

Contents lists available at ScienceDirect

Global Ecology and Conservation



journal homepage: www.elsevier.com/locate/gecco

Precision foraging: Bats in organic desert palm plantations hunt where it is most needed

Danilo Russo^a, Fabiana Soprano^a, Luca Cistrone^a, Adi Einav^{b,c}, Jessica Schäckermann^{d,e,*}, Ioannis Ekklisiarchos^f, Carmi Korine^c

^a Laboratory of Animal Ecology and Evolution (AnEcoEvo), Dipartimento di Agraria, Università degli Studi di Napoli Federico II, Piazza Carlo di Borbone 1, 80055 Portici (Napoli), Italy

^b Albert Katz International School for Desert Studies, Jacob Blaustein Institutes for Desert Research, Ben-Gurion University of the Negev, Midreshet Ben-Gurion, 8499000, Israel

^c Mitrani Department of Desert Ecology, Swiss Institute of Dryland, Environmental and Energy Research, Jacob Blaustein Institutes for Desert

Research, Ben-Gurion University of the Negev, Midreshet Ben-Gurion, 8499000, Israel

^d Southern Arava R&D, Eilot Regional Council, D.N. Hevel Eilot, 8882000, Israel

^e The Arava Institute for Environmental Studies, D.N. Hevel Eilot, Ketura 8884000, Israel

^f Department of Biology, School of Sciences and Engineering, University of Crete, Voutes, Heraklion, Crete 70013, Greece

ARTICLE INFO

Keywords: Bats Biological control Chiroptera Desert Ecosystem Service Feeding Palm tree

ABSTRACT

Bats are crucial in suppressing pest arthropods in agroecosystems, contributing vitally to sustainable agriculture. However, the importance of bats in agriculture in extreme environments. such as deserts, has received far less attention. Date palm plantations represent one of the few productive systems in hyper-arid regions. We studied habitat use in an organic date palm plantation in the Arava Valley (Southern Israel) employing acoustic surveys to assess bat activity and foraging behaviour. According to our predictions, bats preferentially foraged in the plantation's most productive areas, with most of the 13 recorded species exhibiting significant activity in older, sheltered plots. Higher wind speeds correlated with decreased foraging across most species, but sheltered habitats often buffered this effect. While species richness remained stable across habitats, according to our prediction, activity levels varied according to habitat type and wind conditions. In general, bat activity increased in old productive plots in the plantation's core section and decreased elsewhere in response to strong winds. These results highlight the importance of maintaining older productive areas within the interiors of date palm plantations to support bat populations and enhance their pest-suppressing roles. Management strategies should design wind-buffering plantations to protect critical bat foraging areas and provide water sources. As date palm plantations act as "oases" in unproductive landscapes, many bats likely travel significant distances to forage there. Protecting bat habitats on a large scale and prioritising multiscale conservation is crucial to preserving bats and their ecosystem services.

1. Introduction

As farming systems evolve, balancing high production with ecological sustainability is crucial. Natural enemy management

* Corresponding author at: Southern Arava R&D, Eilot Regional Council, D.N. Hevel Eilot, 8882000, Israel. E-mail address: MopRes@aravard.org,il (J. Schäckermann).

https://doi.org/10.1016/j.gecco.2025.e03467

Received 12 December 2024; Received in revised form 25 January 2025; Accepted 28 January 2025

Available online 29 January 2025

^{2351-9894/© 2025} The Authors. Published by Elsevier B.V. This is an open access article under the CC BY license (http://creativecommons.org/licenses/by/4.0/).

enhances pest control by promoting beneficial organisms and reducing chemical inputs (Bianchi et al., 2006; Rusch et al., 2016; Russo et al., 2018). However, this approach often fails in intensive agriculture due to excessive pesticide use, pest resistance, and habitat loss for predators (Buzhdygan and Petermann, 2023). Modern agriculture must develop productive systems that mitigate environmental impacts while ensuring food security and preserving biodiversity through natural pest management integration.

The date palm (*Phoenix dactylifera* L.) is one of the world's earliest domesticated fruit trees and has played a significant role in human history, particularly in the Old World (Johnson et al., 2015). This unisexual fruit tree, native to hot, arid regions, is primarily grown across the Middle East and North Africa. The palm's remarkable ability to flourish in harsh climates has made it indispensable in areas where food security and human well-being rely heavily on its cultivation (Aleid et al., 2015). The date palm cultivation's monocultural nature increases susceptibility to pest infestations due to limited plant diversity, involving 112 mite and insect species (El-Shafie, 2012). Extensive monoculture areas combined with climate change expose these crops to biotic stresses that disrupt natural pest control mechanisms and create ideal conditions for pests (Wakil et al., 2015). Initial management often relied on pesticides; however, drawbacks and rising demand for healthy food have led farmers to adopt more sustainable practices, such as Integrated Pest Management and organic farming (Cohen and Glasner, 2015; Wakil et al., 2015). The lesser date moth (*Batrachedra amydraula* Meyerick), a key pest, specifically targets date palms (Perring et al., 2015). Its larvae feed on fruits, causing yield losses (Blumberg, 2008). Managing pests like the lesser date moth and date mites in organic systems is difficult, and ineffective control of the red palm weevil further threatens organic date production in countries like Israel (Cohen and Glasner, 2015). Understanding the ecology and behaviour of natural enemies is thus crucial for promoting sustainable pest control in organic systems.

