

## RESEARCH ARTICLE

# A whispering bat that screams: bimodal switch of foraging guild from gleaning to aerial hawking in the desert long-eared bat

 Talya D. Hackett<sup>1</sup>, Carmi Korine<sup>2</sup> and Marc W. Holderied<sup>1,\*</sup>
**ABSTRACT**

Echolocating bats have historically been classified as either loud aerial hawkers or whispering gleaners. Some bat species can forage in multiple ways and others have demonstrated limited flexibility in the amplitude of their echolocation calls. The desert long-eared bat, *Otonycteris hemprichii*, has been said to be a passive gleaning whispering bat preying on terrestrial arthropods such as scorpions. Using an acoustic tracking system, we recorded individuals flying at foraging and drinking sites and compared their flight height, flight speed, call duration, pulse interval and source levels with those of gleaning individuals previously recorded using the same setup. We found differences in all variables with the strongest difference in source levels, where bats called at a mean of 119 dB peSPL (compared with 75 dB peSPL when gleaning). Bat faecal analysis indicated that their diet differed from previous studies and that prey species were capable of flight. We conclude that the bats switched from passive gleaning to capturing airborne insects (aerial hawking). Although whispering bats have been known to opportunistically catch insects on the wing, in the present study we show a full bimodal switch between foraging guilds with the respective changes in source level to those typical of a true aerial hawker.

**KEY WORDS:** Acoustic Tracking, Arthropod prey, Echolocation, Foraging guilds, Source level

**INTRODUCTION**

All animals require accurate sensory information in order to interact with their environment, particularly with regard to foraging. Vision is often the dominant sense; however, for animals in poorly lit environments, other senses such as olfaction or hearing become more important. Another solution is biosonar, whereby individuals emit echolocation pulses and gain sensory information from the returning echoes, as used by most members of Chiroptera and some cetaceans (Griffin, 1958; Thomas et al., 2004). Echolocating animals can control the sensory input they receive by manipulating the outgoing signal. All echolocating bats (except *Rousettus*) emit ultrasound calls by pushing air through the larynx and out through either the nose or the mouth (Schnitzler and Kalko, 2001; Jones and Teeling, 2006). This sound is reflected by objects in their environment and returning echoes are detected by the bats' specialised ears (Griffin, 1944).

Recording from bats in the hand, Griffin (Griffin, 1958) classified echolocating bats into two groups: 'loud' aerial insectivores that

catch insects on the wing and 'whispering' bats that are frugivores, nectarivores, carnivores or glean insects off the ground/vegetation. More recently, bats have been classified into broad foraging guilds including aerial hawkers that catch flying insects on the wing, gleaners that take prey off the substrate, which they detect by either listening for prey-generated sounds (passive gleaners) or by echolocation (active gleaners), and trawlers that catch prey from water surfaces (Norberg and Rayner, 1987). The echolocation calls of the bats in each guild conform to similar properties (Fenton, 1990).

However, foraging modes are not always fixed and animals may switch strategies depending on prey availability or environmental conditions. Orca (*Orcinus orca*) will use a variety of hunting strategies including creating waves that knock seals from ice floes (wave washing) and hunting in open water (Pitman and Durban, 2012). Hummingbirds (Trochilidae) and honeyeaters (Meliphagidae) have diets consisting of both nectar and arthropods (Pyke, 1980). This is true also for insectivorous bats, which may choose foraging strategies from multiple guilds (Fenton, 1990). For example, *Myotis evotis* is equally adept at gleaning moths from the substrate and aerial-hawking flying moths, and the duration and frequency of their echolocation calls change depending on the mode of attack (Faure and Barclay, 1994). Two further species of *Myotis*, one traditionally labelled as an aerial hawker (*M. lucifugus*) and the other a gleaner (*M. septentrionalis*), are both capable of catching insects using both tactics (Ratcliffe and Dawson, 2003). This is also true of *M. emarginatus*, which change the temporal structure of their calls (e.g. pulse duration and pulse interval), and *Macrophyllum macrophyllum*, which will use or omit distinct echolocation phases including a terminal buzz, depending on the tactic in use (Krull et al., 1991; Schumm et al., 1991; Weinbeer et al., 2013). Hence, foraging guilds in bats are not mutually exclusive as at least some species are able to use different tactics when necessary.

