitation community, bumblebee nest, and background elements were generated using artificial intelligence (AI)-assisted image tools. Bumblebee images were derived from original photographs taken by the first author and subsequently processed into graphical elements. The overall design, layout, and final assembly of the figure were completed by the first author.

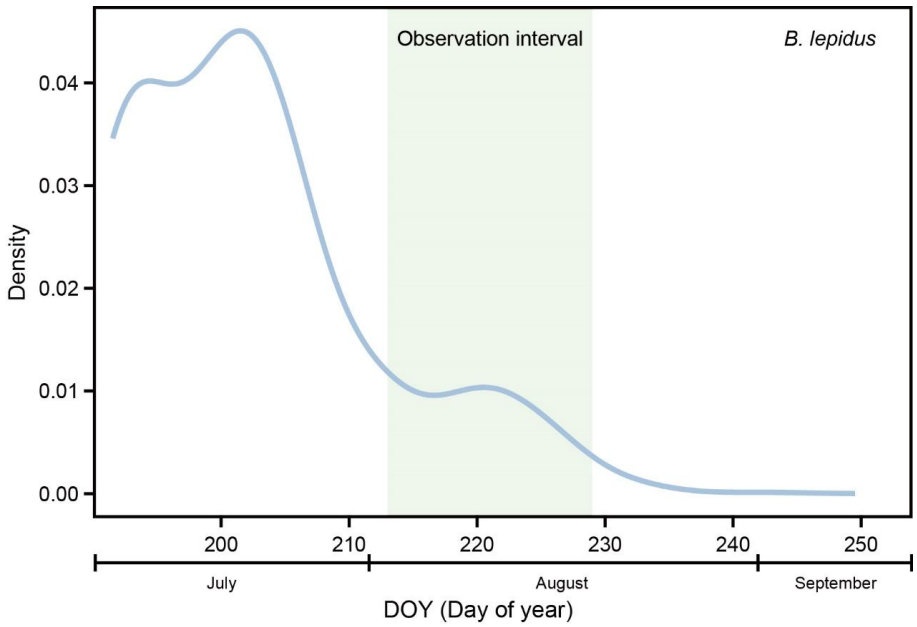


Figure 2. Seasonal dynamics of visitation activity and the specific timing of nest departure and return observations for *Bombus lepidus*. The blue line indicates the floral visitation dynamics of *B. lepidus* across the Day of Year (DOY). The light green shaded area represents the nest observation period.

subsequently monitored under natural conditions. The nest was located underground, adjacent to a rocky wall bordering a flower bed in the Yunnan Lijiang Forest Ecosystem National Observation and Research Station. This rare finding provided a unique opportunity to observe bumblebee nesting activity under natural conditions, which motivated us to initiate this component of the study. The nest was located between the forest and meadow plots described by Xu et al. (2021), more than 100 m from each. This provided an opportunity to compare nest activity with floral visitation patterns in the surrounding habitats. .

We conducted field observations of the nest from August 2 to August 17, 2019. The analysis of *B. lepidus* visitation phenology during the peak flowering season of 2019 (July–September) showed that peak visitation occurred in early July and subsequently declined throughout the flowering season. By late August and September, visitation activity was very low (Fig. 2). Therefore, our observation period (August 2–17) corresponded to the later stage of the flowering season, when floral visitation had already declined from its seasonal peak. Most active individuals observed at the nest entrance were workers, although males and new queens were occasionally recorded during this period (Fig. 2).

Under sunny day conditions, we conducted a six-day continuous field observation of a *B. lepidus* nest located in a crevice between roadside rocks under forest canopy (from 8:00 to 20:00). During this period, we systematically recorded the timing of individual workers leaving and returning to the nest. For each returning worker, we also recorded whether it carried obvious pollen loads on its corbiculae, allowing us to determine the proportion of individuals returning with pollen. To ensure consistent observations and minimize observer-related variation and disturbance to nest activity, one observer was seated 1.5 m away from the nest entrance and recorded all the data. These observations allowed us to characterize the diurnal rhythm of nest-related activity and to link it with community-level floral visitation patterns collected along the meadow and forest transects (Fig. 1).

We extracted the daily floral visitation data of *B. lepidus* from Xu et al. (2021) from the meadow and forest transects near the nest on sunny days in 2019. The original survey included three meadow transects and three adjacent forest transects, with each transect measuring 100 m in length and 3 m in width. Plant–pollinator interactions were systematically recorded during daylight hours (08:00–20:00) using standardized transect surveys (Xu et al., 2021) on 16 days: 14, 17, 20, 22, 25, 26, 27, 28, 30, 31 July and 1, 2, 6, 8, 11, 15 August. For the present study, we selected the nearest meadow and forest transects to the *B. lepidus* nest, and the daily floral visitation data were aggregated from *B. lepidus* visitation records across these two habitat transects.

The floral-visitation and nest-activity datasets were collected during the same season and study period but were not sampled on identical dates; comparisons between them therefore concern their aggregated diurnal activity distributions rather than contemporaneous responses on individual days.

Environmental abiotic factors

To investigate whether abiotic factors influenced the diurnal rhythm of *B. lepidus* nest activity, we recorded half-hourly averages of ambient temperature (°C; AT), relative humidity (%; RH), wind velocity (m/s; WV), and solar radiation ($\mu mol \cdot m^{-2} \cdot s^{-1}$, SR) on all observation days using data from the local weather station located in the meadow–forest ecotone at one of our field sites (Fig. 3), managed by the Yunnan Lijiang Forest Ecosystem National Observation and Research Station. The weather station is located about 50 m away from our observed nest and was used to characterize broader ambient environmental conditions around the study site rather than the exact microclimate experienced by bees at the nest entrance.

In addition, we measured environmental conditions specifically at the nest entrance, including temperature (°C; NT) and relative humidity (%; NH), using HOBO data loggers (Onset Computer Corporation, USA) to characterize the microclimatic conditions experienced by workers when entering and leaving the nest (Fig. 3).

Statistical analysis

All statistical analyses were conducted using R Statistical Software (version 4.3.1; R Core Team, 2023) with the RStudio interface (version 2023.9.0.463; RStudio Team, 2023).

Analysis of daily nest dynamics of bumblebee

To understand better the temporal dynamics of *B. lepidus* nest activity, we analysed the diurnal patterns of worker departures from and returns to the nest based on continuous field observations. The activity data were analysed using a non-parametric kernel density estimation method (Ridout & Linkie 2009), following the analytical approach for diurnal activity patterns described by Xu et al. (2021). The analyses were performed using the "overlap" package (Ridout & Linkie 2009) and the "activity" package (Rowcliffe, 2019). Specifically, temporal overlap in departure and return nest activity patterns with foraging activity was quantified using the overlap coefficient (Δ), derived from fitted kernel density distributions using the *overlapEst* function in the "overlap" package. The statistical significance of the overlap was evaluated via non-parametric bootstrapping with 10,000 resamples using the *compareCkern* function in the "activity" package.

