

SHORT COMMUNICATION

Bats probe the aerosphere during landscape-guided altitudinal flights

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ABSTRACT

As the only mammals capable of powered flight, bats make efficient use of the aerosphere. Yet, our understanding of how bats use the three-dimensional air column is sketchy. By attaching miniaturised Global Positioning System tags to cave bats near a mountain ridge in Thailand, we show that these bats perform undulating ascending and descending flights in quick succession. Bats repeatedly used mountain slopes to ascend to altitudes of more than 550 m above the ground. We infer that mountain ridges are key habitat features for some open-space foraging bats, facilitating altitudinal movements which may aid effective foraging and navigation. Therefore, the development of wind farms along mountain ridges might lead to conflicts with the conservation of some open-space foraging bats.

INTRODUCTION

Aerial movements are an essential part of bat biology, yet our understanding of the movement ecology of bats is usually limited to the two-dimensional scale (reviewed by Frick et al. 2013). Recently, attempts have been made to explore the third dimension of flights using aircraft-assisted very high frequency (VHF) tracking (Dechmann et al. 2014, McCracken et al. 2016) or radar (Chilson et al. 2012). In addition, miniaturised Global Positioning System (GPS) tags have largely improved the accessibility of altitudinal information in small to medium-sized bats. For example, GPS-tracking studies have revealed that flying foxes may fly at altitudes of between 100 and 300 m when commuting (Tsoar et al. 2011) and medium-sized insectivorous bats may fly at altitudes of up to 800 m above the ground (Cvikel et al. 2015). However, we have no information about whether and how bats use the topography of the landscape for altitudinal flights, since most previous studies of GPS-tagged insectivorous bats have been conducted in flat terrain (Cvikel et al. 2015, Roeleke

et al. 2016). Egyptian fruit bats *Rousettus aegyptiacus* have been observed to use visual landmarks when released in unknown terrain (Tsoar et al. 2011), yet it has not been studied quantitatively whether or not they actively follow landscape topography. Here, we hypothesise that open-space foraging Theobald's tomb bats *Taphozous theobaldi* respond to the landscape's topography when performing nightly foraging trips. We studied altitudinal flights of *Taphozous theobaldi* by equipping individuals with GPS tags in central Thailand. On the basis of GPS tracks, we followed how bats adjust their flight altitude to the topography of the local limestone ridge at our study site.

METHODS

The study was conducted in early December 2016 in the Lopburi Province, Thailand. The local landscape is dominated by a north-to-south oriented mountain ridge of about 35 km long and 9 km wide, reaching elevations of more than 600 m above sea level (asl). We caught four individuals of *Taphozous theobaldi* (one male, three females)

in a mist net when they emerged from a cave shortly after sunset. We glued a GPS logger (Robin GPS Loggers, CellGuide Ltd., Israel) and a VHF radiotransmitter (Telemetrie-Service Dessau, Dessau-Roßlau, Germany) on to the back of each bat using non-toxic glue (Sauer Hautkleber, Manfred Sauer, Germany). We used the VHF transmitters to locate GPS units that fell off bats in the cave after 2–4 days. We released all bats individually within about 300 m from the cave entrance. GPS loggers recorded three-dimensional locations once every 30 seconds for whole nights. From data derived from the four retrieved GPS loggers, we reconstructed four full flight paths for the first night; in two cases, we reconstructed partial paths for the second night. We discarded data from the first 5 min after the release of bats, to avoid potential bias due to our handling of the bats. This resulted in a total of about 1400 GPS locations, ranging from 58 to 337 GPS locations per flight path.

With a combined mass of 4.9 g, the loggers and transmitters exceeded the commonly recommended maximum (5% of body mass). However, we expected the loggers to have only minor effects on the flight behaviour and performance of *Taphozous theobaldi*, since we regularly use the same loggers on slightly lighter *Nyctalus noctula* without an observable effect on their behaviour or body condition (Roeleke et al. 2016). If the loggers did influence the behaviour of *Taphozous theobaldi*, we would expect them to show reduced altitudinal movements.