Modern advances in ultrasound recording technology have allowed for more accurate measurements of source levels, a measure of the sound intensity at 10 cm from the source of a call (i.e. mouth of the bat). Aerial-hawking bats (e.g. *Eptesicus* spp.) emit calls in the range of 103 to 137 dB peak-equivalent sound pressure level (peSPL) (Surlykke et al., 1993; Jensen and Miller, 1999; Boonman and Jones, 2002; Holderied and von Helversen, 2003; Holderied et al., 2005; Surlykke and Kalko, 2008), while quieter passive gleaning bats (e.g. gleaning *Myotis* spp.) only call with a source level of between 77 and 102 dB peSPL (Faure et al., 1990; Faure et al., 1993; Miller and Treat, 1993). There is also greater flexibility in the calls produced by bats than previously understood. *Eptesicus fuscus* decreases call intensity during the landing approach (Koblitz et al., 2010) and the decrease in source levels during the target approach has been well documented (Boonman and Jones, 2002; Holderied et al., 2005; Nørnum et al., 2012). Following the initial discovery that *M. macrophyllum* and *Artibeus jamaicensis*, both said to be whispering bats, emit calls louder than previously thought (Brinkløv

<sup>1</sup>School of Biological Sciences, University of Bristol, Bristol BS8 1UG, UK. <sup>2</sup>Mitrani Department of Desert Ecology, Swiss Institute for Dryland Environmental and Energy Research, Jacob Blaustein Institutes for Desert Research, Ben-Gurion University of the Negev, Sede Boqer Campus 84990, Midreshet Ben-Gurion, Israel.

\*Author for correspondence (Marc.Holderied@bristol.ac.uk)

Received 22 November 2013; Accepted 10 June 2014

et al., 2009), Brinklöv et al. (Brinklöv et al., 2010) found that source levels in *M. macrophyllum* increased from flying in a flight room to semi-cluttered foraging, with the loudest calls being produced during open-space foraging.

*Otonycteris hemprichii* Peters 1859 is a desert passive gleaner that feeds primarily on non-aerial arthropods in dry, sparsely vegetated environments (Arlettaz et al., 1995; Gharaibeh and Qumsiyeh, 1995; Fenton et al., 1999; Korine and Pinshow, 2004; Holderied et al., 2011; Hackett et al., 2013). As with most gleaning species, it has long ears, low wing loading and a low aspect ratio (Gharaibeh and Qumsiyeh, 1995). Gleaning *O. hemprichii* fly close to the ground (40–100 cm) and land for 2–5 s to catch prey, which are then consumed while the bat adopts a slow, gliding and widely circling flight 3–7 m above the ground (Arlettaz et al., 1995; Holderied et al., 2011); thus these bats forage in a background-cluttered environment with echoes coming from a non-uniform ground surface. Holderied et al. (Holderied et al., 2011) recorded *O. hemprichii* gleaning tethered scorpions from the ground using a microphone array and recorded frequency modulated (FM) multi-harmonic echolocation calls typical of a whispering gleaner bat at  $75.25 \pm 6.9$  dB peSPL. However, anecdotal evidence suggests that, on occasion, *O. hemprichii* calls louder and adopts a different flight pattern than is typically reported (T.D.H. and C.K., personal observations).

Here we test the hypothesis that *O. hemprichii* can switch between foraging modes, namely passive gleaning and aerial hawking. We therefore predict that aerial-hawking individuals will change their flight behaviour with regard to flight height and flight speed. We also expect that aerial-hawking individuals will alter their call behaviour, namely call duration, pulse interval and, in particular, source level, which we expect to be significantly higher than during gleaning attacks and in the range of typical aerial hawkers.

## RESULTS

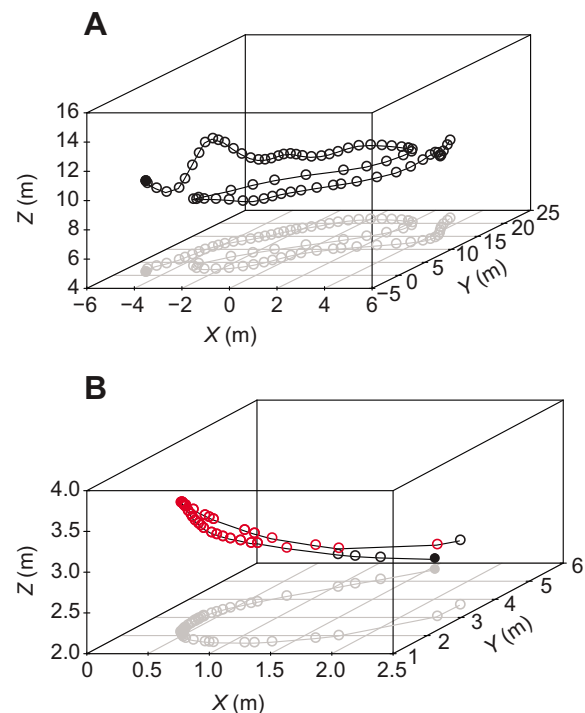
### Flight behaviour

In total, we recorded 849 individual echolocation calls in 60 flight paths from four different sites (mean:  $15.38 \pm 11.25$  calls per flight path; range: 4–76): 20 paths from Zefira (natural pool) and 40 paths from foraging sites (one from Nahal Bitaron, seven from the Moshav Hatzeva pool area and 32 from the Moshav Hatzeva date palm garden). We did not record or observe any drinking attempts by *O. hemprichii* at Zefira, but cannot fully exclude this as the behavioural context, so we did not pool Zefira with the other sites and will refer to it as the drinking site.

