Biodiversity and Conservation (2026) 35:109
https://doi.org/10.1007/s10531-026-03307-x

ORIGINAL RESEARCH

Assessing vertical stratification of bats and nocturnal insects to infer potential collision risk at wind turbines in central Thailand

Supawan Srilopan[1] · Jennifer J. Krauel[4] · Kamonporn Srilopan[5,6] · Christian C. Voigt[2,3] · Sara Bumrungsri[1]

Received: 5 August 2025 / Revised: 17 January 2026 / Accepted: 27 February 2026 /

Abstract

The global growth of wind energy can harm wildlife and ecosystems, especially airborne animals, which face high collision risks with turbine blades. While detailed knowledge of bird and bat collision risk exists for temperate regions, risk assessments for insects and bats in the Global South remain lacking. To fill this gap, we investigated the activity of bats and nocturnal insects in Thailand at different heights above the ground. To this end, we suspended ultrasonic detectors and sticky traps from a helium-filled balloon kite at 25, 50, 75, and 100 m above ground, and also mounted them on a 2 m post to record ground-level activity. We documented the rotor-swept zone of local wind turbines to range between 21 and 159 m above ground. Mostly bat species from the guild of open-space foragers were active within this zone, namely Mops plicatus, Taphozous theobaldi, T. melanopogon, Scotophilus kuhlii, S. heathii, and Myotis siligorensis. Aerial insects, including Diptera, Hemiptera, Lepidoptera, and others, were also present within the rotor-swept zone of local wind turbines. Our findings demonstrate that aerial hawking bats, specialized for hunting insects in open space, face a high collision risk at wind turbines in Southeast Asia. Wind turbines may also kill airborne insects like Diptera, Hemiptera, and Lepidoptera. To reduce bat fatalities at wind turbines, we advocate for effective mitigation measures, such as limiting turbine operation at night during periods of high bat activity and specific environmental conditions. Further, wind turbines should only be built at great distance of ecologically important habitats.

Keywords Open space bats · Rotor-swept zone · Balloon-kite · Altitudes · Wind energy production

---

Christian C. Voigt and Sara Bumrungsri shared senior author position.

Communicated by Daniel Hending.

Extended author information available on the last page of the article

Introduction

Wind energy is expanding globally at an unprecedented rate to generate electricity at low cost and to combat climate change by reducing greenhouse gas emissions (Agency 2023; Global Wind Energy Council 2023). However, wind energy production comes at some environmental cost (Saidur et al. 2011; Gibson et al. 2017), for example by causing high numbers of casualties among aerial vertebrates (Thaxter et al. 2017), by displacing animals from their habitats (Conkling et al. 2022; Tolvanen et al. 2023), and by altering the local weather of adjacent habitats (Diffendorfer et al. 2022). As a consequence, wind energy production may impact biodiversity if practiced without considering the local fauna and flora, or when established at high densities over large spatial scales, particularly in sensitive biodiversity hotspots (Rehbein et al. 2020). To achieve a biodiversity-friendly transition from fossil fuel–based energy systems to renewable energy sources, it is imperative to identify and account for adverse ecological impacts, following the avoidance-mitigation-compensation hierarchy (Arlidge et al. 2018). However, from a global perspective, conservation practices at utility-scale wind energy facilities suffer from a lack of data and guidelines, unspecified monitoring schemes, or a simple unwillingness to comply with legal requirements (Barré et al. 2022). This is particularly true for tropical and subtropical countries, where global biodiversity is highest (Voigt et al. 2024).

Among airborne animals, bats and insects account for a large proportion of fatalities at wind turbine facilities, particularly in temperate regions (Thaxter et al. 2017; Voigt 2021). That said, the exact number of insects that collide and die at wind turbines remain obscure (Voigt et al. 2021). For bats, turbine-related casualties constitute a major cause of human-induced deaths for some aerial-hawking bat species (O’Shea et al. 2016). Besides being killed by wind turbines when colliding with the rotating blades, bats also lose habitat when wind turbines are established, e.g., at forested sites. Forest losses associated with the erection of wind turbines range between 1 ha per wind turbine in Germany (Quentin and Tucci 2022) and 3.5 ha for a 2.5 MW producing wind turbine in North America (Denholm et al. 2009). Also, bats may avoid wind turbines over hundreds of meters, sometimes even kilometers, which can cause additional losses of habitats in proximity of wind turbines (e.g., Barré et al. 2022; Ellerbrok et al. 2022, 2024; Scholz et al. 2025). Most studies to date on the negative effects of wind energy generation on bats have been conducted in temperate zones, although the wind energy industry in the emerging markets of subtropical tropical South America, Africa, and Asia is growing at an annual rate of 10% (Voigt et al. 2024). This geographic bias poses a big problem for global conservation efforts, since local stakeholders lack even fundamental information about the collision risk of airborne taxa (Voigt et al. 2024). Therefore, these countries rarely, if ever, implement appropriate mitigation schemes to protect airborne animals at wind turbines.

Central Thailand is home to a diverse bat fauna, with species varying greatly in morphology and echolocation call parameters. This indicates not only a high species richness, but also a high functional diversity (Suksai and Bumrungsri 2019). Wind energy facilities are already operating in the region, with approximately 415 turbines currently installed and further expansion planned in the near future, indicating a growing scale of potential ecological impact (The Wind Power 2025). Post-construction monitoring at nearby multi-turbine wind farms has documented bat fatalities involving predominantly open-space foraging species, including *Mops plicatus*, *Taphozous melanopogon*, and *Scotophilus kuhlii* (Asian Development Bank 2023; Crane et al. 2025). Reported carcass counts included 130 bats in 2019 (first year of operation), followed by 48 in 2020, 33 in 2021, and 30 in 2022. Although these data provide evidence of bat–turbine interactions in the region, detailed information on survey effort and detection probability was not publicly available. The true fatality rates of bats at local wind turbines may be significantly higher, since search efficiency ranges usually between 20 and 30% and removal of carcasses by scavenger, such as stray dogs, may be substantial in Thailand. Past studies of insectivorous bat activity in agricultural areas have primarily relied on ultrasonic recordings at ground level (e.g., at 1–3 m above ground, Put et al. 2018; Azofeifa et al. 2019; Suksai and Bumrungsri 2019), yet acoustic monitoring of bats foraging at higher altitudes is rare, due to methodological reasons. Acoustic monitoring of bats with ultrasonic detectors suspended from helium-filled kite balloons has been established as a feasible option to monitor bat activity beyond the detection range of ground-based ultrasonic detectors. These studies demonstrate that bat activity is unevenly distributed along the vertical axis (Griffin and Thompson 1982; Fenton and Griffin 1997; Nguyen et al. 2019). For example, aerial-hawking bats that are adapted to hunt insects in the open-space (hereafter called open-space foraging bats) are primarily active at altitudes of 100–200 m above ground (Nguyen et al. 2019). Some of these open-space foraging bats, like *Mops plicatus* and *Taphozous theobaldii*, fly at exceptionally high altitudes, with sensor tag data showing ascents of more than 550 m above ground level in *T. theobaldi* and more than 1,600 m above ground level in *M. plicatus* (Roeleke et al. 2018; Voigt et al. 2019b; Srilopan et al. 2025). Despite these first insights into the spatial use of Southeast Asian bats, there is still a large gap in our understanding on which species of bat is active within the rotor-swept zone of local wind turbines in Thailand. To establish baseline data, we aimed to explore the flight altitudes of bats in this region, particularly in areas where utility-scale wind energy facilities are either already operational or planned for the near future. Accordingly, we monitored the entire community of insectivorous bats that are active within the operation range of local wind turbines. We recorded the activity of bats across five vertical levels, ranging from 2 m (ground level) to 100 m above ground, in various habitat types, including arable land, forest edges, and areas near water bodies. Furthermore, we address the question which taxonomic group of nocturnal insects is vulnerable at wind turbines in central Thailand. Insect collisions with turbine rotors can result in the accumulation of insect debris on rotor blades, which necessitates regular cleaning and maintenance. However, systematic analyses of blade-cleaning residues as a quantitative measure of insect collision rates are currently absent. Anecdotal observations suggests that it is reasonable to assume that large numbers of insects die at wind turbines through collisions with rotating blades, yet conclusive evidence quantifying insect collision risk remains scarce (Voigt 2021). Accordingly, we examined the flight altitude of aerial insects at the same sites where we monitored the activity of bats. To complement our dataset, we also monitored the operation range of wind turbines (rotor-swept area) in the proximity of our study site. This comprehensive assessment provides valuable insights into the vertical habitat use of bats and insects in relation to their threat of colliding with local wind turbines.