To evaluate how much time bats spent in consistent ascending or descending flight, we classified each location into movement categories, using the R package *moveHMM* (Michelot et al. 2016). This package builds on two-dimensional tracking data between successive points. We thus tilted the height profiles of flight paths into a two-dimensional plain to concur with the assumptions of the package. Subsequently, the flight altitude (m asl) was displayed on the *x*-axis, and the regularly spaced timestamps (displayed in 0.1 m spacing for minimum influence on the model outcome) were displayed on the *y*-axis. We allowed the model to classify two states (ascending or descending vs. quasi-horizontal movement). The model fits two-dimensional distributions (step-length and turning angle between three consecutive points) for a defined number of movement states, and calculates the probability of each observed pair of values belonging to these. We assigned each observed location to a movement state when this probability was at least 75%, which was true for the majority of points (97%). Whenever classification of consecutive GPS locations was consistent over a time period of at least 2 min, we categorised the sequence as ascending or descending; all other points were classified as quasi-horizontal.

To test whether or not bats adjust their flight in response to the topography, we compared the topography

they used with the available topography. We calculated the area of the 95% utilisation distribution kernel for each bat trip (R package *adehabitatHR*; Calenge 2006) and randomly sampled five times as many surface elevation levels as there were GPS locations from within the respective areas to reflect the available habitat. Eventually, we used a generalised mixed model, with bat trip as a random factor, to predict the presence of bats based on the underlying landscape elevation. We used a similar model to test whether the different movement behaviours introduced before would allow us to predict the underlying landscape elevation. Asking whether altitude gain relative to ground level could be explained by topography, we deployed a third generalised mixed model applying a gamma-distribution and a log link. For the fixed effect, we used the altitude gain of bats relative to the ground between the start and endpoints of the defined movement categories (ascent, descent, quasi-horizontal).

We used the software R (version 3.3.2, R Foundation for Statistical Computing, Austria) for all statistical analysis, and QGIS 2.18 (version 2.18.2, Free Software Foundation, Inc., USA) for map creation; we assumed significant differences when 95% confidence intervals in effect plots of model estimates did not overlap.

RESULTS

After emerging from the cave, the four *Taphozous theobaldi* foraged in the vicinity of the mountain ridge where the cave was located (Fig. 1; Appendix S1). They spent about 135 min (median) in flight and covered a median distance of 45.5 km per night (Table 1). Bats engaged in quasi-horizontal movements during 54% of time (range: 28–62%). The other half of the time was equally divided between ascending flight (median 23%, range: 21–38%) and descending flight (median 23%, range: 17–34%). The median ascent rate equalled 0.44 m s⁻¹ (range: 0.37–0.55) and the median descent rate -0.46 m s⁻¹ (range: -0.33 to -0.69). Individual bats reached peak altitudes of about 550 m above ground (median = 552 m; range: 516–814 m; Fig. 2). Individuals of *Taphozous theobaldi* were more likely to fly above exposed landscape structures (ridges and hilltops) than expected by chance (Fig. 3a). The higher the elevation of the underlying landscape, the more likely we were to observe consistently ascending flights (Fig. 3b). Descending flights were more likely to take place over low elevations (Fig. 3b). The tagged bats not only preferred to ascend where slopes and ridges were present, they also repeatedly used local ridges and hilltops to gain even further altitude relative to the surface elevation (Fig. 3c, see also the peaks of bat01, bat08 and to some extent bat02 in Fig. 2).

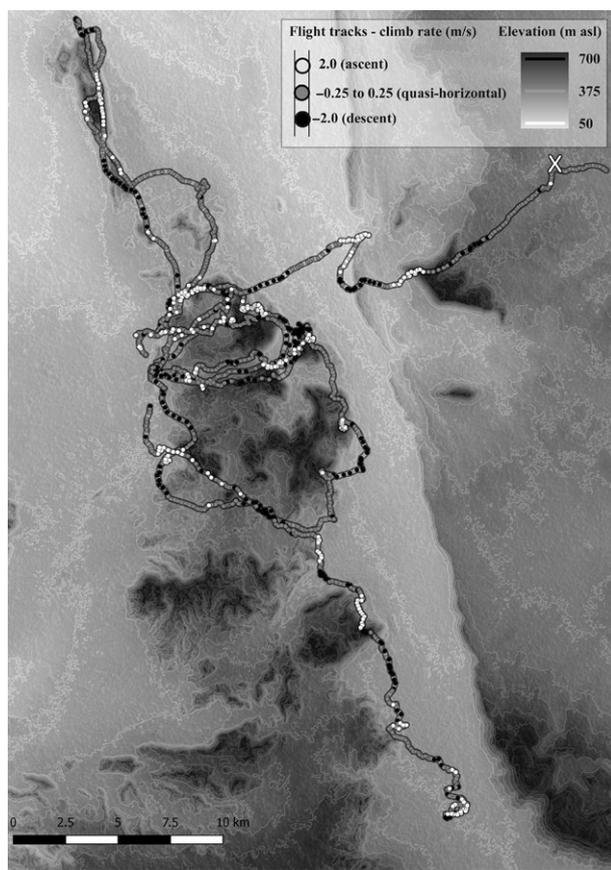


Fig. 1. Map of the study area in central Thailand. Contour lines and shading depict the landscape elevation. Flight tracks of bats are indicated by dots, varying in colour according to ascending (white), quasi-horizontal (grey) or descending flights (black). The white X in the north-east marks a wind farm.