Two typical flight paths from foraging sites in Moshav Hatzeva are presented in Fig. 1. The bats recorded here did not fly in the typical search pattern as described in Holderied et al. (Holderied et al., 2011), having a different flight height ( $F_{2,120}=17.577$ ,  $P<0.001$ ; Table 1) and flight speed ( $F_{2,120}=13.893$ ,  $P<0.001$ ; Table 1). Bats at both the drinking site and the foraging sites flew higher (Tukey's HSD; drinking–gleaning:  $P<0.001$ , foraging–gleaning:  $P=0.01$ , drinking–foraging:  $P=0.001$ ; Table 1) and slower (Tukey's HSD; drinking–gleaning:  $P=0.004$ , foraging–gleaning:  $P<0.001$ , drinking–foraging:  $P=0.34$ ; Table 1) than during gleaning at Park Sapir (Holderied et al., 2011).

### Echolocation behaviour

All recorded calls were of a higher source level than expected for a bat typically considered to be whispering with an overall mean of  $118.8 \pm 7.7$  dB peSPL (range: 93.5–140.5 dB peSPL). The mean frontal on-axis calls were  $124.2 \pm 9.0$  dB peSPL (range: 106.6–142.9 dB peSPL; 86 calls from 32 individuals) and the mean



**Fig. 1.** Two three-dimensional flight paths of *Otonycteris hemprichii* at the Moshav Hatzeva date garden. Points are each a recorded echolocation call. The grey paths are the 2D projections of the original 3D paths. The solid circles are the first call in the flight path. (A) Search flight. (B) Aerial attack. In B the red calls are the calls in the spectrogram in Fig. 2 representing a late approach or abandoned buzz. Sixteen calls that could not be localised were interpolated in B.

lateral (perpendicular to on-axis) calls were  $119.8 \pm 6.4$  dB peSPL (range: 109.7–132.3 dB peSPL; 68 calls from 24 individuals). The overall echolocation calls differed between the drinking site, foraging sites and while gleaning in pulse duration ( $F_{2,130}=33.064$ ,  $P<0.001$ ; Table 1), pulse interval ( $F_{2,120}=10.37$ ,  $P<0.001$ ; Table 1) and source levels ( $F_{2,120}=635.39$ ,  $P<0.001$ ; Table 1). There was no difference in pulse duration (Tukey's HSD;  $P=0.29$ ; Table 1) or source levels (Tukey's HSD;  $P=0.29$ ; Table 1) between the drinking and foraging sites, but calls were longer (Tukey's HSD; drinking–gleaning:  $P<0.001$ , foraging–gleaning:  $P<0.001$ ; Table 1) and louder (Tukey's HSD; drinking–gleaning:  $P<0.001$ , foraging–gleaning:  $P<0.001$ ; Table 1) than calls recorded while gleaning. Individuals showed no difference in the pulse interval between gleaning and at the foraging site (Tukey's HSD;  $P=0.96$ ; Table 1), but at the drinking site the pulse interval was greater (Tukey's HSD; drinking–gleaning:  $P<0.001$ , drinking–foraging:  $P<0.001$ ; Table 1). One of the flight trajectories contained an apparent abandoned aerial attack on an insect at a height 3.5 m from the ground (Fig. 1B). The corresponding echolocation behaviour, consisting of short-duration FM sweeps, resembled that of the approach phase of an aerial attack, with the pulse interval in this sequence decreasing to 18 ms (Fig. 2).

### Diet analysis

We collected five faecal pellets from five individual females, caught on three nights at the Moshav Hatzeva sites. Four of the pellets consisted of only one prey type – 100% by volume Diptera, Lepidoptera, Isopoda and Coleoptera each – and one pellet contained 75% Hymenoptera and 25% Lepidoptera.