Based on past studies on temperate zone bats (e.g., Roeleke et al. 2016; Roemer et al. 2017, 2019; Reusch et al. 2023), we hypothesized that bats exhibit niche partitioning in the vertical dimension by using different heights to forage for insects. We predicted that the flight altitude of open-space foragers would largely overlap with the operation range of local wind turbines, whereas bats specialized to forage for insects at forest edges (hereafter called edge-space foraging bats) or in dense vegetation (hereafter called narrow-space foraging bats) would not be susceptible to collisions with the rotating blades because of their low flight height close to the ground. Furthermore, we hypothesized that aerial insects are unevenly distributed along the vertical axis, with most insects being active at ground level. Specifically, we predicted that more aerial insects are active at ground level than at any of the higher sampling points.

Materials and methods

Study site

We conducted this study from February to March 2021 in Tha Luang District, located in Lopburi province, Thailand, which hosts several areas with multi-turbine wind energy facilities. This province is characterised by a karst landscape with many small and large caves, providing important habitats for various bat species. Previous studies have identified the following species in this area: *Hipposideros pomona*, *H. armiger*, *H. larvatus*, *H. diadema*, *Rhinolophus coelophyllus*, *R. malayanus*, *R. pusillus*, *R. pearsonii*, *Myotis muricola*, *M. siligorensis*, *Scotophilus kuhlii*, *S. heathii*, *Taphozous melanopogon*, *T. theobaldi*, *and Mops plicatus* (Ruadreo et al. 2018; Suksai and Bumrungsri 2019). The area is dominated by arable land, where local farmers plant crops like sugarcane, corn, and cassava. Next to arable and urban areas, the most common landscape elements are water bodies and forests. For this study, we selected three main habitat types: arable land, areas next to water bodies, and forest edges (Fig. 1). In total, 12 recording sites were established. Three replicate sites were selected for each habitat type, and because recordings at 2 m above ground level could not be conducted directly at forest edges, three additional forest-edge sites were added specifi-

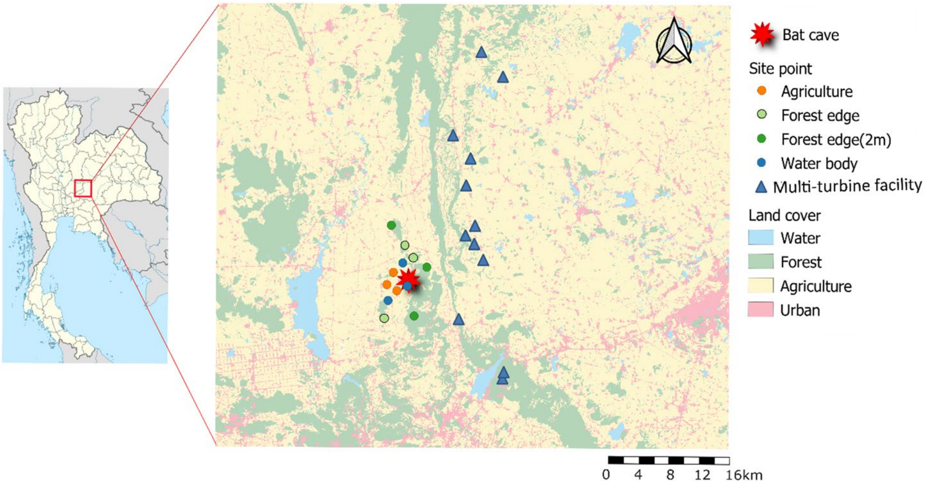

Fig. 1 Map showing the location of the cave with a colony of *M. plicatus* (red multi-pointed star symbol) and recording sites: Orange points indicate recording sites located in agricultural areas, light green points represent those at forest edges (25–100 m), dark green points those at forest edges (2 m), and blue points mark recording sites next to water bodies. Blue triangles indicate the locations of multi-turbine facilities. The map also illustrates the land cover in the study area as outlined in the legend

cally for the 2 m recordings (Fig. 1). Sites were selected based on direct field verification to represent distinct and unambiguous habitat types. The water bodies in this area are relatively small, often representing only small ponds of a few 100 m^2. The forest patches are variable in size and typically isolated by farmland. To select recording sites, we applied the following criteria. Sites were located 2–20 km from the nearest *M. plicatus* colony, a species that is particularly abundant locally (approximately 140,000 bats per cave; Bumrungsri 2018). In addition, each site was at least 2 km from the nearest other site to minimise potential overlap and ensure adequate spatial representation. Final site selection was also influenced by practical constraints, including proximity to roads, power lines, and cultivated areas, as well as access restrictions; therefore, only safe and accessible locations approved by landowners were used.

Wind farm characteristics

We identified 16 multi-turbine facilities for wind energy production within a 100 km radius of the recording sites (Table 1). We chose this distance of 100 km because *M. plicatus*, the locally dominant open-space forager bat species, is capable of flying such distances during a single nightly foraging trip (Srilopan et al. 2025). To calculate key wind turbine parameters, we obtained the diameter (m) of the rotor-swept zone, which is typically provided directly by the manufacturer (The Wind Power 2025) and can also be calculated as twice the blade length (m). The hub height (m) is the distance from the ground to the center of the rotor hub and is often specified in the turbine's technical documentation (The Wind Power 2025). The tip height (m) is the sum of the hub height and the blade length, while the lowest blade height (m) is the distance from the ground to the lowest point of the operating blade. The total number of turbines in a wind farm, the capacity per turbine (MW), which refers to the rated power output of an individual turbine, and the total capacity (MW), calculated by multiplying the number of turbines by the capacity per turbine, are listed in project reports or specifications (The Wind Power 2025).

Acoustic sampling

We recorded echolocation calls of bats using AudioMoth 1.0.0 (Open Acoustic Devices, Southampton, United Kingdom), which store acoustic information as 16-bit uncompressed waveform audio (WAV) files to a microSD card. The devices record frequencies up to approximately 192 kHz over a distance of about 10 m, depending on the call frequency, the source level and ambient conditions (Benjamins 2020; Open Acoustic Devices 2023). We set each AudioMoth to record for 10 s with a 5-second interval between recordings,

Table 1 Summary of wind turbine characteristics across 16 wind farms near the study area in Thailand

Variable	Range	Mean ± SD
Tip height (m)	112.2–158.5	141.4 ± 11.8
Lowest blade height (m)	21.5–48.2	26.0 ± 5.9
Blade length (m)	32.2–68.5	59.1 ± 8.8
Rotor diameter (m)	64.3–137.0	118.0 ± 14.5
Capacity per turbine (kW)	1,250–3,450	2,398 ± 533
Number of turbines/farms	1–103	25.3 ± 25.9

continuously from 6:30 pm to 6:30 am each night, and then placed it in a waterproof box with small perforations at the microphone opening to allow ultrasonic detection. Recordings were conducted at five different heights: (a) 2 m above ground ("ground level"), (b) 25 m above ground, (c) 50 m above ground, (d) 75 m above ground, and (e) 100 m above ground. Each night, recordings were simultaneously taken at all five levels. We lifted the balloon (11 cubic Helikite Balloon, Tichuan International Co., Ltd., Beijing, China) into the air in the late afternoon, and it remained airborne between 6 pm in the evening and 6.30 am the next morning. Recordings were collected for 2 nights per site. We did not collect any data when it was raining or in case of strong winds (> 12 m/s). Echolocation calls were analysed using Kaleidoscope Pro (version 5.1.9). Raw AudioMoth recordings were batch-processed in Kaleidoscope to reduce background noise and split into 5-second WAV files. Signal detection parameters targeted pulses between 8 and 120 kHz, with durations of 2–500 ms, a maximum inter-syllable gap of 500 ms, and a minimum of two pulses per detection. Processed files were screened for bat activity, and all detections were manually verified. Species identification was based on call characteristics including peak frequency, bandwidth, call duration, and call shape, following established regional echolocation call references (Utthammachai et al. 2008; Pham et al. 2021; Hughes et al. 2010, 2011; Wordley et al. 2014; Nguyen et al. 2019). To validate these references under local conditions, a subset of bats was additionally captured during the study, and echolocation calls recorded from morphologically identified individuals were used to confirm consistency with published call characteristics. Feeding buzzes were identified as rapid call sequences characterised by a marked decrease in inter-pulse interval and call duration immediately prior to prey capture. Feeding buzzes were quantified separately from commuting or search-phase calls and used as an indicator of active foraging behaviour (Jameson 2024).

We estimated the altitude of bat detectors in relation to ground level by the formula $h = 0.9\ L\ x\ \sin(\alpha)$ (Griffin and Thompson 1982); where h is the height (in meters) above ground altitude of the operating bat detector, L is the length (in meters) of the line and (α) the angle of the line. In parallel, we confirmed the altitude of the detectors at the start of recording sessions using a rangefinder (Ak-305B, XunTian, China). At the forest edge, it was unsafe to operate a balloon at low altitudes. Therefore, we put the 2 m Audiomoth on a bamboo pole. For all other recording altitudes at forest edges, we used the helium balloon.