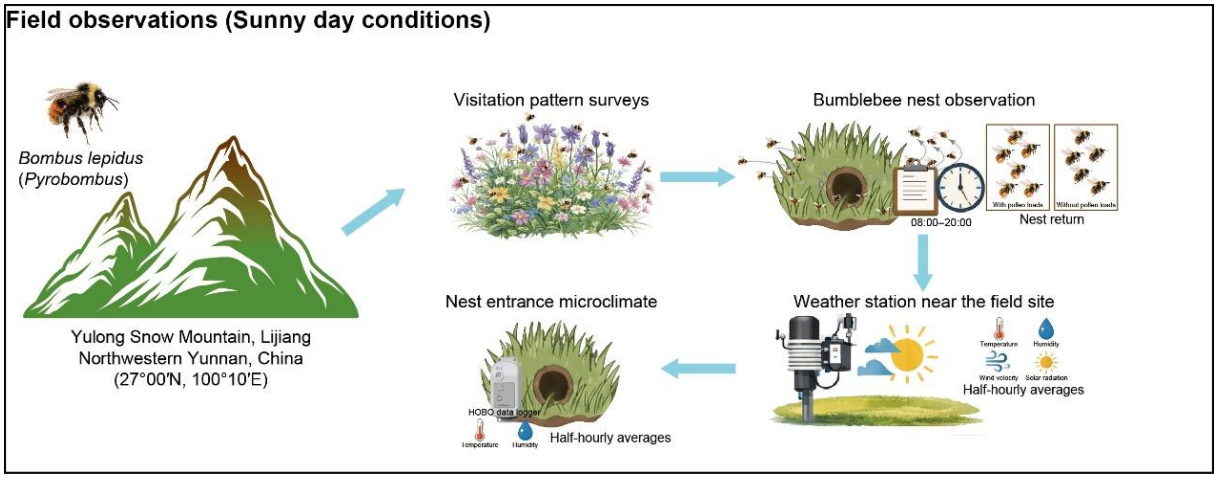


Figure 3. Field observation scheme and data collection design for investigating nest activity patterns, flower visitation, and their associations with environmental conditions in *Bombus lepidus* at Yulong Snow Mountain. Illustrations of the flower visitation community, bumblebee nest, and meteorological station were generated using artificial intelligence (AI)-assisted image tools. Bumblebee images were derived from original photographs taken by the first author and subsequently processed into graphical elements. The overall design, layout, and final assembly of the figure were completed by the first author.

Effects of environmental factors on the departures from and returns to the nest in Bombus lepidus

To determine whether abiotic factors influenced nest-departure and nest-return activity of *B. lepidus*, we fitted generalized linear mixed models (GLMMs) with a negative binomial distribution using the "*glmmTMB*" package (Bates et al. 2015; Brooks et al. 2017), following Xu et al. (2021). Nest-departure and nest-return were analysed separately, with the number of workers recorded during each 30-min observation interval as the response variable. Explanatory variables included ambient temperature, relative humidity, solar radiation, wind velocity, and nest entrance air temperature and humidity, with observation day as a random factor. Continuous predictors were standardized, and quadratic terms were included for temperature, humidity, and solar radiation to account for nonlinear effects. To assess whether zero inflation was present, we used simulation-based diagnostics using the "DHARMa" package (Hartig 2024); it was not detected (all $P > 0.6$). Model selection used AICc-based dredging using the "MuMIn" package (Bartoń 2025), starting from a global model containing all candidate predictors. Models were ranked according to AICc values, and the model with the lowest AICc was considered the most supported model. Model selection used AICc-based dredging in the "MuMIn" package (Bartoń 2025), starting from a global model containing all candidate predictors. Models were ranked according to AICc values, and the model with the lowest AICc was considered the most supported model. Because multiple models often received comparable support, we performed model averaging across all candidate models with ΔAICc < 2 to account for model uncertainty. Inference was based primarily on model-averaged coefficients across models with ΔAICc < 2; the highest-ranked individual model is also presented for comparison. Final parameter estimates and 95% confidence intervals were derived from the model-averaged coefficients. The most supported model was also reported for comparison. This approach was used to identify the combination of predictors that provided the strongest support among the candidate models, while recognizing that model selection may introduce uncertainty. The significance of fixed effects in the final models was assessed using Type III Wald chi-squared tests via the Anova function in the "car" package (Fox & Weisberg 2019). Model assumptions and multicollinearity were checked via residual diagnostics and variance inflation factors (VIFs) implemented in the "performance" package (Lüdecke et al. 2021), and correlation coefficients among environmental predictors included in the global models. The VIF values for predictors retained in the most supported models and the global models combining departure and return data were calculated and are presented, respectively (Tables S1 and S4). Pairwise Spearman correlation coefficients among environmental predictors were also calculated (Table S6).

To evaluate the relative importance of diel cycles versus environmental covariates, we compared three nested models using AIC: an environment-only model (without time terms), a time-only model and a combined model including both. The environment-only model was best (AIC = 929.16, AIC weight = 0.854), followed by the combined model (AIC = 932.69, ΔAIC = +3.53, weight = 0.146), while the time-only model performed considerably worse (AIC = 952.34, ΔAIC = +23.18, weight < 0.001). Thus, time terms did not improve fit and were therefore excluded from the final model, confirming that nest activity was primarily associated with environmental conditions.

Furthermore, to evaluate temporal autocorrelation within observation days, we employed two complementary methods. First, temporal autocorrelation of model residuals was assessed separately for each observation day using the *acf* function, with lag-1 autocorrelation evaluated against the 95% confidence intervals. Autocorrelation function (ACF) analyses of model residuals showed limited and inconsistent temporal autocorrelation, with significant lag-1 autocorrelation detected on two of six observation days for both nest departure and nest return behaviours (Table S7). Second, we conducted formal model comparisons by fitting competing models: a baseline model with a random intercept for Day only (assuming independence of within-day residuals), and an alternative model incorporating a first-order autoregressive [AR1] correlation structure for residuals within each day. The AR1 model showed better fit than the random-

intercept model for both behaviours, with more pronounced improvement for nest-return behaviour (AR1: 533.67 vs. RI: 540.53; ΔAIC = 6.85; ϱ = 0.70; P = 0.004) than for nest-departure behaviour (AR1: 419.28 vs. RI: 422.87; ΔAIC = 3.59; ϱ = 0.55; P = 0.022). The AR1 structure was selected if it produced a substantially lower AIC (ΔAIC > 2) and a significant likelihood ratio test (P < 0.05), indicating that within-day temporal dependence required explicit modelling.

Based on the observed bimodal pattern of *B. lepidus* nest activity, with distinct peaks in the morning and afternoon, we further conducted separate GLMMs analyses to identify the abiotic factors associated with each activity peak. A categorical variable distinguishing observations made before and after 13:00 was used to separate the two activity phases. We selected 13:00 as the threshold because previous work (Xu et al. 2021) showed that pollinator visitation activity reached a low level at this time of day. Moreover, 13:00 approximately corresponds to the period of peak daily solar radiation at the study site (Xu et al. 2021). Each model included the same explanatory variables and quadratic terms as described above. We calculated the coefficient of determination (R^2; Nakagawa & Schielzeth 2013) for each model and adjusted the significance levels using the Benjamini–Hochberg false discovery rate (FDR) procedure (Benjamini & Hochberg 1995; Benjamini & Yekutieli 2001; Benjamini 2010).

RESULTS

During the observation period, *B. lepidus* nest departures, returns, and total activity were highest at the beginning of the season and gradually declined over time. Departure and return trips followed similar decline trends, with return counts generally exceeding departures (Fig. 4A). Furthermore, the number of returns with pollen loads was highest at the beginning of the observation period and gradually decreased. In contrast, the proportion of returns with pollen loads showed an increasing trend, reaching the highest levels in later observations (Fig. 4B).