DISCUSSION

This is the first study to show that open-space foraging bats, such as *Taphozous theobaldi*, actively interact with the topography of the landscape using slopes and mountain ridges during foraging flights, particularly for performing ascending flights towards high altitudes. Altitudinal flights of *Taphozous theobaldi* frequently exceeded the elevation of mountain ridges and hilltops, reaching top altitudes of 552 m (median; maximum = 814 m above ground).

Ascending flights may be easier to perform when flying close to a slope. For example, bats may benefit from upward winds that carry them to higher altitude without much effort. Straw-coloured fruit bats *Eidolon helvum* adjust their flight paths in response to wind drift (Sapir et al. 2014). The overall wind speed in the wider area around the mountain ridge was rather low during the study period (about 3 m s^{-1} from SSW direction at surface level, <https://earth.nullschool.net>), and relating our observations to wind is difficult since conditions may have been different on the local scale of the heterogeneous terrain and at different altitudes.

We speculate that *Taphozous theobaldi* may use high-altitude flight for navigation, as has been suggested for common swifts *Apus apus* (Dokter et al. 2013). Since the sky was clear and the moon provided some light during the study period (33% of the moon was visible), *Taphozous theobaldi* might have used visual orientation to overlook the mountain ridge. A second explanation might be that *Taphozous theobaldi* foraged on insects that were driven into high strata by upward winds or that aggregated above the peaks for mating (Alcock 1986). However, the fact that bats normally did not stay long at high altitudes seems to contradict extensive foraging at peak altitudes.

The two possible reasons for high altitude flights in *Taphozous theobaldi* are not mutually exclusive, and we cannot distinguish between them given the limited sample size of this study and the lack of fine-scale background information, such as data on insect availability or meteorological data.

Overall, bats spent about half of their foraging time in sequences of undulating ascending and descending flights, similar to some GPS-tagged individuals of *Rhinophylla microphyllum* (Cvikel et al. 2015). In *Taphozous theobaldi*, ascent and descent rates were not markedly different from each other, and they did not deviate largely from those observed in similar-sized birds (Bowlin et al. 2015). The similarity of ascent and descent rates in *Taphozous theobaldi* might indicate that, during descent, bats engaged in powered flight and not gliding, since a descending glide might result in higher descent rates. Nightly flight durations were similar to those observed for 30 g insectivorous bats of the temperate zone, *Nyctalus noctula*, yet the distances

Table 1. Metadata and flight metrics for the four *Taphozous theobaldi*

Bat ID #night	Bat mass	Sex	Distance travelled (km)	Flight time (min)	Logger mass (% of bat mass)
bat01 #1	37.0	Male	48.8	169	13
bat02 #1	38.0	Female	10.3	29	13
bat02 #2	—	—	30.8	86	—
bat04 #1	44.0	Female	45.4	141	11
bat04 #2	—	—	39.6	128	—
bat08 #1	36.0	Female	47.5	159	14