We categorized the guild structure of insectivorous bats following Schnitzler and Kalko (2001) and Denzinger and Schnitzler (2013). Species were assigned to guilds based on their echolocation call characteristics (e.g., call type, frequency range), wing morphology (aspect ratio, wing loading), and foraging behaviour reported in previous studies (Suksai and Bumrungsri 2020; Table 2).

Sampling aerial insects

We collected insects using sticky traps (25.5 × 18 cm sheets, Shopee Thailand, Bangkok, Thailand) shaped into cylinders. To collect aerial insects during a given sampling night, we attached 5 cylinders, one at each altitude along the rope, always 2–3 m below the AudioMoths, following past studies (Nguyen et al. 2019; Petkliang et al. 2017; Fritz et al. 2011). Captured insects were kept frozen and identified to order level using standard taxonomic keys (Triplehorn and Johnson 2005). We collected insect biomass by measuring body length

Table 2 Foraging guild classification of insectivorous bat species recorded in central Thailand, following Schnitzler and Kalko (2001), Denzinger and Schnitzler (2013), and Suksai and Bumrungsri (2020)

Foraging guild	Species	Key justification
Open-space foragers	*Mops plicatus*, *Taphozous melanopogon*, *T. theobaldi*	Long, narrow wings; high wing loading; quasi-constant frequency (QCF) calls; foraging in open air
	Scotophilus kuhlii, *S. heathii*	Intermediate wing morphology; frequency-modulated and quasi-constant frequency (FM–QCF) calls; foraging in open and semi-open space
Edge-space foragers	*Myotis siligorensis*, *M. muricola*	Intermediate wing morphology; broadband FM calls; foraging along vegetation edges
	Hipposideros diadema, *H. larvatus*	Broad wing morphology; CF–FM calls; foraging near vegetation edges
	Miniopterus magnater	Long, narrow wings; FM calls; foraging along forest edges
Narrow-space foragers	*Rhinolophus coelophyllus*, *R. pearsonii*, *R. stheno*	Broad wing morphology; FM–CF–FM calls; foraging in cluttered habitats

(Lumsden and Bennett 2005) and using the formula: $W = 0.0305L^{2.62}$, where W is dry mass in mg and L is length in mm (Rogers et al. 1976).

Data analysis

We assessed the activity of bats based on the number of bat passes per minute, defining a bat pass as a sequence of one or more echolocation calls separated from other sequences by a period of silence (Miller 2001). We conducted recordings each night from 6:30 pm to 6:30 am. We grouped less frequently detected species into an “others” category, including *Miniopterus magnater*, *Myotis muricola*, *Rhinolophus coelophyllus*, *R. pearsonii*, *R. stheno*, *Hipposideros diadema*, and *H. larvatus*. We fitted a gaussian distribution generalized linear mixed models (GLMMs) using the “glmmTMB” function from the “glmmTMB” package in R (Brooks et al. 2017). Fixed effects included bat species, altitude (2, 25, 50, 75, and 100 m), habitat (agriculture, forest edge, water), and their interactions. Site and night were included as random intercepts to account for spatial and temporal non-independence. Model selection was based on corrected Akaike Information Criterion (AICc) values using the “model.sel()” function from the “MuMIn” package in R (Bartoń 2024).

Insect biomass was analyzed using gaussian distribution generalized linear mixed models (GLMMs) with fixed effects: insect order, altitude (2, 25, 50, 75, and 100 m), and habitat (agriculture, forest edge, water) and its interaction. Recording date and site were included as random effects. Model selection was based on corrected Akaike Information Criterion (AICc) values using the “model.sel()” function from the “MuMIn” package in R (Bartoń 2024). All statistical analyses were conducted using R software (version 4.2.2), and R Studio (version 4.3.1).

Results

Flight altitude of species and foraging guilds

In total, we analyzed 219.1 h of recordings across five altitude levels, 2 m, 25 m, 50 m, 75 m, and 100 m, documenting 62,239 recognizable bat passes. The recording effort was distributed as follows: 2 m (171.3 h), 25 m (147.1 h), 50 m (147.1 h), 75 m (147.1 h), and 100 m (147.1 h). The analysed recordings captured bat activity from five families, seven genera, and 13 species, as summarised in Table 3.

We observed 6 bat species at a flight altitude of 25 to 100 m, and thus within the rotor-swept zone of wind turbines: *Mops plicatus*, *Taphozous theobaldi*, *T. melanopogon*, *Scotophilus kuhlii*, *S. heathii*, and *Myotis siligorensis*. Five species were found across all recorded altitudes, and included four open-space foragers (*M. plicatus*, *T. melanopogon*, *T. theobaldi*, and *S. kuhlii*) and one edge-space forager (*M. siligorensis*). *Scotophilus heathii*, an open-space forager, was recorded only up to a maximum altitude of 50 m (Fig. 2).

Altitude influenced bat species activity. Among the tested generalized linear mixed models (GLMMs), the best-supported model was provided by the model including the interaction between species and altitude (AICc = 1402.2; Table S2). Compared to *M. plicatus*, all other species showed significantly lower activity: *T. melanopogon* ($\beta = -2.96$, $p < 0.001$), *T. theobaldi* ($\beta = -3.18$, $p < 0.001$), *S. heathii* ($\beta = -5.83$, $p < 0.001$), *S. kuhlii* ($\beta = -5.09$,

Table 3 Proportion of total recorded bat passes by foraging guild, family, and species

Foraging guild	Family	Species	% of total bat passes
Open-space foragers	Molossidae	*Mops plicatus*	83.6
	Emballonuridae	*Taphozous melanopogon*	4.5
	Emballonuridae	*Taphozous theobaldi*	3.4
	Vespertilionidae	*Scotophilus kuhlii*	0.5
	Vespertilionidae	*Scotophilus heathii*	0.3
Total open-space			92.3
Edge-space foragers	Vespertilionidae	*Myotis siligorensis*	7.1
	Vespertilionidae	*Myotis muricola*	0.09
	Hipposideridae	*Hipposideros diadema*	0.005
	Miniopteridae	*Miniopterus magnater*	0.004
	Hipposideridae	*Hipposideros larvatus*	0.0001
Total edge-space			7.2
Narrow-space foragers	Rhinolophidae	*Rhinolophus coelophyllus*	0.4
	Rhinolophidae	*Rhinolophus pearsonii*	0.1
	Rhinolophidae	*Rhinolophus stheno*	0.001
Total narrow-space			0.5

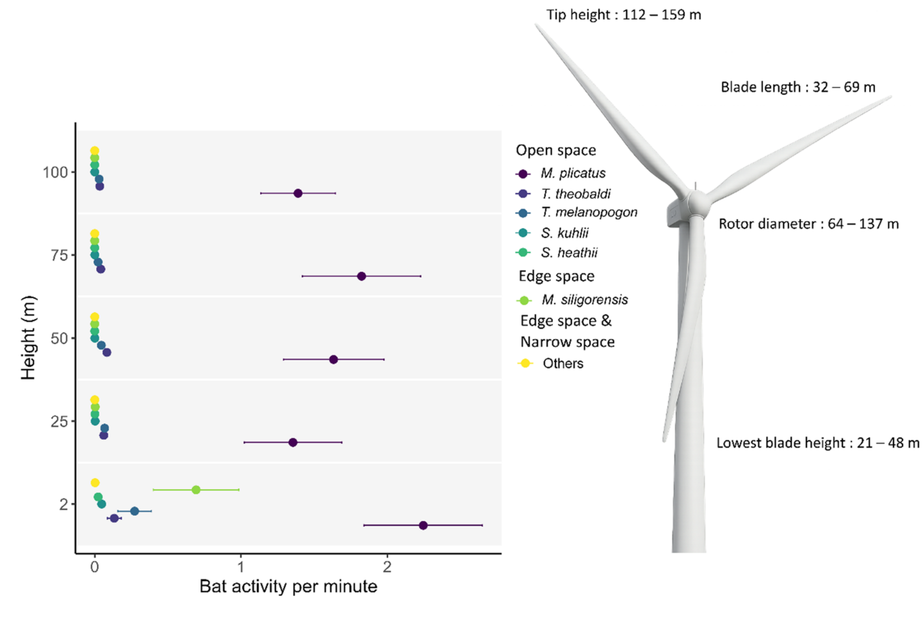

Fig. 2 Bat activity per minute (mean ± SE) at different altitudes in agricultural landscape of central Thailand. Bat species are categorized into three foraging guilds: open-space, edge-space, and narrow-space foraging bat guild. The category "Others" includes less common species, such as *M. magnater*, *M. muricola*, *R. coelophyllus*, *R. pearsonii*, *R. stheno*, *H. diadema, and H. larvatus*

$p<0.001$), and other less common species grouped as "Others" ($\beta = -4.53$, $p<0.001$). Bat activity also declined significantly with increasing height for the reference species (*M. plicatus*): 25 m ($\beta = -0.84$, $p<0.001$), 50 m ($\beta = -0.67$, $p=0.002$), 75 m ($\beta = -0.60$, $p=0.005$), and 100 m ($\beta = -0.84$, $p<0.001$), relative to 2 m. All open-space, edge-space, and narrow-space foraging species were recorded at ground level (2 m, Fig. 2). Open-space foragers exhibited significantly higher activity than edge-space bats ($\beta=2.64$, $p<0.001$), while narrow-space foragers showed significantly lower activity ($\beta = -3.41$, $p<0.001$). No significant differences were found in the number of feeding buzzes across the altitudes analyzed (2, 25, 50, 75, and 100 m; $p>0.1$).