DAILY NEST DYNAMICS OF *BOMBUS LEPIDUS*

We found a consistent diurnal pattern of flower visitor activity for *B. lepidus*, which exhibited a distinct bimodal activity pattern. Visitation activities reached two peaks: the first occurred around 11:00 am to 12:00, and the second appeared between 16:00 and 17:00 (Fig. S1A).

The nest departure behaviour of the bumblebees showed a similar bimodal temporal pattern to visitation activity (Fig. S1B). The return behaviour to the nest also followed a bimodal pattern, but the afternoon peak was slightly delayed compared to the nest departure peak, indicating a time delay in returning to the nest after foraging (Fig. S1C). Further analysis of whether the bumblebees return to the nest with pollen loads showed that both carrying and not carrying pollen loads follow a bimodal pattern, with more individuals carrying pollen loads during both peaks compared to those not carrying pollen loads (Fig. S1D–E).

During the observation period, we recorded a total of 205 floral visits by *B. lepidus*, 171 nest departures, and 286 nest returns. Among the returning workers, 163 individuals carried pollen loads, whereas 123 individuals returned without pollen loads. All behaviours exhibited bimodal activity patterns with substantial temporal overlap despite slight differences in peak time (Table 1; Fig. 5). Nest departure and return behaviours showed similar temporal patterns and did not differ significantly in their activity patterns. Floral visitation differed significantly from both nest departure and return behaviours. The morning visitation peak occurred approximately 1.5 hours later than the peaks of both nest behaviours, whereas the afternoon visitation peak coincided with nest departure but not with nest return (Table 1; Fig. 5). Similarly, returns with and without pollen loads showed substantial temporal overlap and no significant differences in activity patterns. Their morning peaks were nearly identical, whereas the afternoon peak of pollen-carrying returns occurred approximately 2.5 hours later than that of returns without pollen loads (Table 1; Fig. 5). Floral visitation also differed significantly

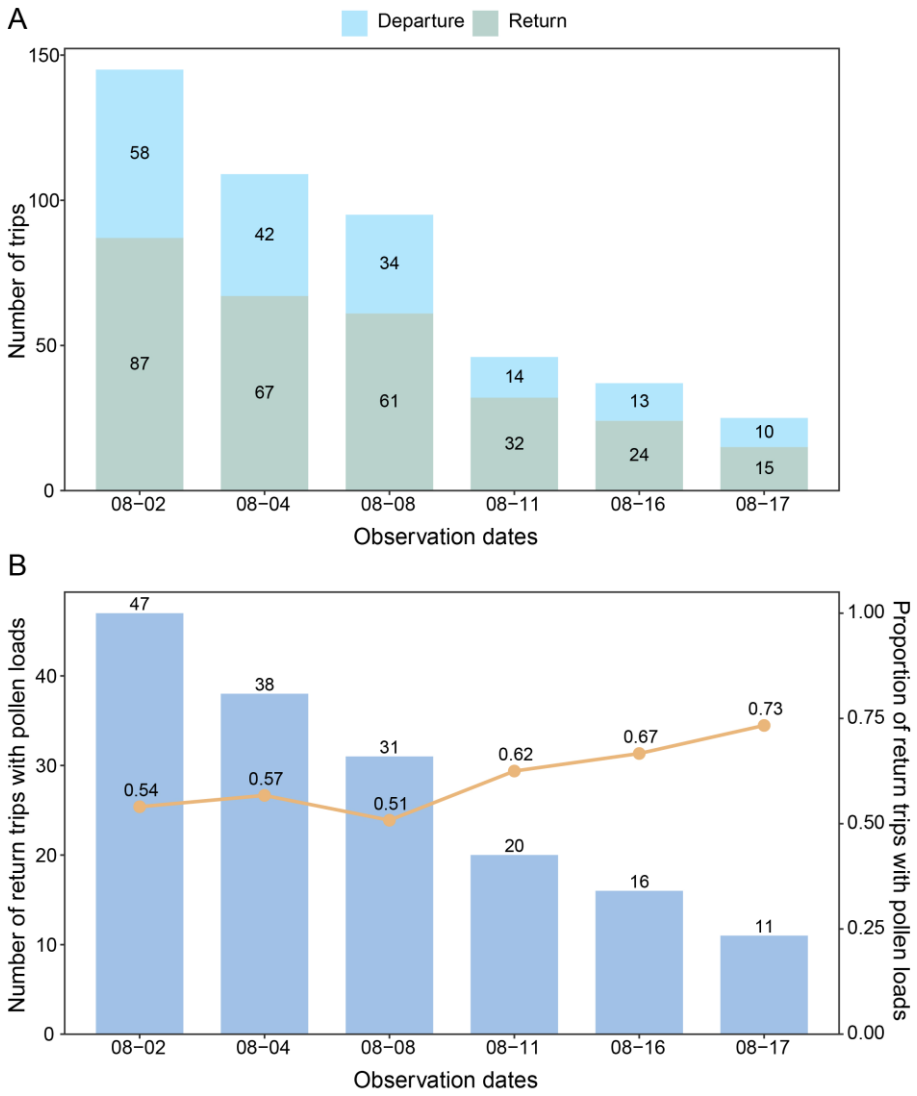


Figure 4. Dynamics of nest departure and return activities and the proportion of returns with pollen loads during the observation period. (A) Variation in the numbers of nest-departure trips and nest-return trips across different observation dates. (B) The number of return trips with pollen loads and their proportion relative to the total number of return trips.

from both return types. In the morning, the visitation peak occurred approximately 1.5 hours later than both return peaks. In the afternoon, pollen-carrying returns peaked about 1.5 hours later than floral visitation, whereas returns without pollen loads peaked about one hour earlier (Table 1; Fig. 5).

Effects of environmental factors on nest departure and return

During the observation period, ambient temperature ranged from 10.0 to 22.8°C (mean ± SD = 16.68 ± 3.12°C), relative humidity ranged from 37.4 to 99.8% (mean ± SD = 69.7 ± 18.2%), solar radiation ranged from 5.0 to 742.0 μmol·m^{-2}·s^{-1} (mean ± SD = 268.00 ± 223.34 μmol·m^{-2}·s^{-1}), and wind velocity ranged from 0 to 4.8 m s^{-1} (mean ± SD = 1.32 ± 1.09 m s^{-1}). At the nest entrance, air temperature ranged from 10.6 to 44.7°C (mean ± SD = 18.38 ± 5.44°C), and nest entrance relative humidity ranged from 13.1 to 99.8% (mean ± SD = 70.1 ± 19.6%).

For nest departure behaviour, model selection identified 970 competing models with varying levels of support. The highest-ranked model had a ΔAICc of 0 and an AICc weight of 0.073, while 3 models showed similar support (ΔAICc < 2, weights ranging from 0.033 to 0.053), indicating model selection uncertainty (Table S2). For nest return behaviour, 970 competing models were retained, with the highest-ranked model having a ΔAICc of 0 and an AICc weight of 0.092. Three other models also received comparable support (ΔAICc < 2, weights ranging from 0.035 to 0.055; Table S2).

Generally, nest entrance air temperature was the strongest predictor associated with both nest

Table 1. Results of the degree of overlap between diurnal activity patterns for different activity comparisons. Values were estimated using non-parametric bootstrap iterations comparing pairs of activity patterns. Significant differences ($P < 0.05$) are shown in bold.