Insectivorous bats are well known for their ability to control arthropod pests in agroecosystems (Russo et al., 2018, 2024; Cohen et al., 2020; Maslo et al., 2022; Tuneu-Corral et al., 2023), and there is increasing evidence of the economic benefits this provides, ranging from local to larger scales (Boyles et al., 2011; 2013; Kolkert et al., 2021; Ancillotto et al., 2024). While species richness and overall bat activity are well documented in various agroecosystems, analyses at the foraging guild level are rarely conducted. Bat foraging strategies have been classified based on the bat's proximity to clutter-producing backgrounds and manoeuvrability (Norberg and Rayner, 1987; Schnitzler and Kalko, 1998; Denzinger and Schnitzler, 2013). In the Negev Desert of Israel, bats have been classified as aerial hawkers or gleaners depending on their foraging style (Korine and Pinshow, 2004). Aerial hawkers catch prey in flight, while gleaners seize it from the substrate. These foraging strategies may play a crucial role in shaping insectivory and ecosystem service delivery, as they influence how bats access different cultivation types based on the degree of clutter.



Fig. 1. Map of the date plantation where this study was set (Samar, Arava Valley, Southern Israel) showing the surveyed plots, the habitat categories and the location of bat recording points. Plots in black were excluded from sampling because they were recently cut or hosted male palms.

We conducted our study in an organically managed date palm plantation in the hyper-arid Arava Valley, Israel, located in the southern section of the Negev Desert, near the shores of the Red Sea. Bats in this plantation exhibited higher species richness than in conventionally managed plantations, with more species observed during the harvest (July) than in the pre-harvest (September) period, while bat activity remained stable across these periods (Schäckermann et al., 2022). Metabarcoding analysis revealed that all bat species consumed nine of the sixteen known date pest species, highlighting their important role in pest control (Schäckermann et al., 2022). This remarks the considerable potential of bats in date palm plantations for delivering valuable ecosystem services, making them essential allies in mitigating yield loss from key pests.

Date palm plantations are typically managed as a mosaic of small plots, each at different stages of growth and production. This creates diverse habitat structures, with only productive plots especially susceptible to pest attacks due to fruit availability (Blumberg, 2008). A key question is whether bats, given their high mobility and large home ranges, can focus their foraging activity precisely where needed in these small, productive plots. Bat activity may also be influenced by strong winds (Russo and Jones, 2003), which are prevalent in the area and visibly affect even tree inclination (Ziv et al., 2004). These winds might deplete insect numbers or alter their distribution, depending on how the plantation's structure interacts with the wind. Understanding the interplay between habitat and wind could help manage the spatial patterning of cultivation to direct bat foraging activity to the most vulnerable areas, enhancing pest control.

We hypothesised that bats would concentrate their foraging activity in the most productive plots of the date palm plantation, where pest pressure is potentially highest. This behaviour would enable them to maximise their ecological impact despite the plantation's small-scale mosaic structure and their capacity for long-range movements. Specifically, bat activity was predicted to be highest in the older, more productive parts of the plantation, where crop production and pest pressure are greatest (Prediction 1.1). Furthermore, we predicted that differences in bat species richness would be more pronounced between these older, productive areas and younger growth sections (Prediction 1.2).

We also hypothesised that wind conditions would influence bat foraging behaviour, reducing overall activity at higher wind speeds, although habitat structures providing shelter could buffer this effect. Specifically, we predicted that bat activity would decrease with increasing wind speeds across all habitat types (Prediction 2.1) and bat species richness would negatively correlate with wind speed (Prediction 2.2). However, in more sheltered habitats, such as denser areas or locations adjacent to larger palms, we anticipated smaller reductions in bat activity than in more exposed areas during periods of strong winds (Prediction 2.3).

2. Materials and methods

2.1. Study Area

We recorded bat activity in July-September 2022 in the organic date palm plantation of Kibbutz Samar (Fig. 1), in the Arava Valley of southern Israel (29.8158 N, 35.0370 E). The plantation, one of the few organic agricultural farms in this desert region, spans over 100 ha. It contains date palms of varying ages and cultivars (Medjoul, Dekel Nour, Barhi, and Zahidi; Arzi et al., 2023). The surrounding landscape is characterised by dunes and loess soil, creating a mosaic of habitats interspersed with patches of date palms. The Arava Valley is a hyper-arid desert, with an average annual temperature of 25.4°C, ranging from mean temperatures of 15.8°C in January to 33.8°C in July, and maximum temperatures of 48°C. Rainfall is minimal, annually averaging 27.6 mm, and only occurs outside the summer months (Arzi et al., 2023). This makes water a scarce and carefully managed resource in the region.

The plantation's organic farming practices distinguish it from other area's farms. Herbicides are not used; instead, machinery is employed to cut weeds. Pest management relies on high-pressure irrigation rather than chemical pesticides for date mites, and organic pesticides against the lesser date moth. Vegetation is deliberately maintained around the base of the trees to protect the soil and support natural predators of pests (Schäckermann et al., 2022; Arzi et al., 2023). These sustainable farming practices, in combination with the plantation's size and location, provide a unique opportunity to study bat activity in an agriculturally managed desert environment.

2.2. Experimental design

To assess bat activity in different stages of date palm growth, the plantation was divided into several plots, classified according to the palms' growth stages and productivity (Fig. 1). We excluded from surveys plots cleared recently or not destined for production, such as those where male palm trees were grown for pollen production. We classified palm habitats based on age and productivity: Youngest (<4 years), Young unproductive (5–8 years), Young productive (8–10 years), and Old productive (>10 years). The Youngest stage focuses on root and vegetative growth (Zaid and Arias-Jimenez, 1999). Young unproductive palms rapidly grow but do not produce fruit yet (Chao and Krueger, 2007). By 8–10 years, they become what we classified as "Young productive" with limited yield. Old productive palms (>10 years) reach their full potential, producing up to 100 kg of dates per tree (Zaid and Arias-Jimenez, 1999). Additionally, we sampled the surrounding desert ('open habitat') as a control set in a natural habitat.

We established 54 sampling points across nine habitat categories, each further subdivided into core and edge areas, with all points spaced at least 100 m apart. Each subcategory was allocated six sampling points, except for the 'Old productive' habitat, where we set seven points in the core and five on the edge due to insufficient edge points that met the 100 m criterion. This setup also included the six points in open habitats outside the plantation (Fig. 1).