Habitat use of species and foraging guilds

Bat activity varied significantly among habitats. Among the tested generalized linear mixed models (GLMMs), the best fit was provided by the model including the interaction between species and habitat (AICc = 1293.5; Table S2). Compared to agricultural areas, overall bat activity across all species was significantly lower at forest edges ($\beta = -0.44$, $p<0.001$) and water bodies ($\beta = -0.17$, $p<0.001$). We found no significant differences in the number of feeding buzzes between the habitats analyzed (agricultural area, edge forest, water body; $p>0.1$).

Bat activity differed significantly among habitat types and species ($p<0.001$; Fig. 3). Overall bat activity, pooled across species, was highest in agricultural areas and significantly lower at forest edges ($\beta = -0.44$, $p<0.001$) and near water bodies ($\beta = -0.17$, $p=0.001$). Across all habitats, *M. plicatus* exhibited significantly higher activity than all other species ($p<0.001$). However, species–habitat interactions indicated that several less common species showed relatively higher activity at forest edges and water bodies compared to agricultural areas. Forest edges and water bodies supported greater species diversity despite lower overall bat activity (Fig. 3). Some species were habitat-exclusive, with *H. diadema* recorded only at forest edges and *M. magnater* only near water bodies.

Insect abundance at different altitudes above ground

Insect biomass varied significantly with altitude and taxonomic order ($p<0.001$). Among the candidate generalized linear mixed models, the best-fit model included an interaction between insect order and altitude (AICc = 5072.6; Table S3), indicating that altitude effects differed among insect orders. Models including habitat effects were poorly supported (ΔAICc > 30), suggesting that altitude was a stronger predictor of insect biomass than habitat type.

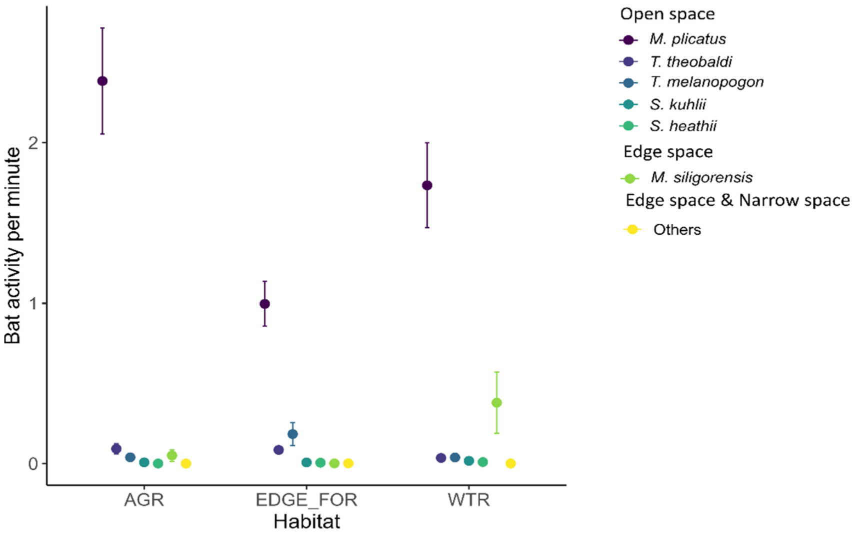

Fig. 3 Bat activity per minute (mean ± SE) in different habitats (AGR: agricultural area, EDGE_FOR: edge forest, WTR: water body) and different bat guilds (open space, edge space, narrow space), and different bat species within the agricultural landscape of central Thailand. "Others" category includes fewer common species: *M. magnater*, *M. muricola*, *R. coelophyllus*, *R. pearsonii*, *R. stheno*, *H. diadema*, *and H. larvatus*

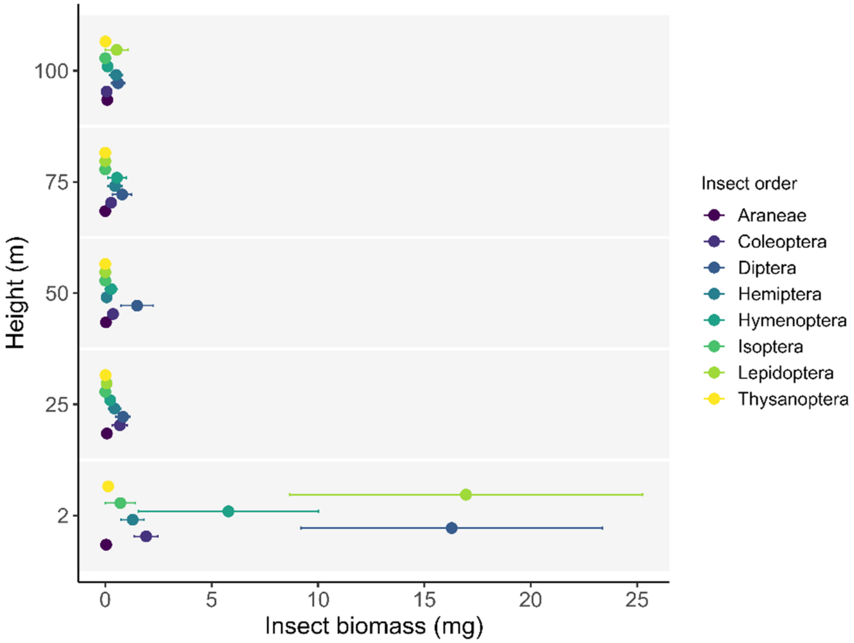

Fig. 4 Insect biomass (mean ± SE) at different altitudes above ground (m) and for different insect orders in the agricultural landscape of central Thailand

Sticky-trap data showed that total insect biomass was highest at ground level (2 m) and declined significantly with increasing altitude ($p < 0.001$). At 2 m, Lepidoptera accounted for the highest biomass and were therefore used as the reference group. Relative to Lepidoptera at 2 m, biomass did not differ significantly for Diptera ($\beta = -0.67, p > 0.01$) or Hymenoptera ($\beta = -11.17, p > 0.01$), whereas Coleoptera ($\beta = -15.03, p < 0.001$), Hemiptera ($\beta = -15.67$, $p < 0.001$), Isoptera ($\beta = -16.25, p < 0.001$), and other insect orders had significantly lower biomass. Although insect biomass decreased with altitude across all orders, Diptera, Hemiptera, Coleoptera, Hymenoptera, Lepidoptera, and other taxa were still detected at higher altitudes between 25 and 100 m, indicating vertical stratification in nocturnal insect availability (Fig. 4).