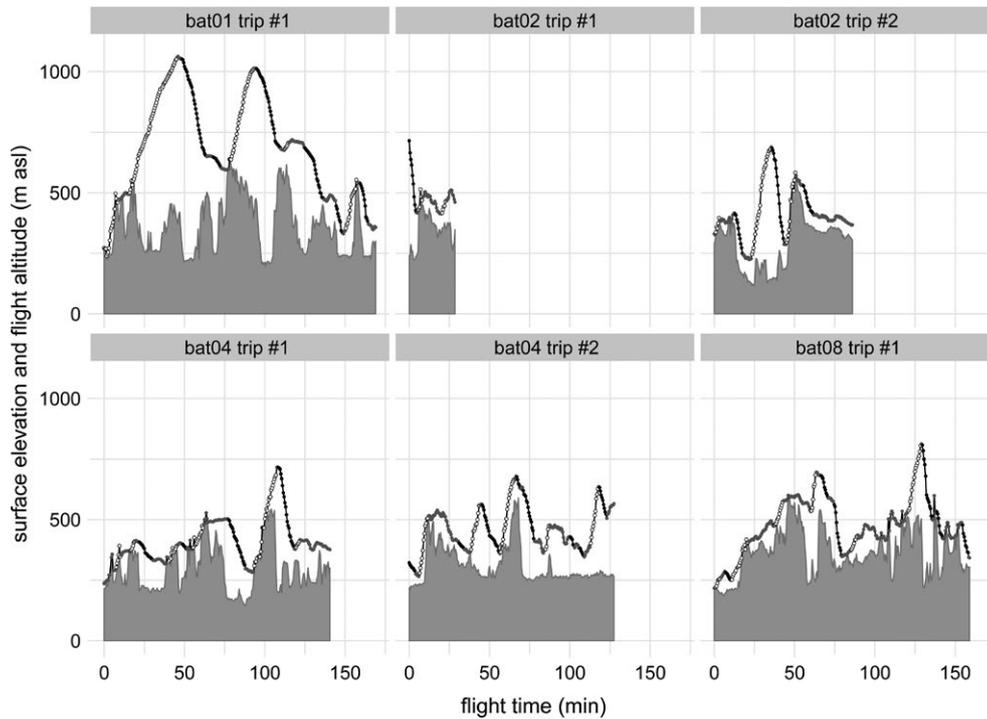


Fig. 2. Altitudinal flights of the four *Taphozous theobaldi*. Each circle indicates a spatial position. Filling indicates altitudinal movement behaviour; white = ascent, black = descent, grey = quasi-horizontal movement.

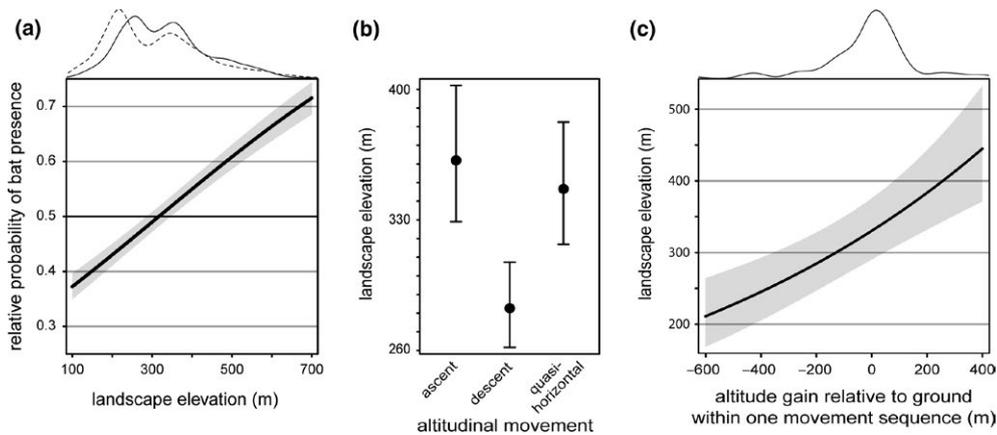


Fig. 3. Effect plots for the three models. (a) Preference of *Taphozous theobaldi* for elevation of underlying landscape, and density plots for the underlying data (solid line = bat, dashed line = pseudo-absence data represented by random points). Values higher 0.5 indicate that it was more likely to find bats at a given elevation level than expected from the null model. (b) Altitudinal movement behaviour as a function of elevation of underlying landscape. (c) Altitude gain relative to surface elevation as a function of elevation of underlying landscape, and density plot for the underlying data. Black lines (a,c) and black dots (b) depict the model estimates, whereas grey bands (a,c) and black bars (b) depict the 95% confidence intervals.

covered by *Taphozous theobaldi* were about twice those recorded for *Nyctalus noctula* (Roeleke et al. 2016), indicating that *Taphozous theobaldi* forages at the landscape scale, rather than in restricted habitat patches.

If mountain ridges and hilltops are preferred areas for open-space foraging bats, this may be in conflict with wind energy developments in which exposed landscape

structures are used for wind turbines. In this context, it was striking to us that the only flight path guiding a bat substantially away from the mountain ridge led to a wind farm on top of the neighbouring mountain ridge (Fig. 1). This observation highlights the fact that the placement of wind turbines on mountain ridges and hilltops may increase the mortality risk for open-space foraging bats.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at the publisher’s web-site.

Appendix S1. Flight tracks of the four *Taphozous theobaldi*. Coloured dots indicate ascending (red) or descending flights (blue) in context to the landscape with contour lines and shading depicting the landscape elevation. White arrows indicate the direction of the flight.