2.3. Acoustic surveys

Bat activity was manually recorded from late July to early September, when ripe fruits remained on productive trees, just before the beginning of the harvest in early September. Recording began 30 min after sunset, with each sampling point monitored for 30 min. Each night, a random order was assigned to the sampling points to determine the sequence in which they were visited. We adopted this order to avoid any potential influence of the recording time on bat activity. Between 3 and 8 sampling points were surveyed per night, with the exact number varying from evening to evening.

We recorded ultrasonic calls at a high sampling rate (350 kHz) using the real-time mode of a D1000X bat detector (Pettersson Elektronik AB, Uppsala, Sweden). This detector features an integrated 16-bit recording system and stores sound files in WAV format on a Compact Flash card. When a bat pass was detected – defined as a sequence of at least two calls indicating the bat was within range (Fenton, 1970) – ultrasound sampling was manually triggered. The detector's microphone was positioned at a 45-degree angle to the horizontal plane, and randomly oriented.

Wind speed was estimated at the beginning and end of each recording session and an average value was obtained using the Beaufort scale (Fry, 1967). This was later converted to the corresponding average km/h speed for analysis. Each sampling night was categorised using Julian days.

2.4. Sound analysis

The acoustic recordings were analysed using BatSound software ver. 4.7 (Pettersson Elektronik AB, Uppsala, Sweden). We analysed 3 > calls with the best signal-to-noise ratio for each sequence, excluding those with poorer quality. For each call, we produced a spectrogram and an oscillogram, along with a power spectrum. The spectrograms and power spectra were generated using a Fast Fourier Transform (FFT) with a Hamming window (window size of 512 samples, 98 % overlap). All spectrograms were generated using the same threshold (16) in the BatSound settings to ensure consistency. For each echolocation call, we measured the start frequency, end frequency, frequency of maximum energy, and duration (Russo and Jones, 2002). Time variables (expressed in ms) were derived from oscillograms, and frequency variables (in kHz) were taken from spectrograms, except for the frequency of maximum energy, measured from power spectra. Species identification was conducted manually by comparing the observed values with Hackett et al. (2016) for the bat species occurring in the study area and using reference recordings from bats of known identity. We recorded the number of bat passes (expressing bat activity) and feeding buzzes for each habitat type. Feeding buzzes are rapid sequences of echolocation calls emitted by a bat as it approaches and attempts to capture prey (Fenton and Bell, 1979).

2.5. Statistical analysis

The moon's per cent illuminated surface was obtained for all nights (https://meteogram.org/moon/israel/jerusalem/). However, a preliminary analysis of the effects of the moon phase and Julian Day on the dataset revealed these factors to be negligible.

A Kruskal-Wallis test using the recording start time at each site as the dependent variable showed no difference across habitats, confirming that the random allocation of recording sites each night avoided temporal biases towards specific habitats ($\chi^2 = 8.60$, d.f. = 8, p = 0.377). Therefore, any differences observed were due to bat habitat use rather than the time of night. We focused our analysis on the impacts of habitat type and wind speed on bat species richness and activity. For the bat activity analysis, we examined the total activity levels of species for which at least 100 passes were recorded to ensure sufficient statistical power. Preliminary data assessments relied on scatterplots, correlation tests, and regression analyses.

To evaluate bat activity and species richness, we employed Generalized Linear Mixed Models (GLMMs) with a negative binomial distribution, suitable for accommodating count data that exhibited overdispersion. Habitat type and wind speed were entered as fixed terms, and the recording site was included as a random factor to account for variation among sites. We generated full (interactive), additive, partial, and null models for each variable assessed. We selected the best models based on the Akaike Information Criterion,

Та	ble	1
		-

Bat species, foraging guild, and corresponding numbers of passes recorded at Samar date palm plantation, Arava Valley, Southern Israel.

Species	Number of passes	Foraging guild
Eptesicus bottae	1239	Aerial hawker – Edge specialist
Hypsugo ariel	965	Aerial hawker – Edge specialist
Pipistrellus kuhlii	319	Aerial hawker – Edge specialist
Rhinopoma cystops	237	Aerial hawker – Open space forager
Taphozous nudiventris	133	Aerial hawker – Open space forager
Rhinopoma microphyllum	116	Aerial hawker – Open space forager
Pipistrellus rueppellii	103	Aerial hawker – Edge specialist
Otonycteris hemprichii	36	Substrate gleaner
Barbastella leucomelas	16	Aerial hawker – Edge specialist
Plecotus christii	4	Substrate gleaner
Asellia tridens	3	Aerial hawker – Open space forager
Tadarida teniotis	1	Aerial hawker – Open space forager
Unidentified	28	

AIC (Akaike, 1974), model simplicity, and the number of statistically significant variables. The AIC values were used to evaluate the model fit vs. complexity trade-off, with lower values indicating a better fit. We used a log link function for the GLMMs to ensure appropriate handling of the response variable.

To validate the models, we first examined the residuals to confirm their random distribution around zero without any discernible patterns. We then assessed model fit using deviance statistics to evaluate how well the model described the data compared to a saturated model. Additionally, we estimated the Chi-squared statistic per degree of freedom to check for overdispersion in the data. The differences across habitats were tested using Fixed Effects Parameter Estimates, with the "Old productive/core" habitat entered as the reference category. All analyses were conducted using JAMOVI version 2.3.28.

3. Results

We recorded 3240 bat passes and 130 feeding buzzes (5.6 % of total passes) corresponding to 12 species (Table 1). Pearson's correlation coefficient between the number of feeding buzzes and the number of passes was 0.70 (P < 0.001), legitimating our use of the number of passes as a proxy for bat foraging activity. We present the results of the best models here, while the fixed effects parameter estimates are provided in the supplementary material.