Comparisons	Overlap coefficient (Δ)	Null	SE-Null	*P*-value
Nest–departure vs. Nest–return	0.928	0.921	0.024	0.583
Visitation vs. Nest–departure	0.835	0.935	0.021	**< 0.001**
Visitation vs. Nest–return	0.824	0.943	0.017	**< 0.001**
Nest–return: With vs. Without pollen loads	0.860	0.902	0.030	0.099
Visitation vs. With pollen loads	0.795	0.938	0.021	**< 0.001**
Visitation vs. Without pollen loads	0.853	0.930	0.024	**0.007**

departure and return behaviours. Both behaviours increased with nest entrance temperature, reached a maximum, and then declined, showing a unimodal relationship with nest entrance temperature (Table 2; Table S1). Departure behaviour was also associated with relative humidity. Similarly, return behaviour was primarily associated with nest entrance air temperature (Table 2; Table S1). These relationships were supported by the statistical analyses (departure: NT, $P < 0.001$; NT^2, $P < 0.001$; RH, $P < 0.001$; return: NT, $P < 0.001$; NT^2, $P < 0.001$; Table 2; Table S1). The selected best models were consistent with the model-averaged results from the competing models (ΔAICc < 2), further supporting the robustness of these relationships (Table S3). The nest-entrance air temperature was positively correlated with air temperature at the nearby weather station (~1.5 m above ground; r = 0.768, $P < 0.05$, Table S6), suggesting that nest entrance temperature was related to both ambient conditions and the microclimate experienced by the bees. Departure behaviour showed a stronger association with humidity.

By analysing the effects of environmental factors on bumblebee nest departure and return behaviour separately for before 13:00 and after 13:00, we found clear diurnal differences in behavioural responses. Before 13:00, both nest departure and return behaviours exhibited relatively weak associations with ambient and nest-entrance microclimates, characterized by low model explanatory power (marginal R^2 = 0.002–0.257; Table 3; Table S5; Fig. S4). The only exception was the significant linear effect of NT on return behaviour ($P = 0.028$; Table 3; Table S5; Fig. S3A), whereas its quadratic term was not significant.

After 13:00, both departure and return behaviours showed stronger responses to environmental conditions, with higher explanatory power (marginal R^2 = 0.133–0.822; Table 3; Table S5; Fig. S4). Departure frequency increased with ambient temperature and wind velocity, while exhibiting unimodal responses to solar radiation, nest entrance temperature, and nest entrance humidity. Peak departure activity occurred at approximately 450 $\mu mol \cdot m^{-2} \cdot s^{-1}$ solar radiation, 24°C nest entrance temperature, and 50% nest entrance humidity (Fig. S2). Nest entrance temperature remained the strongest predictor variable associated with departure behaviour (Table 3; Table S5). Similarly, return frequency was positively associated with wind velocity and negatively associated with relative humidity, while exhibiting unimodal responses to ambient temperature, solar radiation, nest entrance temperature, and nest entrance humidity. Peak return activity occurred at approximately 21°C ambient temperature, 450 $\mu mol \cdot m^{-2} \cdot s^{-1}$ solar radiation, 24°C nest entrance temperature, and 55% nest entrance humidity before declining (Fig. S3). Nest entrance temperature again emerged as the most important predictor associated with return behaviour (marginal R^2 = 0.822; Table 3; Table S5).

DISCUSSION

This study provides one of the first quantitative descriptions of nest-departure and nest-return behaviours in a naturally occurring colony of the alpine bumblebee *Bombus lepidus* in the Hengduan

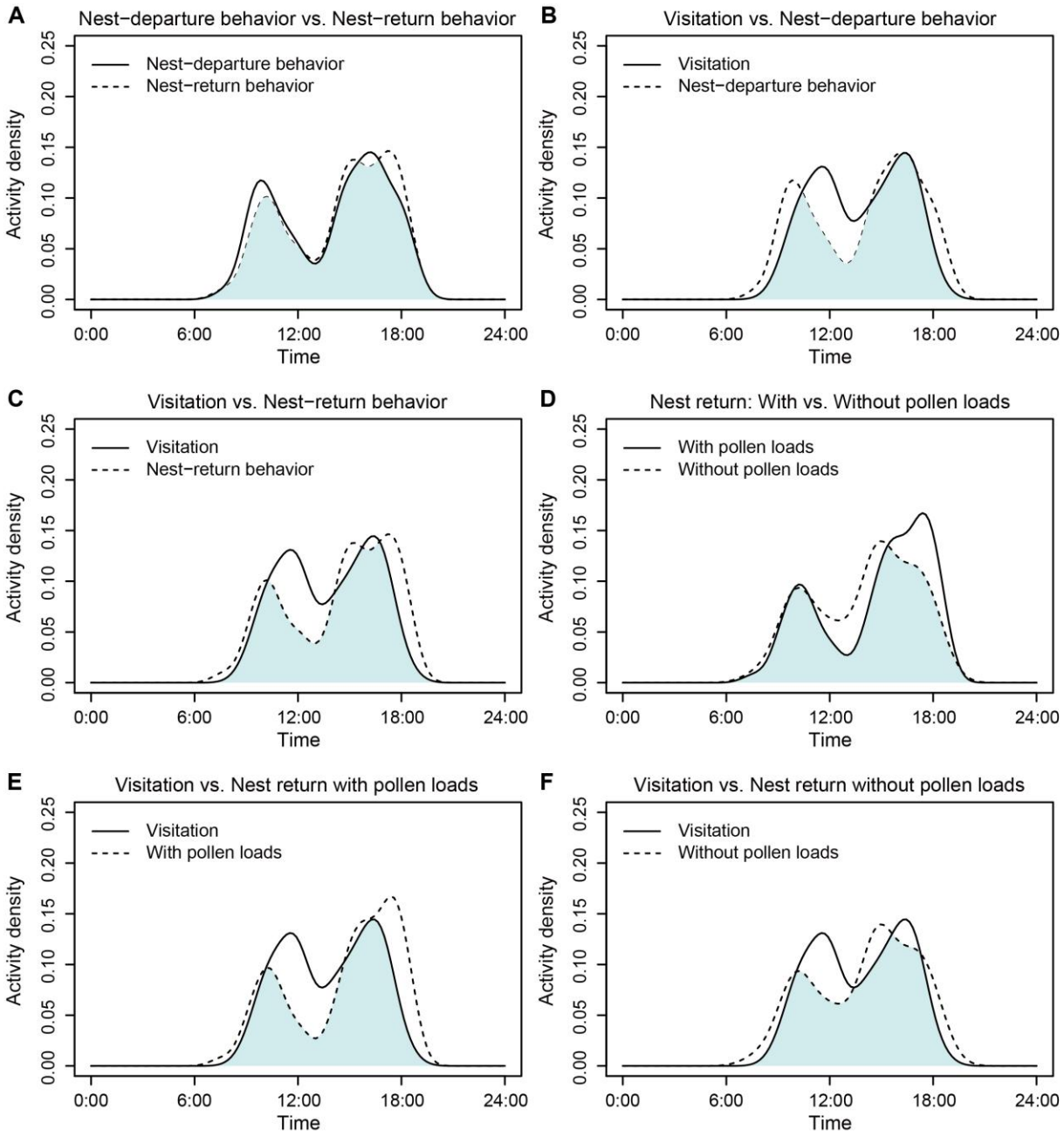


Figure 5. Comparison of diurnal activity patterns between flower visitation and nest-related behaviours of *Bombus lepidus*. (A) Nest-departure vs. nest-return behaviour; (B) Visitation vs. nest-departure behaviour; (C) Visitation vs. nest-return behaviour; (D) Nest return with vs. without pollen loads; (E) Visitation vs. nest return with pollen loads; (F) Visitation vs. nest return without pollen loads. The solid and dashed curves are fitted circular kernel distributions for the respective behaviours. The overlapping coefficient equals the area in light blue.