**Table 1. Mean  $\pm$  s.d. flight and echolocation parameters for *Otonycteris hemprichii* while gleaning, at the drinking site and at the foraging sites in desert areas of Israel**

Behavioural context	N	Flight height (m)	Flight speed (m s <sup>-1</sup> )	Pulse duration (ms)	Pulse interval (ms)	Source level (dB peSPL)
Gleaning	23	2.19 $\pm$ 1.0 <sup>a</sup>	3.52 $\pm$ 1.3 <sup>a</sup>	2.46 $\pm$ 1.1 <sup>a</sup>	131.6 $\pm$ 82.0 <sup>a</sup>	75.3 $\pm$ 6.9 <sup>a</sup>
Drinking site	20	5.35 $\pm$ 4.2 <sup>b</sup>	2.68 $\pm$ 0.9 <sup>b</sup>	4.13 $\pm$ 0.8 <sup>b</sup>	216.25 $\pm$ 93.0 <sup>b</sup>	119.0 $\pm$ 7.7 <sup>b</sup>
Foraging sites	40	3.61 $\pm$ 2.1 <sup>c</sup>	2.32 $\pm$ 1.0 <sup>b</sup>	3.80 $\pm$ 1.0 <sup>b</sup>	136.16 $\pm$ 45.1 <sup>a</sup>	116.8 $\pm$ 5.3 <sup>b</sup>

Different superscripts in each column indicate significant differences (in all cases  $P < 0.01$ ). Gleaning data are from Holderied et al. (Holderied et al., 2011).

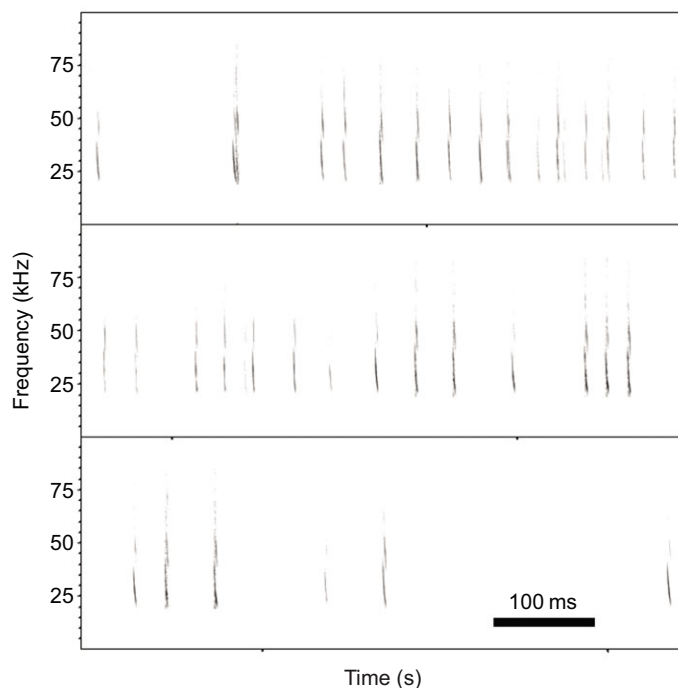
## DISCUSSION

Our results indicate that *O. hemprichii* can operate as an aerial hawk, as supported by a late approach or potential abandoned feeding buzz at a height 3.5 m from the ground, consistent differences in flight (speed and height) and echolocation (duration and source levels) behaviour between bats recorded here and those recorded while gleaning, and dietary differences from previous studies (Arlettaz et al., 1995; Fenton et al., 1999; Daniel, 2005). A decrease in call interval to 18 ms is slightly longer than typical pulse intervals during a terminal buzz of an aerial-hawking bat, but similar to late-approach and pre-buzz call intervals (Britton and Jones, 1999). Other bats have been shown to use multiple foraging tactics (Faure and Barclay, 1994; Ratcliffe and Dawson, 2003; Levin et al., 2009), and it is likely that most bats will catch insects on the wing when possible (Fenton, 1990). In fact, even primarily frugivorous and nectarivorous bats have been shown to catch insects on the wing opportunistically (Howell, 1974). Thus it is in line with previous research on bats' foraging adaptability that *O. hemprichii* is able to aerial hawk. The presence of insect wings in the majority of the faecal pellets indicates that *O. hemprichii* are feeding at least partly on winged insects, although this does not rule out the possibility that these were gleaned from substrates rather than

taken in flight. Previous studies on this species' diet have found a higher prevalence of non-flying arthropods (e.g. Coleoptera, Solifugidae, Scorpionidae and Araneae), and only occasionally Diptera, Hymenoptera, Lepidoptera and Orthoptera (Arlettaz et al., 1995; Fenton et al., 1999; Daniel, 2005).