Discussion

Our study illustrates the potential overlap between flight altitude of bats and insects and the operational range of local wind turbines in Thailand. In particular, we observed six bat species flying at altitudes between 25 and 100 m (the latter being the maximum recording height), which is within the rotor impact zone of nearby turbines operating between 21 and 159 m. The following bat species were active within the rotor-swept zone of local wind turbines: *M. plicatus*, *T. theobaldi*, *T. melanopogon*, *S. kuhlii*, *S. heathii* and *M. siligorensis*. These results explain the presence of bat carcasses at nearby multi-turbine plants, where species such as *M. plicatus*, *T. melanopogon*, and *S. kuhlii*, all open-space foraging bats, have been found (Asian Development Bank 2023; Crane et al. 2025). While *M. muricola* was not detected in our recordings, we documented high-altitude activity by *M. siligorensis*, an edge-space forager, suggesting that some edge-space species may also be at risk of turbine collisions due to their occasional use of higher airspace (Asian Development Bank 2023; Crane et al. 2025). According to the Asian Development Bank (2023), the number of documented bat fatalities at the site was 130 in 2019 (the first year of operation), followed by 48 in 2020, 33 in 2021, and 30 in 2022. These data were collected through post-construction monitoring programs conducted by consulting teams contracted by the wind energy operator. However, detailed information on survey effort, such as search frequency, area coverage, scavenger correction, or detection probability, was not provided in the report. The relatively high number of carcasses in 2019 may reflect greater search effort during the initial monitoring phase, or possibly a behavioral response, such as increased exploratory activity by bats around newly built turbines (Rydell et al. 2010; Arnett et al. 2016). A recent study suggests that several bat species in Southeast Asia may be at high risk of collisions with wind turbines, particularly those with wing traits similar to species known to experience fatalities globally. However, the results also highlight the need for region-specific data to validate and refine these risk assessments (Crane et al. 2025). Studies from the temperate zone, mainly North America and Europe, have shown that wind turbines with rotor blades between 130 m and 180 m diameter are associated with high numbers of bat casualties, as the strong overlap of bat flight altitude with the rotor swept zone dramatically increases the risk of collision (Roeleke et al. 2016; Roemer et al. 2017; Reusch et al. 2023; Garvin et al. 2024; Arnett et al. 2008). As blade length increases, wind turbines begin to generate energy at lower wind speeds, conditions under which bat activity and collision risk are known to be higher, thereby potentially exacerbating conflicts between renewable energy production and bat conservation as larger turbines are deployed in the future (Voigt et al. 2015, 2024).

High altitudes are an important habitat for bats. As some members of this taxon are equipped with the ability to quickly ascend into the sky (Roeleke et al. 2022; O’Mara et al. 2021), they are able to hunt insects or birds in the open airspace (Popa-Lisseanu et al. 2007, Kunz et al. 2008; Davy et al. 2017a, b; Krauel et al. 2018a; Voigt et al. 2019a). Our results show that, within the local bat community in central Thailand, molossid and emballonurid species, as well as one vespertilionid species, were frequently detected at high altitudes (25–100 m), suggesting regular use of the airspace within the rotor-swept zone. Such vertical activity may be related to foraging behavior, especially on dispersing or migrating insects, as has been observed in *Tadarida brasiliensis* in North America (Krauel et al. 2018a, b). Notably, *M. plicatus* has been documented to track high-altitude flying insects as prey, mostly planthoppers (Nguyen et al. 2019; Leelapaibul et al. 2005; Srilopan et al. 2018, 2024; Thongjued 2019). A recent study shows that *M. plicatus* flies up to 1,600 m above ground level, with individual foraging areas covering up to 1,740 km^2 in a single day (Srilopan et al. 2025). Although sticky trap data showed low insect biomass at higher altitudes, several lines of evidence suggest that bats still locate prey there. Feeding buzzes recorded at these heights indicate active foraging, and prior studies have found that *M. plicatus* consumes large amounts of migratory planthoppers (Homoptera), which were largely absent from our samples (Srilopan et al. 2018, 2024). This likely reflects a sampling bias, as sticky traps may underrepresent fast-flying or swarm-forming insects that occur in dense but patchy distributions. Bats may also improve prey detection at altitude through social foraging, such as eavesdropping on the echolocation calls of nearby conspecifics (Roeleke et al. 2022).

Several open-space foraging species in our study were frequently detected at high altitudes. These species typically have high aspect ratio wings, narrow and elongated structures linked to fast, efficient flight in open environments (Norberg and Rayner 1987; Castillo-Figueroa 2020). While this wing shape may support high-altitude flight, it does not always predict the foraging altitude of these species. This underscores the need to integrate wing morphology, acoustic data, and behavioral patterns when evaluating a species' collision risk with wind turbines (Crane et al. 2025). Open-space foraging bats typically emit long-duration, low-frequency echolocation calls that facilitate long-range prey detection during fast, open-air flight (Schnitzler and Kalko 2001; Fenton 1990). However, exceptions exist, such as *M. siligorensis*, which uses relatively short, high-frequency calls despite being detected at high altitudes (Surlykke et al. 1993). These cases highlight the diversity of echolocation and flight strategies even within foraging guilds and suggest that multiple adaptations may enable bats to exploit vertical space. The dominant open space foraging bat in our study area is *M. plicatus*, a molossid bat, known for roosting in large caves, with some colonies numbering in the millions, making it the most abundant bat species in the region (Srilopan et al. 2018). Its aerodynamic morphology and long-range echolocation calls allow it to exploit a wide range of habitats and altitudes, which likely explains its frequent presence across all sampling locations in our study (Nguyen et al. 2019; Srilopan et al. 2025). Remarkably, they can forage from ground level to altitudes of up to 1,600 m (Nguyen et al. 2019; Voigt et al. 2019a; Srilopan et al. 2025). Similarly, the emballonurid bats *T. theobaldi* and *T. melanopogon* are known to fly at high altitudes, reaching peak altitudes of more than 550 m above ground, and most likely higher (Roeleke et al. 2018). In addition, open-space foraging bats such as *S. heathii*, *S. kuhlii* and *M. siligorensis* are also known to forage above 50 m above ground. Among these, *S. heathii*, being larger and heavier than others (Shahbaz et al. 2014), incurs higher energetic costs during ascending flights, which may limit its ability to forage at high altitudes (Norberg and Rayner 1987). Consistent with this notion, we observed *S. heathii* primarily at altitudes of up to 50 m above ground.

Although some bat species were recorded at high altitude in our study, most bat calls were recorded at ground level (2 m), which is consistent with insect biomass data showing the highest capture rates at ground level (2 m). At ground level, insect samples were dominated by Lepidoptera, followed by Diptera, Hymenoptera, Coleoptera, Hemiptera and Isoptera, many of which are major crop pests (Sukonthaphirom Na Phatthalung et al. 2021). Previous research in this area has shown that open-space foraging bats feed heavily on these pest taxa (Srilopan et al. 2024). At our study site, we identified 13 species of bats foraging at ground level. Ground level habitats are essential for species such as *Myotis muricola*, *Miniopterus magnater*, *Rhinolophus pearsonii*, *R. coelophyllus*, *R. stheno*, *Hipposideros diadema*, and *H. larvatus*, which were observed exclusively at this level, suggesting that these species have a limited ability to forage above 25 m above ground level. The listed species typically have broad wings with rounded wingtips and a relatively slow and highly manoeuvrable flight style (Norberg and Rayner 1987; Furey and Racey 2016; Senawi and Kingston 2019). Their short, high-frequency echolocation calls facilitate precise localisation in cluttered spaces, such as in vegetation or along forest edges, but limit foraging at higher altitudes, where low-frequency echolocation calls are required to increase the detection distance of insects (Denzinger and Schnitzler 2013). The detection of species-specific differences in altitude use may reflect spatial niche partitioning, potentially shaped by past or present competition. However, since many open-space foragers were also active near the ground, overlap with clutter-adapted species is possible, and we therefore interpret these patterns cautiously (Collins 2015).

Our results demonstrate pronounced habitat-related differences in bat activity within the agricultural landscape. Overall activity was highest in agricultural areas, largely driven by the dominance of the open-space forager *M. plicatus*, a pattern commonly reported for open-space bats in open and simplified habitats (Suksai and Bumrungsri 2019; Srilopan et al. 2025). In contrast, forest edges and water bodies supported lower overall activity but higher species diversity, consistent with previous studies showing that structurally complex habitats and aquatic features disproportionately benefit edge-space and narrow-space foragers (Fukui et al. 2006; Suksai and Bumrungsri 2019). The exclusive occurrence of *H. diadema* at forest edges and *M. magnater* near water bodies further underscores the importance of these habitats for maintaining bat diversity within agricultural landscapes, despite their lower contribution to total bat activity.

Several insect orders, including Diptera, Hemiptera, and Lepidoptera, were detected between 25 and 100 m, within the rotor-swept zone of wind turbines. This aligns with reports of large-scale insect migrations in East Asia, where Lepidoptera, Hemiptera, and Diptera commonly fly up to 1 km above ground (Huang et al. 2024), suggesting that windborne insects frequently occupy turbine altitudes and may face elevated collision risks. This is further supported by previous estimates suggesting that approximately 1.2 trillion insects are killed annually by onshore wind turbines in Germany, with a single turbine responsible for up to 40 million insect fatalities per year (Voigt 2021). Insect interactions with wind turbines may also influence predators that hunt near turbines. Aerial insectivores, such as bats, are known to forage around wind turbines (Roeleke et al. 2016; Valdez and Cryan 2013). A previous study suggested that the presence of diurnal Diptera in the stomachs of bat carcasses found beneath turbines indicates that bats may hunt these insects while they are around turbine structures (Rydell et al. 2016). Insect attraction to wind turbines may affect trophic interactions, including insect-mediated ecosystem functions and aerial predation by insectivores near turbines (Scholz and Voigt 2022). Thus, insect interactions with wind turbines may have wide-ranging effects that extend across trophic levels and broader spatial scales.