3.1. Species richness

The model including only wind speed (Species richness ~ Wind speed + (1 | Sampling point)) had the lowest AIC (246.17), vs. the null model's AIC = 260.65. In this model, wind speed negatively affected species richness (Table 2; Fig. 2). The exponentiated coefficient for wind speed, exp(B) = 0.979, indicates that for each 1 km/h increase in wind speed, species richness decreases by approximately (1 - exp(B)) × 100, which equals about 2.1 %.

3.2. Total bat activity

The best-performing model was the additive GLMM (Total number of passes ~ Habitat + Wind speed + (1 | Sampling point)), which showed the lowest AIC (519.200). In this model, both "habitat" and "wind speed" were significant predictors (Table 2). The parameter estimates showed that "Old productive/core" had significantly more bat passes than most other habitats except for "Old productive/edge" and "Young unproductive/edge". A borderline (0.05) significance value was recorded for the comparison between "Old productive/core" and "Young productive/edge" (Supplementary material). Wind speed negatively affected total bat activity across most habitats (Estimate = -0.0469, P < 0.001), indicating that higher wind speeds generally reduced bat activity.

3.3. Species-level effects

We recorded numbers of bat passes that we deemed sufficient for quantitative analyses (>100) for seven species only, i.e., Taphozous nudiventris, Rhinopoma cystops, Rhinopoma microphyllum, Eptesicus bottae, Hypsugo ariel, Pipistrellus kuhlii and Pipistrellus rueppellii.

3.4. Aerial hawkers – open space

For *Rhinopoma cystops*, the best model was the partial model including wind speed (Number of passes ~ Wind speed + (1 | Sampling point)), with the lowest AIC = 172.540 (the null model's AIC was 179.14). In this model, wind speed had a significant negative effect (Table 2). Based on the parameter estimate (Supplementary Material), for each 1 km/h increment in wind speed, bat activity significantly (p = 0.005) decreased by approximately 8.95 % (calculated as 1 - exp(-0.0938) = 0.0895) (Supplementary material).

Table 2

Log-likelihood ratio tests for the best models selected to assess bat responses to habitat and wind speed at Samar date palm plantation, Arava Valley, Southern Israel.

Dependent variable	Factor	χ^2	d.f.	Р
Species richness	Wind speed (km/h)	17.2	1	< 0.001
Total activity	Habitat	20.4	8	0.009
	Wind speed (km/h)	13.7	1	< 0.001
Rhinopoma cystops	Wind speed (km/h)	7.86	1	0.005
Rhinopoma microphyllum	Wind speed (km/h)	3.24	1	0.072
Eptesicus bottae	Habitat	71.7	8	< 0.001
	Wind speed (km/h)	11.1	1	< 0.001
	Habitat*Wind speed (km/h)	25.1	8	0.001
Hypsugo ariel	Habitat	31.1	8	< 0.001
	Wind speed (km/h)	12.1	1	< 0.001
Pipistrellus kuhlii	Habitat	41.88	8	< 0.001
	Wind speed (km/h)	3.62	1	0.057
Pipistrellus rueppellii	Habitat	27.4	8	< 0.001



Fig. 2. Scatterplot and corresponding regression line illustrating the response of bat species richness to wind speed in the date palm plantation of Samar, Arava Valley, Southern Israel. The confidence interval was calculated using the standard error. Data points appear fewer than the actual number (54) due to overlap in their coordinates.

For *Rhinopoma microphyllum*, the partial GLMM model including wind speed (Number of passes \sim Wind speed + (1 | Sampling point)) performed best, demonstrating the lowest AIC (153.85). However, the effect of wind only approached significance (Table 2).

No GLMM model for *Taphozous nudiventris* reached significance, and the AIC values were either greater than or equivalent to the value reached by the null model (185.733).



Fig. 3. A scatterplot of *Eptesicus bottae* activity (number of passes) against wind speed, featuring habitat-specific regression lines in the date plantations of Samar, Arava Valley, Southern Israel. All habitats, except for "Old productive/core", exhibited a general decline or stabilisation in activity with increasing wind speed. In contrast, the "Old productive/core" habitat demonstrated increased bat activity. The confidence interval was calculated using the standard error. Data points appear fewer than their actual number due to overlapping coordinates or being obscured by the confidence intervals.

3.5. Aerial hawkers – edge

For *Eptesicus bottae*, we selected the full model (Number of passes $\sim 1 + \text{Habitat} + \text{Wind speed (km/h)} + \text{Habitat: Wind speed (km/h)} + (1 | Sampling point)) as the best one. Its AIC (424.75) was only marginally higher (+1.756) than that of the additive model, but it included all significant effects (Table 2). The null model's AIC was 434.900. Habitat type significantly influenced the species' activity (Table 2), with the "Old productive/core" habitat showing higher activity levels than all other habitat types (Supplementary material).$

Increasing wind speeds were associated with decreased *E bottae*'s activity (Table 2). The exponentiated coefficient for wind speed is exp(B) = 0.9514, so the estimated activity decreased for each 1 km/h in wind speed is $(1-0.9514) \times 100 = 4.86$ %. However, the interaction term (Table 2) and the parameter estimates (Supplementary material) indicated that activity decreased with wind speed or remained relatively stable in all habitats, except for the "Old productive/core", where higher wind speeds were associated with an activity increase (Fig. 3).

The additive GLMM model (Number of passes ~ Habitat + Wind speed + 1 | Sampling point)), performed best for *Hypsugo ariel*, demonstrating the lowest AIC (341.460). In this model, the log-likelihood ratio tests were significant for "habitat" and "wind speed"(Table 2). Increasing wind speeds were associated with a decrease in *H. ariel* activity. The parameter estimates (Supplementary material) showed that the "Old productive/core" had significantly higher bat passes than all other habitat types except "Old productive/edge".