The source levels that we report here are considerably louder than those previously reported for *O. hemprichii* during gleaning (Holderied et al., 2011). This species adjusts its source level by more than 43 dB, corresponding to an increase in sound pressure by a factor of 141. We used the same tracking equipment and identical calculation methods as used to determine gleaning *O. hemprichii* source levels (Holderied et al., 2011), so this is not an artefact of experimental differences. This adaptability is considerably greater than the 11 dB reported for *M. macrophyllum* moving from open to cluttered environments (Brinklöv et al., 2010) as well as the 30 dB difference recorded during target approach in *Myotis daubentonii* (Nørum et al., 2012). The typical on-axis source levels of aerial-hawking bats are between 120 and 130 dB (Holderied and von Helversen, 2003); *O. hemprichii* in the recordings presented here are calling at almost the same level. Interestingly, there is no apparent change in call design that might serve to increase detection range even further, i.e. away from this species' typical short-duration, broadband, FM sweep towards a more narrowband, lower-frequency call (Jones and Holderied, 2007). Using the same selection criterion as Holderied et al. (Holderied et al., 2011), we included all calls, and not just on-axis calls. On-axis recordings were 5 dB louder, so rejecting off-axis calls would have artificially inflated the source level difference between our measurements and those from gleaning individuals in Holderied et al. (Holderied et al., 2011). Actually, as *O. hemprichii* looks down with ears pointing forward while searching for terrestrial prey (M.H., personal observation), lateral rather than on-axis calls may provide a better comparison, and even the lateral calls were only 1 dB different from the mean of all calls as used here. In conjunction with concurrent changes in flight and echolocation behaviour, we conclude that *O. hemprichii* is indeed able to switch between the two foraging modes of passive gleaning and aerial hawking. This is the first study to our knowledge showing a link between source level and foraging mode in the same species without a concurrent change in habitat clutter, and *O. hemprichii* shows the largest known adaptability in the sound pressure level of its call.

There are trade-offs in morphology when specialising in one foraging mode. Gleaning bats usually have long ears for the detection of faint sound cues and low wing loading to allow them to carry heavy loads. But these features increase drag and are linked to slower flight (Norberg and Rayner, 1987). Hence a long-eared bat such as *O. hemprichii* that specialises in gleaning is less adapted to aerial hawking, which is associated with higher flight speeds and agility (Gardiner et al., 2008; Gardiner et al., 2011). Interestingly, *O. hemprichii* recorded here during aerial hawking adopted a slower flight speed than during gleaning. Aerial-hawking bats of the genus *Molossus* have greater metabolic costs associated with more manoeuvrable flight in confined spaces, presumably because they are flying slower than the optimal speed predicted by their



**Fig. 2. Spectrogram (fast Fourier transform window size=1024, frame 100%, overlap 98.43%, window flat top) of a late approach or abandoned buzz echolocation call sequence of *Otonycteris hemprichii* in the Moshav Hatzeva date garden.** To reduce background noise, we applied a finite impulse response filter with the inverse noise spectrum. The short-duration frequency modulated sweep is consistent with previous recordings of gleaning individuals (Holderied et al., 2011). In the top row, faint calls of a second individual are visible.

physiology and increased centripetal acceleration in curves (Voigt and Holderied, 2012). The slower aerial-hawking flight of *O. hemprichii* might thus allow for abrupt initiation of tight turns to chase more manoeuvrable flying prey.

It is thought that most bats will opportunistically switch to aerial hawking from their normal foraging mode if they detect flying prey; for instance, *Myotis daubentonii* switches between trawling and aerial hawking depending on prey availability (Todd and Waters, 2007). However, it does not appear that this is what we recorded; all flight paths consisted of loud calls that are atypical of usual gleaning behaviour and we did not observe any classic *O. hemprichii* low-flying search tactics (Holderied et al., 2011). Thus, the individuals in our study were most likely exclusively aerial hawking.

One possible reason for a bat adapted to one foraging mode adopting another is changes in environmental conditions or prey availability. The time of recording was toward the end of an exceptionally hot and dry summer with multiple record-breaking days, so it is likely that usual prey items were scarcer. Desert scorpions (e.g. *Scorpio maurus palmatus*), for instance, become more inactive during dry conditions (Shachak and Brand, 1983). It is therefore possible that *O. hemprichii* enters different habitats with artificial irrigation or attacks different prey and then adopts a different foraging mode in times of scarcity of its typical prey. Indeed, *O. hemprichii* in the region are typically found in natural habitats and rarely in artificial habitats such as the date palms and village gardens where we recorded (Hackett et al., 2013). Additionally, on moonlit nights, adult common yellow scorpions (*Buthus occitanus israelis*) are less active, and those that are active tend to ambush from under vegetation (Skutelsky, 1996). The moon was in its first quarter and setting between 22:00 and 00:15 h during this study, so it is unlikely that this was affecting the scorpions' behaviour. However, it is possible that *O. hemprichii* also switches to alternative prey and thus a different foraging mode on moonlit nights, when ambush predators such as desert scorpions are less active. Both *S. maurus palmatus* and *B. occitanus israelis* are common in the study area and, when presented, are readily taken as prey by *O. hemprichii* (Holderied et al., 2011).

The evidence that we present here indicates that not only does *O. hemprichii* switch foraging modes to aerial hawking, but when doing so they drastically alter both their call and flight behaviour. The malleability in source levels is the most extensive change seen in any bat species, indicating that perhaps bats are more flexible in their echolocation behaviour than previously understood.