Mountains. Our findings suggest that nest-level activity schedules are closely aligned with community-level flower visitation, indicating a potential temporal link between colony activity and pollination-related behaviour in alpine ecosystems.

The observed activity patterns were associated with nest-entrance microclimatic conditions, suggesting that local environmental variation may contribute to the regulation of bumblebee activity under high-altitude conditions. Although overall activity decreased later in the season, the proportion of returning bees carrying pollen increased, potentially indicating a seasonal shift in foraging outcomes. These results provide insights into temporal relationships between nest activity

Table 2. Results from the highest-ranked individual models. Candidate models were constructed from a global generalized linear mixed model including linear and quadratic terms of environmental predictors. Models were ranked using Akaike's information criterion (AICc) corrected for small sample size, and inference was based on the most supported models. Values are derived from generalized linear mixed models and significance was assessed with Type III Wald Chi-square tests. Significant differences ($P < 0.05$) are shown in bold.

Parameter	Chisq	Df	Pr (>Chisq)
Model (Departure): Abundance ~ RH + NT + NT^2 + (1 | Day) + AR1 (time)			
Intercept	0.020	1	0.888
Relative humidity (RH)	5.084	1	**0.024**
Nest entrance air temperature (NT)	16.502	1	**< 0.001**
Nest entrance air temperature^2 (NT^2)	12.951	1	**< 0.001**
Model (Return): Abundance ~ NT + NT^2 + (1 | Day) + AR1 (time)			
Intercept	1.992	1	0.158
Nest entrance air temperature (NT)	14.717	1	**< 0.001**
Nest entrance air temperature^2 (NT^2)	12.427	1	**< 0.001**

and foraging-related behaviour in the observed *B. lepidus* colony, highlighting the value of incorporating nest-level observations into studies of plant–pollinator interactions in alpine systems.

Although studies based on a single nest are relatively uncommon, such studies have been used to document bee natural history and colony-level behavioural patterns, particularly for rare or difficult-to-study colonies. For example, Koch and Cane (2022) explicitly reported that their study of *Bombus morrisoni* was based on a single nest and used detailed observations to describe nest architecture, colony composition, reproductive output, pollen storage, and wax-canopy construction. Similarly, Jacome-García et al. (2024) repeatedly monitored a single nest of the high-Andean stingless bee *Parapartamona zonata* over multiple months and used statistical analyses to examine temporal and environmental variation in foraging activity in relation to temperature, humidity, and sky conditions. Other bee studies have likewise used single nests to investigate nesting biology, immature development, and unusual nesting behaviour (Rozen 1991; Gibbs 2017; Amala et al. 2017; Rozen et al. 2018). These studies demonstrate that repeated observations from a single nest can provide valuable ecological and behavioural information, while also highlighting the importance of treating the nest as the biological unit of replication and avoiding broad species-level generalisations. Our study follows this precedent by providing detailed repeated observations of a naturally occurring *B. lepidus* colony, with the aim of characterising nest-departure and nest-return rhythms and their associations with environmental conditions rather than making population-level inferences about the species.

The study showed that *B. lepidus* nest activity and flower-visitation behaviour exhibit similar diurnal bimodal patterns, with nest departures and returns closely aligned with foraging peaks occurring around 10:00–11:00 and 15:00–16:00. Similar bimodal activity patterns have been reported in high-elevation pollinator communities, where flower visitation peaks in the morning and afternoon, likely driven by abiotic factors such as solar radiation and temperature thresholds (Xu et al. 2021; Knop et al. 2018; Zoller et al. 2020). Previous studies on bumblebee foraging rhythms have also shown that diurnal activity patterns remain stable even under extended daylight, indicating strong circadian regulation of foraging behaviour (Stelzer & Chittka 2010). This observed correspondence may reflect the combined effects of abiotic conditions and endogenous regulation on colony-level activity patterns, although further studies across multiple colonies are needed to evaluate the generality of this pattern. However, because our observations were obtained from only one natural colony of *B. lepidus*, the observed patterns should be interpreted as colony-specific rather than representative of the species as a whole. In addition, flower visitation patterns

Table 3. Results of the effect of separating the environmental variables associated with each diurnal abundance peak of nest departure and return behaviors independently. Values (including the Marginal R^2 values) are derived from generalized linear mixed models. Environmental variables' significance was corrected for multiple testing using the Benjamini–Hochberg false discovery rate (FDR) procedure and calculated as P adjusted. Significant differences ($P < 0.05$) are shown in bold.

Nest behavior	Environmental factors	*P* adjusted		Marginal R^2	Time of the day
		Variable	Variable^2		
Departure	Ambient temperature	0.503	0.317	0.082	Before 13:00
Departure	Ambient temperature	**0.020**	0.343	0.266	After 13:00
Departure	Relative humidity	0.486	0.861	0.083	Before 13:00
Departure	Relative humidity	0.170	0.794	0.162	After 13:00
Departure	Wind velocity	0.861	-	0.002	Before 13:00
Departure	Wind velocity	**< 0.001**	-	0.165	After 13:00
Departure	Solar radiation	0.794	0.535	0.037	Before 13:00
Departure	Solar radiation	**0.023**	0.145	0.133	After 13:00
Departure	Nest entrance air temperature	0.207	0.252	0.213	Before 13:00
Departure	Nest entrance air temperature	**< 0.001**	**0.002**	0.657	After 13:00
Departure	Nest entrance relative humidity	0.793	0.595	0.041	Before 13:00
Departure	Nest entrance relative humidity	**0.001**	**0.030**	0.263	After 13:00
Return	Ambient temperature	0.371	0.114	0.110	Before 13:00
Return	Ambient temperature	**0.003**	**0.019**	0.359	After 13:00
Return	Relative humidity	0.275	0.368	0.131	Before 13:00
Return	Relative humidity	**0.007**	0.222	0.277	After 13:00
Return	Wind velocity	0.482	-	0.013	Before 13:00
Return	Wind velocity	**< 0.001**	-	0.156	After 13:00
Return	Solar radiation	0.362	0.242	0.049	Before 13:00
Return	Solar radiation	**0.020**	**0.035**	0.140	After 13:00
Return	Nest entrance air temperature	**0.028**	0.109	0.257	Before 13:00
Return	Nest entrance air temperature	**0.019**	**0.006**	0.822	After 13:00
Return	Nest entrance relative humidity	0.222	0.362	0.100	Before 13:00
Return	Nest entrance relative humidity	**0.026**	**0.026**	0.259	After 13:00

recorded across the transects likely involved individuals from multiple nests, meaning that the two datasets represent different spatial scales. Therefore, comparisons between nest activity and community-level flower visitation should be interpreted cautiously. Further studies involving multiple nests and populations are needed to validate the generality of these behavioural patterns.