For *Pipistrellus kuhlii*, the additive GLMM model (Number of passes ~ Habitat + Wind speed + (1 | Sampling point)) demonstrated superior performance, yielding the lowest AIC of 206.480 vs. a null model's AIC = 233.36. In this model, log-likelihood ratio tests were significant for "habitat" and approached significance for "wind speed" (Table 2). Higher wind speeds were linked to a weak negative effect on *P. kuhlii* activity, as indicated by the borderline significance value and the parameter estimates (Supplementary material). The "Old productive/core" habitat had significantly more bat passes than all other habitats (Supplementary material).

Finally, for *Pipistrellus rueppellii*, the best model included habitat as a main effect (Number of passes \sim Habitat + 1 | Sampling point)), with an AIC of 130.110 vs. the null model's AIC value = 141.97. The log-likelihood ratio test showed that the effect of habitat was highly significant (Table 2). The parameter estimates (Supplementary material) indicated that all habitats except "Young unproductive/core" and "Youngest/edge" had significantly fewer bat passes than "Old productive/core".

4. Discussion

4.1. Bats forage in productive habitats while coping with wind disturbance

Previous work showed that bats largely forage in date palm plantations (Schäckermann et al., 2022), where they actively suppress pests (Arzi et al., 2023). However, no study addressed habitat use in these tightly packed environmental mosaics. As hypothesised, despite the fine-grained patterning of plantations, we show that bats concentrate their foraging activity in the most productive areas in date palm plantations, fulfilling their role as effective pest suppressors. We found that wind has a strong effect on bat foraging and that this effect is habitat- and species-specific. The "precision foraging" bats exhibit highlights habitat structure's importance in shaping bat foraging dynamics, particularly under changing wind conditions. Schäckermann et al. (2022) highlighted a temporal link between bat foraging and date palm productivity, with activity peaking during summer harvest. Our work expands on this, emphasising the critical role of space by demonstrating how habitat type and wind interference shape the spatial patterns of foraging within these agroecosystems.

We observed strong support for Prediction 1.1, anticipating that bat activity would be highest in the old productive parts of the plantation. Both total activity and species-level activity of *Eptesicus bottae*, *Hypsugo ariel*, *Pipistrellus rueppellii*, and *Pipistrellus kuhlii* were highest in these internal, high-stand productive areas, emphasising the precision of bats in delivering ecosystem services. Hackett et al. (2013) observed strong winds in the Northern Arava Valley near *Acacia* trees, apparently affecting insect abundance without impacting the general bat activity. They proposed that bats might switch to low-wind areas while foraging, maintaining consistent activity levels throughout the night.

We found that edge specialist species concentrate their efforts where they are most needed, particularly in areas with higher productivity. This capacity to forage where food is most available is especially pronounced in desert environments, where trophic resources are rare and concentrated at sites such as date palm plantations (Schäckermann et al., 2022). However, the three open-space foragers, *R. cystops, R. microphyllum* and *T. nudiventris* showed no habitat preference, probably due to their foraging strategy and hunting altitude. We rejected Prediction 1.2 since habitat did not affect species richness. Our data confirm the presence of 11 out of the 12 species previously recorded in the same plantation (Schäckermann et al., 2022; Arzi et al., 2023), since we did not detect *Rhinolophus clivosus*. Besides, we added *Asellia tridens* to the area's checklist. *Rhinolophus clivosus* has highly directional, high-frequency echolocation calls exposed to significant atmospheric attenuation (Jacobs et al., 2017), which can be overlooked in acoustic surveys. The absence of habitat effects on species richness may stem from species being easily detected in habitats they rarely, if ever, use for foraging, but still cross during commuting.

We also hypothesised that higher wind speeds reduce bat foraging activity, with sheltered habitats potentially buffering this effect – a pattern strongly supported by our results. In line with Prediction 2.1, total bat activity did decrease with increasing wind speeds across all habitat types within the plantation, particularly noted in more exposed areas. At the species level, all species models except that of *Pipistrellus rueppellii* showed a significant, negative effect of wind; for open space foragers, wind was the only factor influencing bat activity. Prediction 2.2, positing that bat species richness would negatively correlate with wind speed, was also confirmed. Wind may affect foraging bats by reducing prey availability and making flight more difficult and energetically costly (Verboom and

Spoelstra, 1999; Russo and Jones, 2003). Given the strong wind characteristic of the study area, the generalised effect of wind as a predictor in our models is well justified.

Finally, Prediction 2.3 proposed that in more sheltered habitats (e.g., denser areas or areas adjacent to larger palms), bat activity would decline less than in exposed areas during high wind conditions. We confirmed this prediction for at least the most active foraging species, *E. bottae*, whose model revealed a significant interaction between wind speed and habitat. While foraging decreased with increasing wind speeds across all habitats, the "Old productive/core" habitat exhibited the opposite trend. This suggests that bats forage more in sheltered, productive areas when strong winds strike the date plantation. Hence, bats likely shifted foraging activity from the less sheltered outer and younger parts of the plantation to the more protected older core areas.

4.2. Management implications

Several bat species we recorded are effective pest suppressors in date palm plantations. *Eptesicus bottae, H. ariel, P. rueppellii* and *Otonycteris hemprichii* consume a wide variety of pests, including different pest moth species, Dubas bug, and spider mites, all known threats to date palms (Schäckermann et al., 2022). Given their role in natural pest suppression, enhancing conditions for these bats to thrive will likely boost pest control. This highlights the importance of protecting bats beyond the plantation, as most roosts are likely found in nearby rock crevices or buildings. Protecting bats across larger landscapes supports biodiversity conservation and pest suppression, making it a win-win strategy, as shown in studies from temperate regions (Froidevaux et al., 2017). Bats crucially depend upon the availability of drinking water for survival (Korine et al., 2016), whose influence on bat activity is strong where water sources are naturally rare (Cistrone et al., 2024). Establishing water sources within plantations is particularly vital, given the water scarcity in these environments. Strategically placing these water sites near productive plots would enhance pest control where most needed (Arzi et al., 2023).