## MATERIALS AND METHODS

### Study site

We collected data in August 2010 at four sites in the Arava and Judean Deserts, Israel: one natural desert area with no water (Nahal Bitaron, 30°49'4N, 35°16'58E); two village gardens in Moshav Hatzeva, one of which was located next to a swimming pool (30°46'08N, 35°16'44E) and the other in an orchard of date palms (30°46'11N, 35°16'39E); and one natural pool where we observed other species of bats drinking (Zefira, 30°20'00N, 35°17'00E). All sites contained background clutter with bats flying less than 5 m from vertical structures, but sites ranged in openness from Nahal Bitaron, a relatively open site in a 200 m wide wadi (dry river bed) with 10 m between the tree and the cliff edge, to the date palm orchard in Moshav Hatzeva with 8 m between trees. Nahal Bitaron and Moshav Hatzeva are located ~20 km from Park Sapir, where Holderied et al. (Holderied et al., 2011) recorded source levels of gleaning *O. hemprichii*.

### Flight and echolocation behaviour

We used an array of 2×4 microphones (Knowles, BT1759) to track flight movements of *O. hemprichii* as described in Holderied and von Helversen

(Holderied and von Helversen, 2003). We constructed flight paths based on the time of arrival differences of echolocation calls between these microphones using the custom-written software BatSonar (University of Erlangen). From these flight paths, we determined flight height and flight speed. To measure source levels, call duration and pulse interval (from start to start of two consecutive calls), we additionally recorded echolocation calls with a calibrated microphone (CO-100K, Sanken Microphone Co. Ltd, Tokyo, Japan, with Quadmic amplifier, RME, Audio AG, Haimhausen, Germany). Holderied et al. (Holderied et al., 2011) measured flight and echolocation behaviour of *O. hemprichii* gleaning tethered scorpions using the same tracking apparatus; see their paper for further details.

### Calculation of source levels

We calculated source levels from the fundamental frequency in dB peSPL using the sonar equation (Möhl, 1988). We determined the bats' distance to the calibrated microphone from the flight paths and, using measured temperature and humidity (Skywatch GEOS No.11, JDC Electronic SA, Yverdon-les-Bains, Switzerland), we compensated for spreading loss following Bazley (Bazley, 1976). We analysed all flight paths with more than four calls and employed three different selection criteria: (1) all calls including those that were not on-axis (these were used for the statistical comparisons); (2) only those calls on-axis, i.e. where the microphone was ±20 deg in azimuth and elevation relative to flight direction vector; and (3) only calls in a ±20 deg range of lateral directions, i.e. where the microphone was ±20 deg in elevation and between 70 and 110 deg or between -70 and -110 deg in azimuth relative to the flight direction vector.

### Diet analysis

On nights when we were not recording flight paths, we collected faecal droppings from five bats caught in mist nets at sites within Moshav Hatzeva. We inspected all pellets visually (Leica EZ5 OEM microscope, Leica Microsystems, Wetzlar, Germany), recorded any identifiable insect remains and report contents as percentage of arthropod type (often order) by volume.

Bat captures were conducted under license no. 34615 given to C.K. by the Israel Nature and Park Authority.

### Statistical analysis

To remove pseudoreplication caused by different numbers of calls in individual flight paths, we calculated a mean value for each flight path for all parameters. All data were normally distributed and homoscedastic, allowing the use of parametric statistics. We used an ANOVA with Tukey *post hoc* tests to determine differences in flight height, flight speed, call duration, pulse interval and source levels between the drinking and foraging sites compared with gleaning data published in Holderied et al. (Holderied et al., 2011). All statistical tests were computed and graphs were created using R2.7.1 (R Foundation for Statistical Computing).

### Acknowledgements

Lauren Holt assisted with data collection. This is publication no. 842 of the Mitrani Department of Desert Ecology.

### Competing interests

The authors declare no competing financial interests.

### Author contributions

T.D.H., C.K. and M.W.H. conceived the research idea and conducted the field work and analysed the data. M.W.H. provided equipment and C.K. access to field sites and capture licenses. T.D.H. wrote the paper with assistance from C.K. and M.W.H.

### Funding

This study was supported by the Israeli Ministry of Science and Technology (to C.K.), The Explorers Club Exploration Fund (to T.D.H.) and European Commission Dryland Research Specific Support Action Plan (to T.D.H.).

### References

Arlettaz, R., Dandliker, G., Kasybekov, E., Pillet, J. M., Rybin, S. and Zima, J. (1995). Feeding habits of the long-eared desert bat, *Otonycteris hemprichii* (Chiroptera, Vespertilionidae). *J. Mammal.* **76**, 873-876.