The observed differences in peak timing among nest departure, flower visitation, and nest return records constitute an important aspect of this study, offering descriptive insights into how aggregated colony activity and flower-visitation patterns are temporally distributed across the sampling periods. The morning flower visitation peak occurred slightly later than the nest activity peak, whereas the afternoon visitation peak preceded nest returns. These temporal offsets may reflect the time required for workers to complete foraging trips, although the underlying mechanisms require further investigation. Importantly, these rhythms are flexible, adjusting to resource availability and sensory limitations. For instance, bumblebees can still forage on known food sources under low-light conditions yet return with substantially smaller pollen loads as evening approaches, indicating a strategic trade-off

between foraging gains and navigation costs (Chapman et al. 2022). Together, these observations suggest a temporal correspondence between nest activity and foraging behaviour in this colony, but extrapolation to species-level pollination efficiency in alpine ecosystems should be made cautiously.

In this alpine environment, the *B. lepidus* colony exhibited pronounced diurnal foraging variation in nest activity and foraging-related behaviour, with changes in the timing and frequency of nest departures, returns, and flower visitation. These behavioural patterns were associated with nest-entrance microclimatic conditions, which may represent one of several environmental factors correlated with colony-level activity patterns. Given the observational nature of this study, these associations should be interpreted cautiously because environmental variables may covary with diel patterns. Similar to previous studies suggesting that bumblebee foraging rhythms involve both environmental conditions and intrinsic rhythms (Stelzer & Chittka 2010), our results suggest that this colony may adjust its activity schedule according to temporal variation in microclimatic conditions. Such patterns may reflect potential trade-offs between the energetic costs of foraging and resource acquisition, although these mechanisms were not directly tested in this study. Previous studies have suggested that temporal changes in foraging costs and benefits, including variation in competition and nectar availability, can influence pollinator activity patterns (Schaffer et al. 1979). However, the relative contributions of these factors to alpine bumblebee foraging dynamics require further investigation.

Evidence for microclimate-mediated behavioural regulation was provided by Karbassioon et al. (2023), who demonstrated that *Bombus terrestris* maintains relatively stable flight activity under adverse environmental conditions (e.g., low temperature and low light) compared with *Apis mellifera*, suggesting a certain degree of environmental tolerance. In our study, returning behaviour showed distinct periodicity and was associated with nest-entrance microclimate. Furthermore, the response to Nest entrance air temperature was non-linear; activity frequency increased with temperature up to a peak of 24°C before declining. This pattern is consistent with previous findings that bumblebee activity and performance may be constrained at high temperatures (Kenna et al. 2021), although the physiological mechanisms underlying the observed temperature–activity relationship remain unclear.

Beyond temperature associations, humidity at the nest entrance was also associated with variation in bumblebee behavioural responses, suggesting the potential importance of nest-entrance microclimate in shaping colony activity. Our results suggest a nonlinear association between nest activity and humidity in this colony, with activity levels highest around 50–55% relative humidity. Given the strong correlations between ambient temperature and relative humidity (–0.870), and between nest-entrance temperature and relative humidity (–0.895), we view these factors as coupled drivers and interpret our findings in terms of combined thermal-humidity conditions rather than separate effects. These findings suggest that nest entrance humidity may be an important microclimatic factor associated with behavioural responses. It may reflect not only external environmental conditions but also microclimatic conditions experienced by workers during nest departure and return.

High humidity is generally considered detrimental to pollen collection because it increases pollen adhesion and reduces handling efficiency (Peat & Goulson 2005). Nevertheless, bumblebees exhibit considerable environmental tolerance, with the proportion of pollen load–carrying foragers remaining relatively stable up to around 57% relative humidity (Karbassioon et al. 2023). At the same time, elevated humidity often enhances nectar secretion, allowing bumblebees to adjust their foraging strategies by shifting resource acquisition toward nectar to offset reduced pollen profitability (Willmer 1983). Such humidity-dependent trade-offs in resource use may be influenced by species-specific morphological traits, particularly those related to pollen transport capacity and proboscis structure (Willmer et al. 1994).

Although several studies have investigated the influence of microclimate on bee foraging activity in the field (e.g., Knop et al. 2018; Xu et al. 2021; Sisk et al. 2025), relatively few studies have

investigated the effects of nest-entrance microclimate on bee behavioural responses. Activity patterns in the nest may be shaped by both thermal constraints and temporal variation in pollen availability. For example, whilst the desert bee *Anthophora pauperata* showed clear morning and afternoon peaks in foraging activity, separated by a 2–3-hour midday period spent in their underground nests, this bimodal pattern was associated with pollen availability of its host plant rather than thermal constraints (Stone et al. 1999). Exploring this possibility in *B. lepidus* and other alpine bumblebees is another avenue of further research, as resource availability may act in concert or conflict with physiologically optimal thermal windows. Further research is also required to determine if bumblebees select their nest locations based on specific microclimatic conditions in alpine environments.

We also observed diurnal variation in pollen-collecting (carrying pollen loads) and non-pollen-collecting foraging (without pollen loads). A previous study showed that under dry, low-humidity conditions, bumblebees were more likely to collect pollen, particularly during midday when temperatures were higher and wind speeds were stronger, whereas they tended to collect nectar during morning and evening periods (Peat & Goulson 2005). Within a colony, larger bumblebees are more likely to collect pollen than smaller ones (Peat & Goulson 2005). In our study, the bimodal patterns of nest departure, return, and pollen-carrying behaviours observed in this *B. lepidus* colony suggest that temporal variation in foraging strategies may also contribute to variation in colony activity rhythms. Although pollen-carrying and non-pollen-carrying returns showed similar bimodal patterns, the afternoon peak of pollen-carrying returns occurred later than that of non-pollen-carrying returns, suggesting temporal differences in resource collection strategies. Further studies integrating floral resource availability are needed to determine whether pollen release dynamics contribute to these patterns.

Early summer is crucial for colony establishment and population growth, requiring a steady intake of energy and protein. Conversely, as colonies prepare for overwintering in late summer, foraging targets shift (Kitaoka & Nieh 2009; Döke et al. 2015). In our study, the proportion of returning *B. lepidus* workers carrying pollen increased as the season progressed. The mechanism underlying this pattern remains uncertain, as colony size, brood development, reproductive status, and seasonal changes in floral resource availability were not directly assessed. Further research is needed to determine whether this pattern reflects changes in colony requirements, resource availability, or foraging behaviour.

Conclusion

In this single observed colony of the alpine bumblebee *B. lepidus*, nest activity declined over the observation period and exhibited a bimodal diurnal pattern, showing temporal correspondence with community-level flower visitation patterns. Colony activity was associated with nest-entrance microclimate, with non-linear relationships detected for temperature and humidity. Seasonal increases in returning individuals carrying pollen may reflect changes in the composition of foraging trips associated with seasonal variation in microclimatic conditions, floral resource availability, and colony state, although these interpretations require further investigation. Although brood rearing may decline toward the end of the colony cycle, this aspect was not directly measured in this study, and therefore continued or increased pollen collection should be interpreted cautiously. Taken together, our observations provide detailed natural-history information on a poorly studied alpine bumblebee and suggest that nest activity patterns may be associated with both microclimatic variation and colony conditions. However, further studies involving multiple colonies and seasons are needed to evaluate the generality of these patterns and their broader ecological significance in alpine pollination systems.

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AUTHOR CONTRIBUTION

XX, ZXR and HW conceived and designed the experiments. XX and DW collected data in the field. XX led the manuscript writing, with contributions from ZXR, KSP, JO and HW in writing and revision. All authors contributed critically to the drafts and gave final approval for publication and agreed to be held accountable for the work performed.

DISCLOSURE STATEMENT

The authors have no conflict of interest to declare. Since co-author Jeff Ollerton is an Associate Editor of the Journal of Pollination Ecology, the peer-review process for this article was handled independently by another member of the editorial board.