Our study is the first to systematically record bat flight altitude in Southeast Asia for a local bat community. We acknowledge some limitations caused by our study design. First, we only recorded in a relatively small area of the Thai landscape dominated by agricultural practices. Although high-altitude flying bats can travel long distances (e.g. *M. plicatus* has been recorded of use a foraging area of up to 1,740 km² in a single night and reaching altitudes of 1,600 m; Srilopan et al. 2025), we acknowledge that the local bat community may vary spatially across Thailand and that the composition of bats foraging at low and high altitudes may change accordingly. We attempted to account for this spatial variation by selecting recording sites in variable landscapes, e.g. on arable land, next to forests and near waterbodies. We also conducted our fieldwork over a relatively short period, which limits our ability to extrapolate our results across seasons. The reasons for our choice of study period were mainly of logistical and technical nature, as weather conditions are less favourable for helium kite based acoustic monitoring during seasons with high winds and precipitation. Furthermore, bat species differ in their echolocation call characteristics, with bats calling at low frequency and high intensity more likely to be detected by ultrasonic detectors than species calling at high frequency and low intensity (Voigt et al. 2021). Therefore, our acoustic data are inherently biased toward detecting bat species that produce low-frequency, high-intensity echolocation calls. Species with high-frequency, low-intensity calls are less detectable, particularly at greater distances or in cluttered environments, which may explain the absence of some known ground-level foragers in our dataset. Additionally, acoustic surveys are unable to detect non-echolocating bats such as pteropodids, which are also known to suffer wind turbine-related mortality in Southeast Asia (e.g., Crane et al. 2025). Nevertheless, our study provides a robust representation of the echolocating insectivorous bat community and a foundation for broader future research. Finally, our insect monitoring using sticky traps was inherently biased towards those insects that were more likely to land on the sticky traps. We suspect that other insect sampling techniques may have yielded slightly different results. However, hoisting UV lamps for collecting insects at greater altitudes was not an option because of the limited carrying capacity of the used helium balloon.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s10531-026-03307-x.

Acknowledgements This research was supported by a Postdoctoral Fellowship from Prince of Songkla University and by the National Research Council of Thailand (NRCT) under grant number NRCT5-RGJ63019-162. We thank Phongsin Inpaen, Tusita Srilopan, and Sunet Nalisa for their assistance during fieldwork. We are also grateful to the members of the Small Mammal, Bird, and Spider Research Unit for their valuable input in developing ideas. Additional thanks go to the Faculty of Science, Prince of Songkla University, for their continued support.

Author contributions SS, SB, JJK and CCV conceived and designed the experiments. SS, KS and SB performed the experiments. SS analyzed the data. SS, SB, JJK and CCV wrote the manuscript.

Funding This research was supported by a Postdoctoral Fellowship from Prince of Songkla University and by the National Research Council of Thailand (NRCT) under grant number NRCT5-RGJ63019-162.

Data availability The datasets generated during and/or analysed during the current study are available from the corresponding author on reasonable request.

Declarations

Consent for publication All authors gave consent for publication.

Competing interests The authors declare no competing interests.

Conflict of interest The authors have no relevant financial or non-financial interests to disclose.

Consent to participate All authors gave consent to participate.

References

Agency IRE (2023) Renewable capacity statistics 2023. IRENA, Abu Dhabi. https://www.irena.org/publications/2023/Mar/Renewable-Capacity-Statistics-2023. Accessed 4 Aug 2024

Arlidge WNS, Bull JW, Addison PFE, Burgass MJ, Gianuca D, Gorham TM, Jacob C, Shumway N, Sinclair SP, Watson JEM, Wilcox C, Milner-Gulland EJ (2018) A global mitigation hierarchy for nature conservation. Bioscience 68:336–347. https://doi.org/10.1093/biosci/biy029

Arnett EB, Brown WK, Erickson WP, Fiedler JK, Hamilton BL, Henry TH, Jain A, Johnson GD, Kerns J, Koford RR, Nicholson CP, O'Connell TJ, Piorkowski MD, Tankersley RD Jr (2008) Patterns of bat fatalities at wind energy facilities in North America. J Wildl Manage 72:61–78. https://doi.org/10.2193/2007-221

Arnett EB, Hein CD, Schirmacher MR, Huso MM, Szewczak JM (2016) Evaluating the effectiveness of an ultrasonic acoustic deterrent for reducing bat fatalities at wind turbines. PLoS ONE 11:e0161194. https://doi.org/10.1371/journal.pone.0161194

Asian Development Bank (2019) Energy absolute green bond for wind power project, Thailand (53255-001). https://www.adb.org/sites/default/files/project-documents/53255/53255-001-escar-en.pdf. Accessed 4 Aug 2024

Asian Development Bank (2020) Environmental and social monitoring report: Energy absolute green bond for wind power project (Project No. 53255-001, January–December 2019). Asian Development Bank, Bangkok. https://www.adb.org/projects/documents/tha-53255-001-esmr. Accessed 4 Aug 2024

Asian Development Bank (2022) Extended annual review report: Energy absolute green bond for wind power project (Project No. 53255-001, Loan No. 3818). Asian Development Bank, Bangkok. https://www.adb.org/projects/documents/tha-53255-001-xarr. Accessed 4 Aug 2024

Asian Development Bank (2023) Environmental and social monitoring report: Annual report (January–December 2022). Project Number: 53255-001 Asian Development Bank(Bangkok):httpswwwadborg projectsdocumentstha–53255

Azofeifa Y, Estrada-Villegas S, Mavárez J, Nassar JM (2019) Activity of aerial insectivorous bats in two rice fields in the northwestern Llanos of Venezuela. Acta Chiropterol 21:149–163. https://doi.org/10.3161/15081109ACC2019.21.1.012

Barré K, Froidevaux JSP, Leroux C, Mariton L, Fritze M, Kerbiriou C, Bas Y, Roemer C (2022) Over a decade of failure to implement UNEP/EUROBATS guidelines in wind energy planning: A call for action. Conserv Sci Pract 4:e12805. https://doi.org/10.1111/csp2.12805

Bartoń K (2024) MuMIn: Multi-Model Inference. R package version 1.47.5. https://CRAN.R-project.org/package=MuMIn. Accessed 4 July 2025

Benjamins S (2020) MASTS Small Grant report–SG499: Bats as Coastal Foragers (BACOF). https://www.masts.ac.uk/media/36942/sg499_final_report.pdf. Accessed 4 June 2024

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

Bumrungsri S (2018) Ecosystem services of *Tadarida plicata* to rice fields. Thailand. Final report, project code p-14-50620. National Science and Technology Development Agency (NSTDA), Pathum Thani, Thailand. 90 pp (In Thai)

Castillo-Figueroa D (2020) Ecological morphology of neotropical bat wing structures. Zool Stud 59. https://doi.org/10.6620/ZS.2020.59-60

Collins CT (2015) Food habits and resource partitioning in a guild of Neotropical swifts. Wilson J Ornithol 127:239–248. https://doi.org/10.1676/wils-127-02-239-248.1

Conkling TJ, Vander Zanden HB, Allison TD, Diffendorfer JE, Dietsch TV, Duerr AE, Fesnock AL, Hernandez RR, Loss SR, Nelson DM, Sanzenbacher PM, Yee JL, Katzner TE (2022) Vulnerability of avian populations to renewable energy production. R Soc Open Sci 9:211558. https://doi.org/10.1098/rsos.211558

Crane M, Silva I, Grainger MJ, Gale GA (2025) Predicting risk to bat species from wind turbine collision in Southeast Asia. https://doi.org/10.1111/cobi.14452. Conserv Biol e14452

Davy CM, Ford AT, Fraser KC (2017a) Aeroconservation for the fragmented skies. Conservation Letters, 10(6), 773-780. https://doi.org/10.1111/conl.12347

Davy CM, Ford AT, Fraser KC (2017b) Aeroconservation for the fragmented skies. Conserv Lett 10:773–780. https://doi.org/10.1111/conl.12347

Denholm P, Hand M, Jackson M, Ong S (2009) Land use requirements of modern wind power plants in the United States (No. NREL/TP-6A2-45834). National Renewable Energy Lab (NREL), Golden, CO. https://doi.org/10.2172/964608

Denzinger A, Schnitzler HU (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

Diffendorfer JE, Vanderhoof MK, Ancona ZH (2022) Wind turbine wakes can impact down-wind vegetation greenness. Environ Res Lett 17:104025. https://doi.org/10.1088/1748-9326/ac8da9

Ellerbrok JS, Delius A, Peter F, Farwig N, Voigt CC (2022) Activity of forest specialist bats decreases towards wind turbines at forest sites. J Appl Ecol 59:2497–2506. https://doi.org/10.1111/1365-2664.14249