- Bazley, E. N. (1976). Sound absorption in air at frequency up to 100 kHz. In *National Physics Laboratory Acoustics Report No Ac 74*. Teddington, UK: National Physics Laboratory.
- Boonman, A. and Jones, G. (2002). Intensity control during target approach in echolocating bats; stereotypical sensori-motor behaviour in Daubenton's bats, *Myotis daubentonii*. *J. Exp. Biol.* **205**, 2865-2874.
- Brinklöv, S., Kalko, E. K. V. and Surlykke, A. (2009). Intense echolocation calls from two 'whispering' bats, *Artibeus jamaicensis* and *Macrophyllum macrophyllum* (Phyllostomidae). *J. Exp. Biol.* **212**, 11-20.
- Brinklöv, S., Kalko, E. K. V. and Surlykke, A. (2010). Dynamic adjustment of biosonar intensity to habitat clutter in the bat *Macrophyllum macrophyllum* (Phyllostomidae). *Behav. Ecol. Sociobiol.* **64**, 1867-1874.
- Britton, A. R. C. and Jones, G. (1999). Echolocation behaviour and prey-capture success in foraging bats: laboratory and field experiments on *Myotis daubentonii*. *J. Exp. Biol.* **202**, 1793-1801.
- Daniel, S. (2005). *Behavioral Body Temperature Regulation and Foraging Activity in Reproductive Female Hemprich's Long-eared Bats (Otonycteris hemprichii) in the Negev Desert*. PhD dissertation, Ben-Gurion University of the Negev, Israel.
- Faure, P. A. and Barclay, R. M. R. (1994). Substrate-gleaning versus aerial-hawking: plasticity in the foraging and echolocation behaviour of the long-eared bat, *Myotis evotis*. *J. Comp. Physiol. A* **174**, 651-660.
- Faure, P. A., Fullard, J. H. and Barclay, R. M. R. (1990). The response of tympanate moths to the echolocation calls of a substrate gleaning bat, *Myotis evotis*. *J. Comp. Physiol. A* **166**, 843-849.
- Faure, P. A., Fullard, J. H. and Dawson, J. W. (1993). The gleaning attacks of the northern long-eared bat, *Myotis septentrionalis*, are relatively inaudible to moths. *J. Exp. Biol.* **178**, 173-189.
- Fenton, M. B. (1990). The foraging behavior and ecology of animal-eating bats. *Can. J. Zool.* **68**, 411-422.
- Fenton, M. B., Shalmon, B. and Makin, D. (1999). Roost switching, foraging behavior, and diet of the vespertilionid bat, *Otonycteris hemprichii*. *Isr. J. Zool.* **45**, 501-506.
- Gardiner, J. D., Codd, J. R. and Nudds, R. L. (2011). An association between ear and tail morphologies of bats and their foraging style. *Can. J. Zool.* **89**, 90-99.
- Gardiner, J. D., Dimitriadis, G., Sellers, W. I. and Codd, J. R. (2008). The aerodynamics of big ears in the brown long-eared bat *Plecotus auritus*. *Acta Chiropt.* **10**, 313-321.
- Gharaibeh, B. M. and Qumsiyeh, M. B. (1995). *Otonycteris hemprichii*. *Mamm. Species* **514**, 1-4.
- Griffin, D. R. (1944). Echolocation by blind men, bats and radar. *Science* **100**, 589-590.
- Griffin, D. R. (1958). *Listening in the Dark*. New Haven, CT: Yale University Press.
- Hackett, T. D., Korine, C. and Holderied, M. W. (2013). The importance of Acacia trees for insectivorous bats and arthropods in the Arava desert. *PLoS ONE* **8**, e52999.
- Holderied, M., Korine, C. and Moritz, T. (2011). Hemprich's long-eared bat (*Otonycteris hemprichii*) as a predator of scorpions: whispering echolocation, passive gleaning and prey selection. *J. Comp. Physiol. A* **197**, 425-433.
- Holderied, M. W. and von Helversen, O. (2003). Echolocation range and wingbeat period match in aerial-hawking bats. *Proc. R. Soc. B* **270**, 2293-2299.
- Holderied, M. W., Korine, C., Fenton, M. B., Parsons, S., Robson, S. and Jones, G. (2005). Echolocation call intensity in the aerial hawking bat *Eptesicus bottae* (Vespertilionidae) studied using stereo videogrammetry. *J. Exp. Biol.* **208**, 1321-1327.
- Howell, D. J. (1974). Acoustic behavior and feeding in glossophagine bats. *J. Mammal.* **55**, 293-308.
- Jensen, M. E. and Miller, L. A. (1999). Echolocation signals of the bat *Eptesicus serotinus* recorded using a vertical microphone array: effect of flight altitude on searching signals. *Behav. Ecol. Sociobiol.* **47**, 60-69.