Wind can have conflicting effects on date palm plantations. Although it may help reduce pest populations by disrupting their activities, it negatively affects palm tree growth and productivity by inhibiting transpiration and damaging flowers and fruits (Brunel et al., 2006; Krueger, 2021). Our findings indicate that in such agroecosystems, wind also reduces bat activity, except in older, more productive, and sheltered plots. Especially under very windy conditions, bats tend to concentrate foraging in the plantation's inner sector. Thus, a key management recommendation is to design plantations with wind-buffering strategies, such as planting younger, non-productive native desert trees around older productive ones.

Native desert tree species such as *Acacia tortilis* and *A. raddiana* are keystone species in arid and semi-arid regions, as many desert animals depend on them, directly or indirectly, for food and shelter (Ward and Rohner, 1997). These trees also serve as important foraging habitats for insectivorous bats in the Arava Valley (Hackett et al., 2013). However, they continue to decline due to anthropogenic influences such as road construction and agricultural practices (Tran et al., 2018). Using these trees as windbreaks may be a win-win strategy for enhancing desert biodiversity and promoting biological pest suppression. This setup would protect the palms and bats, optimising pest control, particularly during high wind conditions when bats concentrate their foraging in sheltered areas.

One caveat of this study was the limited sample size – due to logistical constraints, we could not replicate recordings over time. Nonetheless, the patterns we observed were clear and statistically supported, highlighting the robustness of our findings. Another potential limitation is that our work was conducted in a strictly organic plantation, where herbicides are absent and pesticide use is restricted to organic materials only (Schäckermann et al., 2022). This limits the applicability of our findings to integrated pest management or conventional plantations, where bat pest suppression may differ.

While organic agriculture varies in its importance for bat foraging (Froidevaux et al., 2017; Fialas et al., 2023), several examples from temperate regions demonstrate its value for bats and the ecosystem services they provide (Wickramasinghe et al., 2003; Ancillotto et al., 2023; 2024). In conventional plantations that widely use pesticides and herbicides, bat activity may be less pronounced due to reduced prey availability or direct exposure to harmful chemicals. Even in these environments, bats still play an important role in pest suppression, underscoring the need for their conservation and inclusion in pest management strategies (Schäckermann et al., 2022). However, attracting bats to conventional sites without reducing chemical use could lead to direct and indirect harm to bats, turning agroecosystems into "ecological traps" (Russo et al., 2024).

"Traps" might also be determined by other mortality factors such as roads. Promoting the development of plantations at safe distances from major roads could help mitigate potential roadkill mortality associated with attracting bats to profitable foraging sites near such infrastructures. In our study area, some young plots are located near Highway 90, a major traffic route. As these plots mature and become productive in the coming years, bats may face increased risks of road mortality or foraging interference due to vehicular traffic. Strategic plantation planning prioritising distance from roads may reduce these risks while supporting bat conservation efforts.

In conclusion, a transition toward more sustainable management practices of date palm plantations is strongly recommended. We remark that in such plantations, bats exhibit "precision foraging", focusing their activity in small, productive, sheltered areas, much like precision agriculture targets specific zones for intervention. Accordingly, management should prioritise maintaining and sheltering older productive plots within plantations. Enhancing these areas by placing water sources nearby and designing the plantation's spatial patterning would encourage bats to forage where pest suppression is most needed, improving overall plantation health and yield (Arzi et al., 2023). A comprehensive management strategy across different scales is necessary to increase bat populations in agricultural landscapes, support biological control, and foster sustainable farming practices.

Ethics statement

Not applicable: This manuscript does not include human or animal research.

Funding

Israel Ministry of Agriculture and Rural Development, # 16-38-0032 (CK), KA171 Erasmus+ programme: FS, DR and CK The Jewish National Fund and ICA: J.S.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

We thank the Samar Date team for their constant assistance in field research. This study was supported by the Israel Ministry of Agriculture and Rural Development, #16–38–0032 (CK), FS, DR and CK were supported by the KA171 Erasmus+ funding. The Jewish National Fund and ICA in Israel provided further funding to J.S. We are grateful to two anonymous reviewers for their very constructive feedback on a previous manuscript version.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.gecco.2025.e03467.

Data availability

Data will be made available on request.

References

- Akaike, H., 1974. A new look at the statistical model identification. IEEE Trans. Autom. Control 19 (6), 716–723. https://doi.org/10.1109/tac.1974.1100705. Aleid, S.M., Al-Khayri, J.M., Al-Bahrany, A.M., 2015. Date palm status and perspective in Saudi Arabia. Date Palm. Genet. Resour. Util. Vol. 2: Asia Eur. 49–95.
- https://doi.org/10.1007/978-94-017-9707-8_3.
- Ancillotto, L., Falanga, A., Agostinetto, G., Tommasi, N., Garonna, A.P., de Benedetta, F., Bernardo, U., Galimberti, A., Conti, P., Russo, D., 2023. Predator-prey traits and foraging habitat shape the diet of a common insectivorous bat. Acta Oecologica 118, 103890. https://doi.org/10.1016/j.actao.2023.103890.
- Ancillotto, L., Borrello, M., Caracciolo, F., Dartora, F., Ruberto, M., Rummo, R., Scaramella, C., Odore, A., Pietro Garonna, A., Russo, D., 2024. A bat a day keeps the pest away: bats provide valuable protection from pests in organic apple orchards. J. Nat. Conserv. 78, 126558. https://doi.org/10.1016/j.jnc.2024.126558.
- Arzi, Y., Segoli, M., Schäckermann, J., Korine, C., 2023. Providing water sources to insectivorous bats for conservation biological control in arid date plantations. Biol. Control 187, 105374. https://doi.org/10.1016/j.biocontrol.2023.105374.
- Bianchi, F.J., Booij, C.J.H., Tscharntke, T., 2006. Sustainable pest regulation in agricultural landscapes: a review on landscape composition, biodiversity and natural pest control. Proc. R. Soc. B Biol. Sci. 273 (1595), 1715–1727. https://doi.org/10.1098/rspb.2006.3530.