Ellerbrok JS, Delius A, Peter F, Farwig N, Voigt CC (2024) Forest bat activity declines with increasing wind speed in proximity of operating wind turbines. Glob Ecol Conserv 48:e02782. https://doi.org/10.1016/j.gecco.2023.e02782

Fenton MB (1990) The foraging behaviour and ecology of animal-eating bats. Can J Zool 68:411–422. https://doi.org/10.1139/z90-061

Fenton MB, Griffin DR (1997) High-altitude pursuit of insects by echolocating bats. J Mammal 78:247–250. https://doi.org/10.2307/1382658

Fritz GN, Fritz AH, Vander Meer RK (2011) Sampling high-altitude and stratified mating flights of red imported fire ant. J Med Entomol 48:508–512. https://doi.org/10.1603/ME10185

Fukui D, Murakami M, Nakano S, Aoi T (2006) Effect of emergent aquatic insects on bat foraging in a riparian forest. J Anim Ecol 75:1252–1258. https://doi.org/10.1111/j.1365-2656.2006.01146.x

Furey NM, Racey PA (2016) Can wing morphology inform conservation priorities for Southeast Asian cave bats? Biotropica 48:545–556. https://doi.org/10.1111/btp.12333

Garvin JC, Simonis JL, Taylor JL (2024) Does size matter? Investigation of the effect of wind turbine size on bird and bat mortality. Biol Conserv 291:110474. https://doi.org/10.1016/j.biocon.2024.110474

Gibson L, Wilman EN, Laurance WF (2017) How green is 'green' energy? Trends Ecol Evol 32:922–935. https://doi.org/10.1016/j.tree.2017.09.007

Global Wind Energy Council (2023) Global wind report 2023. Global wind energy council. https://gwec.net/reports/global-wind-report-2023/. Accessed 03 Jan 2024

Griffin DR, Thompson D (1982) High altitude echolocation of insects by bats. Behav Ecol Sociobiol 10:303–306. https://doi.org/10.1007/BF00302821

Huang J, Feng H, Drake VA, Reynolds DR, Gao B, Chen F, Chapman JW (2024) Massive seasonal high-altitude migrations of nocturnal insects above the agricultural plains of East China. Proc Natl Acad Sci USA 121:e2317646121. https://doi.org/10.1073/pnas.2317646121

Hughes AC, Satasook C, Bates PJJ, Soisook P, Sritongchuay T, Jones G, Bumrungsri S (2010) Echolocation call analysis and presence-only modelling as conservation monitoring tools for rhinolophoid bats in Thailand. Acta Chiropterol 12:311–327. https://doi.org/10.3161/150811010X537891

Hughes AC, Satasook C, Bates PJJ, Soisook P, Sritongchuay T, Jones G, Bumrungsri S (2011) Using echolocation calls to identify Thai bat species: Vespertilionidae, emballonuridae, nycteridae and megadermatidae. Acta Chiropterol 13:447–455. https://doi.org/10.3161/150811011X624938

Jameson JW (2024) Buzzfindr: Automating the detection of feeding buzzes in bat echolocation recordings. PLoS ONE 19:e0306063. https://doi.org/10.1371/journal.pone.0306063

Krauel JJ, Brown VA, Westbrook JK, McCracken GF (2018a) Predator–prey interaction reveals local effects of high-altitude insect migration. Oecologia 186:49–58. https://doi.org/10.1007/s00442-017-3995-0

Krauel JJ, Ratcliffe JM, Westbrook JK, McCracken GF (2018b) Brazilian free-tailed bats (*Tadarida brasiliensis*) adjust foraging behaviour in response to migratory moths. Can J Zool 96:513–520. https://doi.org/10.1139/cjz-2017-0284

Kunz TH, Gauthreaux SA Jr, Hristov NI, Horn JW, Jones G, Kalko EKV, Larkin RP, McCracken GF, Swartz SM, Srygley RB, Dudley R, Westbrook JK, Wikelski M (2008) Aeroecology: probing and modeling the aerosphere. Integr Comp Biol 48:1–11. https://doi.org/10.1093/icb/icn037

Leelapaibul W, Bumrungsri S, Pattanawiboon A (2005) Diet of wrinkle-lipped free-tailed bat (*Tadarida plicata* Buchannan, 1800) in central Thailand: insectivorous bats potentially act as biological pest control agents. Acta Chiropterol 7:111–119. https://doi.org/10.3161/1733-5329(2005)7[111:DOWFBT]2.0.CO;2

Lumsden LF, Bennett AF (2005) Scattered trees in rural landscapes: Foraging habitat for insectivorous bats in southeastern Australia. Biol Conserv 122:205–222. https://doi.org/10.1016/j.biocon.2004.07.006

Miller BW (2001) A method for determining relative activity of free-flying bats using a new activity index for acoustic monitoring. Acta Chiropterologica 3(1):93–105

Nguyen TN, Ruangwiset A, Bumrungsri S (2019) Vertical stratification in foraging activity of *Chaerephon plicatus* (Molossidae, Chiroptera) in central Thailand. Mamm Biol. https://doi.org/10.1016/j.mambio.2019.03.003

Norberg UM, Rayner JM (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 316:335–427. https://doi.org/10.1098/rstb.1987.0030

O'Shea TJ, Cryan PM, Hayman DT, Plowright RK, Streicker DG (2016) Multiple mortality events in bats: a global review. Mamm Rev 46:175–190. https://doi.org/10.1111/mam.12064

O'Mara MT, Amorim F, Scacco M, McCracken GF, Safi K, Mata V, Tomé R, Swartz S, Wikelski M, Beja P, Rebelo H, Dechmann DKN (2021) Bats use topography and nocturnal updrafts to fly high and fast. Curr Biol 31:1311–1316e4. https://doi.org/10.1016/j.cub.2020.12.042

Open Acoustic Devices (2023) AudioMoth user guide and specifications. https://www.openacousticdevices.info. Accessed 12 Jan 2024

Petkliang N, Gale GA, Brunton DH, Bumrungsri S (2017) Wetland, forest, and open paddy land are the key foraging habitats for Germain's swiftlet (*Aerodramus inexpectatus germani*) in Southern Thailand. Trop Conserv Sci 10:1–12. https://doi.org/10.1177/1940082917698467

Pham LK, Tran BV, Le QT, Nguyen TT, Voigt CC (2021) Description of echolocation call parameters for urban bats in Vietnam as a step towards a more integrated acoustic monitoring of urban wildlife in Southeast Asia. Diversity 13:18. https://doi.org/10.3390/d13010018

Popa-Lisseanu AG, Delgado-Huertas A, Forero MG, Rodríguez A, Arlettaz R, Ibáñez C (2007) Bats' conquest of a formidable foraging niche: the myriads of nocturnally migrating songbirds. PLoS ONE 2:e205. https://doi.org/10.1371/journal.pone.0000205

Put JE, Mitchell GW, Fahrig L (2018) Higher bat and prey abundance at organic than conventional soybean fields. Biol Conserv 226:177–185. https://doi.org/10.1016/j.biocon.2018.06.021

Quentin J, Tucci F (2022) Entwicklung der windenergie im wald: Ausbau, planerische vorgaben und empfehlungen für windenergiestandorte auf waldflächen in den Bundesländern. Bundesministerium für Wirtschaft und Energie, 6th ed. https://www.bmwi.de/Redaktion/DE/Publikationen. Accessed 14 Jan 2025

Rehbein JA, Watson JE, Lane JL, Sonter LJ, Venter O, Atkinson SC, Allan JR (2020) Renewable energy development threatens many globally important biodiversity areas. Glob Chang Biol 26:3040–3051. https://doi.org/10.1111/gcb.15067

Reusch C, Paul AA, Fritze M, Kramer-Schadt S, Voigt CC (2023) Wind energy production in forests conflicts with tree-roosting bats. Curr Biol 33:737–743. https://doi.org/10.1016/j.cub.2022.12.050

Roeleke M, Blohm T, Kramer-Schadt S, Yovel Y, Voigt CC (2016) Habitat use of bats in relation to wind turbines revealed by GPS tracking. Sci Rep 6:28961. https://doi.org/10.1038/srep28961

Roeleke M, Bumrungsri S, Voigt CC (2018) Bats probe the aerosphere during landscape-guided altitudinal flights. Mamm Rev 48:7–11. https://doi.org/10.1111/mam.12109

Roeleke M, Schlägel UE, Gallagher C, Pufelski J, Blohm T, Nathan R, Toledo S, Jeltsch F, Voigt CC (2022) Insectivorous bats form mobile sensory networks to optimize prey localization: The case of the common noctule bat. Proc Natl Acad Sci USA 119:e2203663119. https://doi.org/10.1073/pnas.2203663119