- Jones, G. and Teeling, E. C. (2006). The evolution of echolocation in bats. *Trends Ecol. Evol.* **21**, 149-156.
- Jones, G. and Holderied, M. W. (2007). Bat echolocation calls: adaptation and convergent evolution. *Proc. R. Soc. B* **274**, 905-912.
- Koblitz, J. C., Stitz, P. and Schnitzler, H. U. (2010). Source levels of echolocation signals vary in correlation with wingbeat cycle in landing big brown bats (*Eptesicus fuscus*). *J. Exp. Biol.* **213**, 3263-3268.
- Korine, C. and Pinshow, B. (2004). Guild structure, foraging space use, and distribution in a community of insectivorous bats in the Negev Desert. *J. Zool.* **262**, 187-196.
- Krull, D., Schumm, A., Metzner, W. and Neuweiler, G. (1991). Foraging areas and foraging behavior in the notch-eared bat, *Myotis emarginatus* (Vespertilionidae). *Behav. Ecol. Sociobiol.* **28**, 247-253.
- Levin, E., Yom-Tov, Y. and Barnea, A. (2009). Frequent summer nuptial flights of ants provide a primary food source for bats. *Naturwissenschaften* **96**, 477-483.
- Miller, L. A. and Treat, A. E. (1993). Field recordings of echolocation and social signals from the gleaning bat *Myotis septentrionalis*. *Bioacoustics* **5**, 67-87.
- Möhl, B. (1988). Target detection by echolocating bats. In *Animal Sonar: Processes and Performance* (ed. P. E. Nachtigall and P. W. B. Moore). New York, NY: Plenum Press.
- Norberg, U. M. and Rayner, J. M. V. (1987). Ecological morphology and flight in bats (Mammalia; Chiroptera): wing adaptations, flight performance, foraging strategy and echolocation. *Philos. Trans. R. Soc. B* **316**, 335-427.
- Nørum, U., Brinklöv, S. and Surlykke, A. (2012). New model for gain control of signal intensity to object distance in echolocating bats. *J. Exp. Biol.* **215**, 3045-3054.
- Pitman, R. L. and Durban, J. W. (2012). Cooperative hunting behavior, prey selectivity and prey handling by pack ice killer whales (*Orcinus orca*), type B, in Antarctic Peninsula waters. *Mar. Mamm. Sci.* **28**, 16-36.
- Pyke, G. H. (1980). The foraging behavior of Australian honeyeaters – a review and some comparisons with hummingbirds. *Aust. J. Ecol.* **5**, 343-369.
- Ratcliffe, J. M. and Dawson, J. W. (2003). Behavioural flexibility: the little brown bat, *Myotis lucifugus*, and the northern long-eared bat, *M. septentrionalis*, both glean and hawk prey. *Anim. Behav.* **66**, 847-856.
- Schnitzler, H. U. and Kalko, E. K. V. (2001). Echolocation by insect-eating bats. *Bioscience* **51**, 557-569.
- Schumm, A., Krull, D. and Neuweiler, G. (1991). Echolocation in the notch-eared bat, *Myotis emarginatus*. *Behav. Ecol. Sociobiol.* **28**, 255-261.
- Shachak, M. and Brand, S. (1983). The relationship between sit and wait foraging strategy and dispersal in the desert scorpion, *Scorpio maurus palmatus*. *Oecologia* **60**, 371-377.
- Skutelsky, O. (1996). Predation risk and state-dependent foraging in scorpions: effects of moonlight on foraging in the scorpion *Buthus occitanus*. *Anim. Behav.* **52**, 49-57.
- Surlykke, A. and Kalko, E. K. V. (2008). Echolocating bats cry out loud to detect their prey. *PLoS ONE* **3**, e2036.
- Surlykke, A., Miller, L. A., Mohl, B., Andersen, B. B., Christensendalsgaard, J. and Jorgensen, M. B. (1993). Echolocation in two very small bats from Thailand – *Craseonycteris thonglongyai* and *Myotis siligorensis*. *Behav. Ecol. Sociobiol.* **33**, 1-12.
- Thomas, J., Moss, C. and Vater, M. (2004). *Echolocation in Bats and Dolphins*. Chicago, IL: The University of Chicago Press Ltd.
- Todd, V. L. G. and Waters, D. A. (2007). Strategy-switching in the gaffing bat. *J. Zool.* **273**, 106-113.
- Voigt, C. C. and Holderied, M. W. (2012). High manoeuvring costs force narrow-winged molossid bats to forage in open space. *J. Comp. Physiol. B* **182**, 415-424.
- Weinbeer, M., Kalko, E. K. V. and Jung, K. (2013). Behavioral flexibility of the trawling long-footed bat, *Macrophyllum macrophyllum* (Phyllostomidae). *Front. Physiol.* **4**, 342.