Blumberg, D., 2008. Date palm arthropod pests and their management in Israel. Phytoparasitica 36 (5), 411–448. https://doi.org/10.1007/bf03020290.

Boyles, J.G., Cryan, P.M., McCracken, G.F., Kunz, T.H., 2011. Economic importance of bats in agriculture. Science 332 (6025), 41–42. https://doi.org/10.1126/ science.1201366.

- Boyles, J.G., Sole, C.L., Cryan, P.M., McCracken, G.F., 2013. On estimating the economic value of insectivorous bats: prospects and priorities for biologists. Bat Evol. Ecol. Conserv. 501–515. https://doi.org/10.1007/978-1-4614-7397-8_24.
- Brunel, J.-P., Ihab, J., Droubi, A.M., Samaan, S., 2006. Energy budget and actual evapotranspiration of an arid oasis ecosystem: Palmyra (Syria). Agric. Water Manag. 84 (3), 213–220. https://doi.org/10.1016/j.agwat.2006.02.005.
- Buzhdygan, O.Y., Petermann, J.S., 2023. Multitrophic biodiversity enhances ecosystem functions, services and ecological intensification in agriculture. J. Plant Ecol. 16 (6), rtad019. https://doi.org/10.1093/jpe/rtad019.
- Chao, C.T., Krueger, R.R., 2007. The date palm (Phoenix dactylifera L.): overview of biology, uses, and cultivation. HortScience 42 (5), 1077–1082. https://doi.org/ 10.21273/hortsci.42.5.1077.
- Cistrone, L., Augusto, A.M., Fichera, G., Rebelo, H., Russo, D., 2024. Agriculture and water availability show contrasting effects on bats in a Mediterranean island of outstanding chiropteran biogeographical value. Ecol. Evol. 14 (12), e70717. https://doi.org/10.1002/ece3.70717.
- Cohen, Y., Glasner, B., 2015. Date palm status and perspective in Israel. Date Palm. Genet. Resour. Util. Vol. 2: Asia Eur. 265–298. https://doi.org/10.1007/978-94-017-9707-8_8.
- Cohen, Y., Bar-David, S., Nielsen, M., Bohmann, K., Korine, C., 2020. An appetite for pests: synanthropic insectivorous bats exploit cotton pest irruptions and consume various deleterious arthropods. Mol. Ecol. 29 (6), 1185–1198. https://doi.org/10.1111/mec.15393.
- Denzinger, A., Schnitzler, H.U., 2013. Bat guilds, a concept to classify the highly diverse foraging and echolocation behaviors of microchiropteran bats. Front. Physiol. 4, 164. https://doi.org/10.3389/fphys.2013.00164.
- El-Shafie, H., 2012. Review: list of arthropod pests and their natural enemies identified worldwide on date palm, *Phoenix dactylifera L.* Agric. Biol. J. North Am. 3 (13), 516–524. https://doi.org/10.5251/abjna.2012.3.12.516.524.
- Fenton, M.B., 1970. A technique for monitoring bat activity with results obtained from different environments in southern Ontario. Can. J. Zool. 48 (4), 847–851. https://doi.org/10.1139/z70-148.
- Fenton, M.B., Bell, G.P., 1979. Echolocation and feeding behaviour in four species of *Myotis* (Chiroptera). Can. J. Zool. 57 (6), 1271–1277. https://doi.org/10.1139/ 279-163.
- Fialas, P.C., Froidevaux, J.S.P., Jones, G., Batáry, P., 2023. Transition to organic farming negatively affects bat activity. J. Appl. Ecol. 60 (10), 2167–2176. https://doi.org/10.1111/1365-2664.14468.
- Froidevaux, J.S.P., Louboutin, B., Jones, G., 2017. Does organic farming enhance biodiversity in Mediterranean vineyards? A case study with bats and arachnids. Agric. Ecosyst. Environ. 249, 112–122. https://doi.org/10.1016/j.agee.2017.08.012.
- Fry, H.T., 1967. The emergence of the beaufort scale. Mar. S. Mirror 53 (4), 311-313. https://doi.org/10.1080/00253359.1967.10659401.

Hackett, T.D., Korine, C., Holderied, M.W., 2013. The importance of acacia trees for insectivorous bats and arthropods in the Arava desert. PLoS ONE 8 (2), e52999. https://doi.org/10.1371/journal.pone.0052999.