GENERATIVE AI DISCLOSURE STATEMENT

Generative AI was used only to create some graphical elements in Figures 1 and 2. All content were reviewed and finalized by the authors. No AI tools were used for generating, analyzing, or altering research data.

DATA AVAILABILITY STATEMENT

Data available in the Figshare repository (DOI: 10.6084/m9.figshare.31943496) at: https://doi.org/10.6084/m9.figshare.31943496.

APPENDICES

Additional supporting information may be found in the online version of this article:

Table S1. Results of the most supported generalized linear mixed models evaluating the effects of ambient and nest-entrance environmental variables on bumblebee nest departure and return abundance, with multicollinearity diagnostics (variance inflation factor, VIF).

Table S2 Supported generalized linear mixed models (ΔAICc < 2) explaining nest departure and nest-return behaviours, with AICc values and model weights.

Table S3 Model-averaged parameter estimates from competing models (ΔAICc < 2) for nest departure and nest-return behaviours.

Table S4. Multicollinearity diagnostics (VIF) of environmental variables in global models of departure and return behaviour.

Table S5. Results of separate analyses of environmental variables associated with each diurnal peak in nest departure and return activity.

Table S6. Spearman correlation coefficients among environmental predictor variables included in the global GLMMs.

Table S7. Autocorrelation function (ACF) analyses of model residuals for nest departure and nest return behaviours across observation days.

Figure S1. Diurnal activity patterns in flower visitation pattern, nest-departure/return behaviour, nest return with/without pollen loads of *B. lepidus*.

Figure S2. The relationship between the number of nest-departure trips and environmental factors during the afternoon.

Figure S3. The relationship between the number of nest-return trips and environmental factors during the two periods.

Figure S4. The marginal R^2 values of environmental factors for nest-departure and nest-return behaviours across different times of the day.

REFERENCES

Abou-Shaara HF (2014) The foraging behaviour of honey bees, *Apis mellifera*: a review. Veterinarni medicina 59. https://doi.org/10.17221/7240-VETMED

Amala U, Shivalingaswamy TM, Kumar V (2017) An unusual nesting site by leaf cutter bee *Megachile* (*Aethomegachile*) *laticeps* Smith. Journal of the Kansas Entomological Society 90:77–81. https://doi.org/10.2317/JKES-D-17-00018.1

Bartoń K (2025) MuMIn: Multi-Model Inference. R package (version 1.48.11)

Bates D, Mächler M, Bolker B, Walker S (2015) Fitting Linear Mixed-Effects Models Using lme4. Journal of Statistical Software 67:1–48. https://doi.org/10.18637/jss.v067.i01

Benjamini Y (2010) Discovering the false discovery rate. Journal of the Royal Statistical Society: Series B (Statistical Methodology) 72:405–416. https://doi.org/10.1111/j.1467-9868.2010.00746.x

Benjamini Y, Hochberg Y (1995) Controlling the false discovery rate: a practical and powerful approach to multiple testing. Journal of the Royal Statistical Society: Series B (Methodological) 57:289–300. https://doi.org/10.1111/j.2517-6161.1995.tb02031.x

Benjamini Y, Yekutieli D (2001) The control of the false discovery rate in multiple testing under dependency.

The Annals of Statistics 29:1165–1188. https://doi.org/10.1214/aos/1013699998

Biesmeijer JC, Nieuwstadt MGLV, Lukács S, Sommeijer MJ (1998) The role of internal and external information in foraging decisions of *Melipona* workers (Hymenoptera: Meliponinae). Behavioral Ecology & Sociobiology 42:107–116. https://doi.org/10.1007/s002650050418

Bloch G (2010) The social clock of the honeybee. Journal of Biological Rhythms 25:307–317. https://doi.org/10.1177/0748730410380149

Bloch G, Bar-Shai N, Cytter Y, Green R (2017) Time is honey: circadian clocks of bees and flowers and how their interactions may influence ecological communities. Philosophical Transactions of the Royal Society B: Biological Sciences 372:20160256. https://doi.org/10.1098/rstb.2016.0256

Boisvert MJ, Sherry DF (2006) Interval timing by an invertebrate, the bumble bee *Bombus impatiens*. Current Biology 16:1636–1640. https://doi.org/10.1016/j.cub.2006.06.064

Borges RM, Somanathan H, Kelber A (2016) Patterns and processes in nocturnal and crepuscular pollination services. The Quarterly Review of Biology 91:389–418. https://doi.org/10.1086/689481

Brooks ME, Kristensen K, van Benthem KJ, Magnusson A, Berg CW, Nielsen A, Bolker BM (2017) *glmmTMB* balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. The R Journal 9:378–400. https://doi.org/10.32614/RJ-2017-066

Chapman KE, Cozma NE, Hodgkinson ABJ, English R, Gaston KJ, Hempel de Ibarra N (2022) Bumble bees exploit known sources but return with partial pollen loads when foraging under low evening light. Animal Behaviour 194:127–137. https://doi.org/10.1016/j.anbehav.2022.09.010

Chapman KE, Smith MT, Gaston KJ, Hempel de Ibarra N (2024) Bumblebee nest departures under low light conditions at sunrise and sunset. Biology Letters 20:20230518. https://doi.org/10.1098/rsbl.2023.0518

Corbet SA, Fussell M, AKE R, Fraser A, Gunson C, Savage A, Smith K (1993) Temperature and the pollinating activity of social bees. Ecological Entomology 18:17–30. https://doi.org/10.1111/j.1365-2311.1993.tb01075.x

Döke MA, Frazier M, Grozinger CM (2015) Overwintering honey bees: biology and management. Current Opinion in Insect Science 10:185–193. https://doi.org/10.1016/j.cois.2015.05.014

Dunlap JC, Loros JJ, DeCoursey PJ (2004) Chronobiology: Biological Timekeeping. Sinauer Associates, Sunderland, MA, USA.

Fox J, Weisberg S (2019) An R Companion to Applied Regression, Third edition., Sage, Thousand Oaks CA.

Fründ J, Dormann CF, Tscharntke T (2011) Linné's floral clock is slow without pollinators – flower closure and plant-pollinator interaction webs. Ecology Letters 14:896–904. https://doi.org/10.1111/j.1461-0248.2011.01654.x

Gibbs J (2017) Notes on the Nests of *Augochloropsis metallica fulgida* and *Megachile mucida* in Central Michigan (Hymenoptera: Halictidae, Megachilidae). The Great Lakes Entomologist 50:17–24. https://doi.org/10.22543/0090-0222.1001

Goulson D (2010) Bumblebees: Behaviour, Ecology, and Conservation, Second Edition. Oxford University Press

Hartig F (2024) DHARMa: Residual Diagnostics for Hierarchical (Multi-Level/Mixed) Regression Models. R package (version 0.4.6)

Heinrich B (1979) Bumblebee Economics. Harvard University Press, Cambridge.

Heinrich B, Heinrich MJE (1983) Size and Caste in Temperature Regulation by Bumblebees. Physiological Zoology 56:552–562. https://doi.org/10.1086/physzool.56.4.30155878

Hines HM (2025) Comparative Evolution of Social and Ecological Traits in Bumble Bees. Annual Review of Entomology 71:189–207. https://doi.org/10.1146/annurev-ento-121423-013636

Huang H (2021) linkET: Everything is Linkable. R package (version 0.1.0).