Roemer C, Disca T, Coulon A, Bas Y (2017) Bat flight height monitored from wind masts predicts mortality risk at wind farms. Biol Conserv 215:116–122. https://doi.org/10.1016/j.biocon.2017.09.002

Roemer C, Bas Y, Disca T, Coulon A (2019) Influence of landscape and time of year on bat–wind turbines collision risks. Landsc Ecol 34:2869–2881. https://doi.org/10.1007/s10980-019-00927-3

Rogers LE, Hinds WT, Buschbom RL (1976) A general weight vs. length relationship for insects. Ann Entomol Soc Am 69:387–389. https://doi.org/10.1093/aesa/69.2.387

Ruadreo N, Voigt CC, Bumrungsri S (2018) Large dietary niche overlap of sympatric open-space foraging bats revealed by carbon and nitrogen stable isotopes. Acta Chiropterol 20:329–341. https://doi.org/10.3161/15081109ACC2018.20.2.005

Rydell J, Bach L, Dubourg-Savage MJ, Green M, Rodrigues L, Hedenström A (2010) Bat mortality at wind turbines in northwestern Europe. Acta Chiropterol 12:261–274. https://doi.org/10.3161/150811010X537846

Rydell J, Bogdanowicz W, Boonman A, Pettersson S, Suchecka E, Pomorski JJ (2016) Bats may eat diurnal flies that rest on wind turbines. Mamm Biol 81:331–339. https://doi.org/10.1016/j.mambio.2016.01.005

Saidur R, Rahim NA, Islam MR, Solangi KH (2011) Environmental impact of wind energy. Renew Sustain Energy Rev 15:2423–2430. https://doi.org/10.1016/j.rser.2011.02.024

Schnitzler HU, Kalko EKV (2001) Echolocation by insect-eating bats. Bioscience 51:557–569. https://doi.org/10.1641/0006-3568(2001)051[0557:EBIEB]2.0.CO;2

Scholz C, Voigt CC (2022) Diet analysis of bats killed at wind turbines suggests large–scale losses of trophic interactions. Conserv Sci Pract 4:e12744. https://doi.org/10.1111/csp2.12744

Scholz C, Klein H, Voigt CC (2025) Wind turbines displace bats from drinking sites. Biol Conserv 284:110968. https://doi.org/10.1016/j.biocon.2025.110968

Senawi J, Kingston T (2019) Clutter negotiating ability in an ensemble of forest interior bats is driven by body mass. J Exp Biol 222:jeb203950. https://doi.org/10.1242/jeb.203950

Shahbaz M, Javid A, Mahmood-ul-Hassan M, Makhdoom S, Hussain SA, Idnan M (2014) Recent record of *Scotophilus heathii* from wheat-rice based agroecosystem of Punjab. Pak J Zool 46:4

Srilopan S, Bumrungsri S, Jantarit S (2018) The wrinkle-lipped free-tailed bat (*Chaerephon plicatus* Buchanan, 1800) feeds mainly on brown planthoppers in rice fields of central Thailand. Acta Chiropterol 20:207–219. https://doi.org/10.3161/15081109ACC2018.20.1.016

Srilopan S, Mata VA, Bumrungsri S (2024) DNA metabarcoding reveals insights into diet partitioning and pest suppression by open space bats in agricultural landscapes. Acta Chiropterol 26:171–187. https://doi.org/10.3161/15081109ACC2024.26.2.003

Srilopan S, Lewanzik D, Bumrungsri S, Voigt CC (2025) Large and high-altitude foraging ranges suggests importance of Wrinkle-lipped free-tailed bats (*Mops plicatus*) for consuming dispersing pest insects. Oecologia 207:1–11. https://doi.org/10.1007/s00442-025-05671-x

Sukonthaphirom Na Phatthaung S, Punwatho P, Phonphunsak S, Srijantra S (2021) Guidelines for safe pest and animal insect management from the 2021 research work. Plant pest management division/entomology group, office of crop research and development, department of agriculture. [In Thai]

Suksai P, Bumrungsri S (2019) Water bodies are a critical foraging habitat for insectivorous bats in tropical agricultural landscapes of central Thailand. Songklanakarin J Sci Technol 42:3

Surlykke A, Miller LA, Møhl B, Andersen BB, Christensen-Dalsgaard J, Buhl Jørgensen M (1993) Echolocation in two very small bats from Thailand: *Craseonycteris thonglongyai* and *Myotis siligorensis*. Behav Ecol Sociobiol 33:1–12. https://doi.org/10.1007/BF00164345

Thaxter CB, Buchanan GM, Carr J, Butchart SH, Newbold T, Green RE, Pearce-Higgins JW (2017) Bird and bat species' global vulnerability to collision mortality at wind farms revealed through a trait-based assessment. Proc R Soc B 284:20170829. https://doi.org/10.1098/rspb.2017.0829

The Wind Power (2025) Wind turbine specifications. https://www.thewindpower.net/. Accessed 13 Feb 2025

Thongjued K (2019) Diet analysis of wrinkle-lipped free-tailed bat (*Chaerephon plicatus* Buchannan, 1800) using direct-PCR DGGE technique. MSc Thesis, Prince of Songkla University, Songkhla, Thailand, 99 pp

Tolvanen A, Routavaara H, Jokikokko M, Rana P (2023) How far are birds, bats, and terrestrial mammals displaced from onshore wind power development? – A systematic review. Biol Conserv 288:110382. https://doi.org/10.1016/j.biocon.2023.110382

Triplehorn CA, Johnson NF (2005) Borror and DeLong's introduction to the study of insects, 6th edn. Thomson Brooks/Cole, Belmont, CA, p 800

Utthammachai K, Bumrungsri S, Chimchome V, Russ J, Mackie I (2008) The habitat use and feeding activity of *Tadarida plicata* in Thailand. Thai J For 27:21–27

Valdez EW, Cryan PM (2013) Insect prey eaten by hoary bats (*Lasiurus cinereus*) prior to fatal collisions with wind turbines. West N Am Nat 73:516–524. https://doi.org/10.3398/064.073.0404

Voigt CC (2021) Insect fatalities at wind turbines as biodiversity sinks. Conserv Sci Pract 3:e366. https://doi.org/10.1111/csp2.366

Voigt CC, Lehnert LS, Petersons G, Adorf F, Bach L (2015) Wildlife and renewable energy: German politics cross migratory bats. Eur J Wildl Res 61:213–219. https://doi.org/10.1007/s10344-015-0903-y

Voigt CC, Bumrungsri S, Roeleke M (2019a) Rapid descent flight by a molossid bat (*Chaerephon plicatus*) returning to its cave. Mamm Biol 95:15–17. https://doi.org/10.1016/j.mambio.2019.01.001

Voigt CC, Kravchenko K, Liechti F, Bumrungsri S (2019b) Skyrocketing flights as a previously unrecognized behaviour of open-space foraging bats. Acta Chiropterol 21:331–339. https://doi.org/10.3161/15081109ACC2019.21.2.008

Voigt CC, Russo D, Runkel V, Goerlitz HR (2021) Limitations of acoustic monitoring at wind turbines to evaluate fatality risk of bats. Mamm Rev 51:559–570. https://doi.org/10.1111/mam.12247

Voigt CC, Bernard E, Huang JCC, Frick WF, Kerbiriou C, MacEwan K, Mathews F, Rodríguez-Durán A, Scholz C, Webala PW, Welbergen J, Whitby M (2024) Toward solving the global green–green dilemma between wind energy production and bat conservation. Bioscience 74:240–252. https://doi.org/10.1093/biosci/biae023

Wordley CFR, Fouli EK, Mudappa D, Sankaran M, Altringham JD (2014) Acoustic identification of bats in the southern Western Ghats, India. Acta Chiropterol 16:213–222. https://doi.org/10.3161/150811014X683408

Authors and Affiliations

Supawan Srilopan[1] · Jennifer J. Krauel[4] · Kamonporn Srilopan[5,6] · Christian C. Voigt[2,3] · Sara Bumrungsri[1]

✉ Sara Bumrungsri
sara.b@psu.ac.th

[1] Division of Biological Science, Prince of Songkla University, Hat Yai, Songkhla, Thailand

[2] Leibniz Institute for Zoo and Wildlife Research, Alfred-Kowalke-Str. 17, Berlin, Germany

[3] Universität Potsdam, Am Mühlenberg 3, Potsdam, Germany

[4] Department of Biology and Microbiology, South Dakota State University, Brookings, South Dakota, USA

[5] Division of Physics, Rajamangala University of Technology Thanyaburi, Pathum Thani, Thailand

[6] Smart Materials Research Unit, Rajamangala University of Technology Thanyaburi, Pathum Thani, Thailand