- Hackett, T.D., Holderied, M.W., Korine, C., 2016. Echolocation call description of 15 species of Middle-Eastern desert dwelling insectivorous bats. Bioacoustics 26 (3), 217–235. https://doi.org/10.1080/09524622.2016.1247386.
- Jacobs, D.S., Catto, S., Mutumi, G.L., Finger, N., Webala, P.W., 2017. Testing the sensory drive hypothesis: geographic variation in echolocation frequencies of Geoffroy's horseshoe bat (*Rhinolophidae: Rhinolophus clivosus*). PLOS ONE 12 (11), e0187769. https://doi.org/10.1371/journal.pone.0187769.
- Johnson, D.V., Al-Khayri, J.M., Jain, S.M., 2015. Introduction: date production status and prospects in Asia and Europe. In: Al-Khayri, J., Jain, S., Johnson, D. (Eds.), Date Palm Genetic Resources and Utilization. Springer, Dordrecht. https://doi.org/10.1007/978-94-017-9707-8_1.
- Kolkert, H., Smith, R., Rader, R., Reid, N., 2021. Insectivorous bats provide significant economic value to the Australian cotton industry. Ecosyst. Serv. 49, 101280. https://doi.org/10.1016/j.ecoser.2021.101280.
- Korine, C., Pinshow, B., 2004. Guild structure, foraging space use, and distribution in a community of insectivorous bats in the Negev Desert. J. Zool. 262 (2), 187–196. https://doi.org/10.1017/s0952836903004539.
- Korine, C., Adams, R., Russo, D., Fisher-Phelps, M., Jacobs, D., 2016. Bats and water: anthropogenic alterations threaten global bat populations. Bats Anthr.: Conserv. bats a Chang. World 215–241. https://doi.org/10.1007/978-3-319-25220-9_8.
- Krueger, R.R., 2021. Date Palm (Phoenix dactylifera L.) Biology and Utilization. In: Al-Khayri, J.M., Jain, S.M., Johnson, D.V. (Eds.), The Date Palm Genome, Vol. 1. Compendium of Plant Genomes. Springer, *Cham.* https://doi.org/10.1007/978-3-030-73746-7_1.
- Maslo, B., Mau, R.L., Kerwin, K., McDonough, R., McHale, E., Foster, J.T., 2022. Bats provide a critical ecosystem service by consuming a large diversity of agricultural pest insects. Agric. Ecosyst. Environ. 324, 107722. https://doi.org/10.1016/j.agee.2021.107722. (https://doi.org/10.1007/978-3-319-24397-9_12).
- Norberg, U.M., Rayner, J.M., 1987. Ecological morphology and flight in bats (*Mammalia; Chiroptera*): wing adaptations, flight performance, foraging strategy and echolocation. Philos. Trans. R. Soc. Lond. B, Biol. Sci. 316 (1179), 335-427. https://doi.org/10.1098/rstb.1987.0030.
- Perring, M.P., Standish, R.J., Price, J.N., Craig, M.D., Erickson, T.E., Ruthrof, K.X., Hobbs, R.J., 2015. Advances in restoration ecology: rising to the challenges of the coming decades. Ecosphere 6 (8), 1–25. https://doi.org/10.1890/es15-00121.1.
- Rusch, A., Chaplin-Kramer, R., Gardiner, M.M., Hawro, V., Holland, J., Landis, D., Bommarco, R., 2016. Agricultural landscape simplification reduces natural pest control: a quantitative synthesis. Agric. Ecosyst. Environ. 221, 198–204. https://doi.org/10.1016/j.agee.2016.01.039.
- Russo, D., Jones, G., 2002. Identification of twenty-two bat species (Mammalia: Chiroptera) from Italy by analysis of time-expanded recordings of echolocation calls. J. Zool. 258 (1), 91–103. https://doi.org/10.1017/s0952836902001231.
- Russo, D., Jones, G., 2003. Use of foraging habitats by bats in a Mediterranean area determined by acoustic surveys: conservation implications. Ecography 26 (2), 197-209. https://doi.org/10.1034/j.1600-0587.2003.03422.x.
- Russo, D., Bosso, L., Ancillotto, L., 2018. Novel perspectives on bat insectivory highlight the value of this ecosystem service in farmland: research frontiers and management implications. Agric., Ecosyst. Environ. 266, 31–38. https://doi.org/10.1016/j.agee.2018.07.024.
- Russo, D., Tanalgo, K., Rebelo, H., Cistrone, L., 2024. To improve or not to improve? The dilemma of "bat-friendly" farmland potentially becoming an ecological trap. Agric. Ecosyst. Environ. 375, 109215. https://doi.org/10.1016/j.agee.2024.109215.
- Schäckermann, J., Morris, E.J., Alberdi, A., Razgour, O., Korine, C., 2022. The contribution of desert-dwelling bats to pest control in hyper-arid date agriculture. Diversity 14 (12), 1034. https://doi.org/10.3390/d14121034.
- Schnitzler, H.U., Kalko, E.K.V., 1998. How echolocating bats search for food. In: Kunz, T.H., Racey, P.A. (Eds.), Bats biology and conservation. Smithsonian Institution Press, Washington, DC, pp. 183–196.
- Tran, T.H., Mayzlish Gati, E., Eshel, A., Winters, G., 2018. Germination, physiological and biochemical responses of acacia seedlings (Acacia raddiana and Acacia tortilis) to petroleum contaminated soils. Environ. Pollut. 234, 642–655. https://doi.org/10.1016/j.envpol.2017.11.067.
- Tuneu-Corral, C., Puig-Montserrat, X., Riba-Bertolín, D., Russo, D., Rebelo, H., Cabeza, M., López-Baucells, A., 2023. Pest suppression by bats and management strategies to favour it: a global review. Biol. Rev. 98 (5), 1564–1582. https://doi.org/10.1111/brv.12967.
- Verboom, B., Spoelstra, K., 1999. Effects of food abundance and wind on the use of tree lines by an insectivorous bat, Pipistrellus pipistrellus. Can. J. Zool. 77 (9), 1393–1401. https://doi.org/10.1139/z99-116.
- Wakil, W., Faleiro, J.R., Miller, T.A., Bedford, G.O., Krueger, R.R., 2015. Date palm production and pest management challenges. Sustain. Pest Manag. Date Palm: Curr. Status Emerg. Chall. 1–11. https://doi.org/10.1007/978-3-319-24397-9 1.
- Ward, D., Rohner, C., 1997. Anthropogenic causes of high mortality and low recruitment in three Acacia tree taxa in the Negev desert, Israel. Biodivers. Conserv. 6 (6), 877–893. https://doi.org/10.1023/b:bioc.0000010408.90955.48.
- Wickramasinghe, L.P., Harris, S., Jones, G., Vaughan, N., 2003. Bat activity and species richness on organic and conventional farms: impact of agricultural intensification. J. Appl. Ecol. 40 (6), 984–993. https://doi.org/10.1111/j.1365-2664.2003.00856.x.
- Zaid, A., & Arias-Jimenez, E.D.J. (1999). Date palm cultivation. FAO Plant Production and Protection Paper No. 156. Food and Agriculture Organization.
- Ziv, B., Saaroni, H., Alpert, P., 2004. The factors governing the summer regime of the eastern Mediterranean. Int. J. Climatol. 24 (14), 1859–1871. https://doi.org/ 10.1002/joc.1113.