Jacome-García JC, Gonzalez VH, Riaño-Jimenez DA, Herrera-Motta AF, Cure JR (2024) Foraging behavior and the nest architecture of a high-Andean stingless bee (Hymenoptera: Apidae: Meliponini) revealed by X-ray computerized tomography. Apidologie 55:33. https://doi.org/10.1007/s13592-024-01074-8

Johnson SD, Balducci MG, Bijl A, Castañeda-Zárate M, Cozien RJ, Ortmann CR, Niet T (2019) From dusk till dawn: camera traps reveal the diel patterns of flower feeding by hawkmoths. Ecological Entomology 45:751–755. https://doi.org/10.1111/een.12827

Karbassioon A, Yearlsey J, Dirilgen T, Hodge S, Stout JC, Stanley DA (2023) Responses in honeybee and bumblebee activity to changes in weather conditions. Oecologia 201:689–701. https://doi.org/10.1007/s00442-023-05332-x

Kenna D, Pawar S, Gill RJ (2021) Thermal flight performance reveals impact of warming on bumblebee foraging potential. Functional Ecology 35:2508–2522. https://doi.org/10.1111/1365-2435.13887

Kitaoka TK, Nieh JC (2009) Bumble bee pollen foraging regulation: role of pollen quality, storage levels, and odor. Behavioral Ecology and Sociobiology 63:625–625. https://doi.org/10.1007/s00265-008-0707-0

Koch JB, Cane JH (2022) Pollen columns and a wax canopy in a first nest description of *Bombus* (*Cullumanobombus*) *morrisoni* (Apidae). Apidologie 53:31. https://doi.org/10.1007/s13592-022-00943-4

Knop E, Gerpe C, Ryser R, Hofmann F, Menz MHM, Trösch S, Ursenbacher S, Zoller L, Fontaine C (2018) Rush hours in flower visitors over a day–night cycle. Insect Conservation and Diversity 11: 267–275. https://doi.org/10.1111/icad.12277

Lüdecke D, Makowski D, Waggoner P, Patil I (2021) performance: an R package for assessment, comparison and testing of statistical models. Journal of Open Source Software 6:3139. https://doi.org/10.21105/joss.03139

Nakagawa S, Schielzeth H (2013) A general and simple method for obtaining R^2 from generalized linear mixed-effects models. Methods in Ecology and Evolution 4:133–142. https://doi.org/10.1111/j.2041-210x.2012.00261.x

Peat J, Goulson D (2005) Effects of experience and weather on foraging rate and pollen versus nectar collection in the bumblebee, *Bombus terrestris*. Behavioral Ecology and Sociobiology 58:152–156. https://doi.org/10.1007/s00265-005-0916-8

Mani MS (1968) The high altitude environment. In Ecology and Biogeography of High Altitude Insects (pp. 9–50). Dordrecht: Springer Netherlands.

Prendergast KS (2022) Assessing climate change impacts on pollinators. In P. Kevan & S. W. Chan (Eds.), Promoting pollination and pollinators in farming. Cambridge, UK: Burleigh Dodds Science Publishing.

R Core Team (2023) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/

Rowcliffe JM (2019) activity: Animal Activity Statistics. R package (version 1.3). https://CRAN.R-project.org/package=activity.

Rozen JG (1991) Nesting biology and mature larva of the bee *Idiomelissodes duplocincta* (Hymenoptera, Anthophoridae, Eucerini). American Museum novitates 3012. https://www.biodiversitylibrary.org/bibliography/196489

Rozen JG, Smith CS, Johnson DE (2018) Preliminary study of the bumble bee *Bombus griseocollis*, its eggs, their eclosion, and its larval instars and pupae (Apoidea: Apidae: Bombini). American Museum Novitates 2018:3898. https://doi.org/10.1206/3898.1

RStudio Team (2023) RStudio: Integrated Development Environment for R. RStudio, PBC, Boston, MA. https://www.rstudio.com/

Ridout MS, Linkie M (2009) Estimating overlap of daily activity patterns from camera trap data. Journal of Agricultural, Biological, and Environmental Statistics 14:322–337. https://doi.org/10.1198/jabes.2009.08038

Schaffer WM, Jensen DB, Hobbs DE, Gurevitch J, Todd JR, Schaffer MV (1979) Competition, foraging energetics, and the cost of sociality in three species of bees. Ecology 60:976–987. https://doi.org/10.2307/1936866

Sisk G, Ostroski A, Dillard T, Hall B, Goslee SC, Grozinger CM, Khanna V, Grab H (2025). Unraveling microclimate effects on pollinator foraging and crop yield in lowbush blueberry. Agriculture, Ecosystems & Environment, 392, 109734. https://doi.org/10.1016/j.agee.2025.109734

Stelzer RJ, Chittka L (2010) Bumblebee foraging rhythms under the midnight sun measured with radiofrequency identification. BMC Biology 8:93. https://doi.org/10.1186/1741-7007-8-93

Stone GN, Gilbert F, Willmer P, Potts S, Semida F, Zalat S (1999) Windows of opportunity and the temporal structuring of foraging activity in a desert solitary bee. Ecological Entomology 24:208–221. https://doi.org/10.1046/j.1365-2311.1999.00181.x

Vicens N, Bosch J (2000) Weather-Dependent Pollinator Activity in an Apple Orchard, with Special Reference to *Osmia cornuta* and *Apis mellifera* (Hymenoptera: Megachilidae and Apidae). Environmental Entomology 29:413–420. https://doi.org/10.1603/0046-225X-29.3.413

Williams PH, Cameron SA, Hines HM, Cederberg B, Rasmont P (2008) A simplified subgeneric classification of the bumblebees (genus *Bombus*). Apidologie 39:46–74. https://doi.org/10.1051/apido:2007052

Willmer PG (1983) Thermal constraints on activity patterns in nectar-feeding insects. Ecological Entomology 8:455–469. https://doi.org/10.1111/j.1365-2311.1983.tb00524.x

Willmer PG, Bataw AAM, Hughes JP (1994) The superiority of bumblebees to honeybees as pollinators: insect visits to raspberry flowers. Ecological Entomology 19:271–284. https://doi.org/10.1111/j.1365-2311.1994.tb00419.x

Woods WA, Heinrich B, Stevenson RD (2005) Honeybee flight metabolic rate: does it depend upon air temperature? Journal of Experimental Biology 208:1161–1173. https://doi.org/10.1242/jeb.01510

Wratt EC (1968) The Pollinating Activities of Bumble Bees and Honeybees in Relation to Temperature, Competing Forage Plants, and Competition from Other Foragers. Journal of Apicultural Research 7:61–66. https://doi.org/10.1080/00218839.1968.11100190

Xu X, Liang H, Ren Z-X, Maruyama PK, Rodrigo Rech A, Trunschke J, Zhao Y-H, Li H-D, Wang H (2025) Generalised bumblebee–flower interactions demonstrate weak floral niche partitioning despite a

high bee diversity. Ecography 2025:e07956. https://doi.org/10.1002/ecog.07956

Xu X, Ren Z-X, Trunschke J, Kuppler J, Zhao Y-H, Knop E, Wang H (2021) Bimodal activity of diurnal flower visitation at high elevation. Ecology and Evolution 11:13487–13500. https://doi.org/10.1002/ece3.8074

Zoller L, Bennett JM, Knight TM (2020) Diel-scale temporal dynamics in the abundance and composition of pollinators in the Arctic summer. Scientific Reports 10:21187. https://doi.org/10.1038/s41598-020-78165-w

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