

The sensory basis of roost finding in a forest bat, *Nyctalus noctula*

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Summary

Tree cavities are a critical resource for most forest-dwelling bats. Yet, it is not known how bats search for new sites and, in particular, find entrances to cavities. Here, we evaluated the importance of different sensory channels for the detection of tree roosts by the noctule bat *Nyctalus noctula*. Specifically, we tested the role of three non-social cues (echo information, visual information and temperature-related cues) and two social sensory cues (conspecific echolocation calls and the presence of bat olfactory cues). We set up an experiment in a flight room that mimicked natural conditions. In the flight room, we trained wild-caught bats kept in captivity for a short while to find the entrance to an artificial tree cavity. We measured the bats' hole-finding performance based on echolocation cues alone and then presented the bat with one of four additional sensory cues. Our data show that conspecific echolocation calls clearly improved the bats'

performance in finding tree holes, both from flying (long-range detection) and when they were crawling on the trunk (short range detection). The other cues we presented had no, or only weak, effects on performance, implying that detection of new cavities from a distance is difficult for noctules if no additional social cues, in particular calls from conspecifics, are present. We conclude that sensory constraints strongly limit the effectiveness of finding new cavities and may in turn promote sociality and acoustic information transfer among bats. As acoustic cues clearly increased the bats' detection performance, we suggest that eavesdropping is an important mechanism for reducing the costs of finding suitable roosts.

Key words: sensory ecology, roost selection, echolocation, social cues, eavesdropping, information transfer, bat.

Introduction

Suitable roosts are a particularly critical resource for bats (Kunz and Lumsden, 2003). Depending on species, bats use stable roosts such as caves or rather more transient roosts such as tree cavities, unfurled leaves, leaf tents or, as an extreme, live termite nests (Lewis, 1995; Kalko et al., 2006). Many temperate forest-dwelling bats exhibit low roost fidelity and change roosts every 1–3 days, even during the breeding season (e.g. Lewis, 1995; Sedgeley and O'Donnell, 1999a; Siemers et al., 1999; Kerth et al., 2001; Willis and Brigham, 2004). Frequent switching may minimise predation risk and potentially reduce exposure to ectoparasites (Lewis, 1996; Reckardt and Kerth, 2006; Bartonička and Gaisler, 2007). Roost switching may reduce the energetic costs of thermoregulation in response to changing weather conditions and bats' physiology with regard to reproduction (e.g. Racey, 1973; Lewis, 1996; Kerth et al., 2001; Dietz and Kalko, 2006). During the reproductive period, bats choose roosts with specific internal features, e.g. particular temperature profiles (Sedgeley and O'Donnell, 1999b; Ruczyński and Bogdanowicz, 2005; Ruczyński, 2006). This selection presumably requires searching for and sampling

roosting options, i.e. tree cavities that are suitable in terms of size and accessibility.

The ability to find new roosts that are not occupied by other bat species or other tree-cavity-dwelling animals is even more important for migratory species, such as noctule bats (*Nyctalus noctula* Schreber 1774; Vespertilionidae), that are faced with the challenge of finding suitable short-term roosts in unknown areas, presumably throughout their lifetime. In addition to providing shelter during migration, adequate roosts in tree cavities are also needed for mating by various species. Male noctules temporarily occupy roosts on migration or dispersal routes and call in an attempt to attract females for mating (Sluiter and van Heerdt, 1966; Petit et al., 2001). Therefore, finding new suitable roosts is a basic and fundamental problem for all bats, particularly for those that frequently switch between sites.

The roost characteristics of tree-cavity-dwelling temperate-zone bat species are reasonably well known (e.g. Ruczyński and Kalko, 2000; Kunz and Lumsden, 2003; Russo et al., 2004; Kalcounis-Ruppell et al., 2005), but there is limited information about how bats actually find new roosts. Once a bat knows a

suitable tree cavity, it might rely on spatial memory to relocate it. However, bats must somehow detect and recognise potential roosts on the first visit to a new cavity.

Our purpose was to determine which sensory modalities and cues play a role in detecting tree roosts by noctule bats (henceforth 'noctules'). Noctules are fast, agile but not very manoeuvrable bats (Norberg, 1987) who forage for insects in open space. Throughout the summer, and even for hibernation, noctules depend on tree cavities as roosts (Ryberg, 1947; Boonman, 2000; Baschta, 2004; Gebhard and Bogdanowicz, 2004). While numerous studies have addressed the sensory basis of prey detection in bats (e.g. Fenton, 1990; Faure and Barclay, 1994; Siemers and Schnitzler, 2000; Arlettaz et al., 2001), to our knowledge this is the first experimental investigation of the sensory basis of roost finding in bats, but also for other cavity-dwelling vertebrates (e.g. birds). Echolocation is the primary sensory modality that microbats use for small-scale spatial orientation (e.g. Schnitzler et al., 2003). However, although they are able to discriminate fine, regularly spaced surface structures in training experiments (e.g. Simmons et al., 1974; Habersetzer and Vogler, 1983), the task of finding an entrance to a cavity within the irregularly structured surface of an extended three-dimensional object (i.e. a tree trunk) should be much more difficult from an echo-acoustical viewpoint. This applies especially to fast-flying bats with limited manoeuvrability, such as the noctule (Baagøe, 1987; Norberg, 1987; Gebhard and Bogdanowicz, 2004), which are unable to inspect trees while in slow hovering flight.

Behavioural activity data predict that visual cues might be used by noctules for finding new tree cavities, because they typically start flying early in the evening when light levels are still high (Jones, 1995). In some bats, vision is known to complement echolocation for foraging and spatial orientation (e.g. Eklöf et al., 2002a; Eklöf et al., 2002b; Rydell and Eklöf, 2003; Winter et al., 2003). At close range, bats might also perceive olfactory stimuli or cues related to temperature differences between a tree cavity and ambient (Ruczyński, 2006). Once a roost is in use, social cues known to be important for intraspecific communication (e.g. Bloss, 1999; Voigt and Helvesen, 1999; Pfalzer and Kusch, 2003; Siemers, 2006), including calls or conspecific odours, may help other bats localise it (Barclay, 1982; Kerth and Reckardt, 2003).

We experimentally assessed hole-finding behaviour in tree-roosting noctules caught in the Białowieża Primeval Forest. Preliminary experiments suggested that hole-finding behaviour is a difficult task. This stimulated us to set up training experiments with wild-caught noctules in a large flight room to gather quantitative data on entrance detection. We trained bats to find a hole in artificial tree cavities. We measured bats' hole-finding performance when using echolocation alone and when one of four additional sensory cue types were also available. These additional cues were either non-social (visual information or temperature-related cues) or social (playbacks of conspecific echolocation calls or bat odours; i.e. olfactory cues). We predicted that adding a cue would increase bats' performance over the echolocation-only condition. We further expected visual cues and conspecific calls to be detectable over larger distances and hence to have a stronger effect than temperature-related or olfactory cues.

Materials and methods

Study animals

We captured individual noctules in the Białowieża Forest (north-eastern Poland) with mistnets (2×6 m and 2.5×4 m; Ecotone, Gdańsk, Poland) set across small rivers (Narewka, 3 sites; Hwoźna, 1 site) and at a pond located at the border of the Białowieża National Park between July and September 2006. The noctule is a good model species because it roosts predominantly, and in Białowieża Forest almost exclusively, in tree cavities (Boonman, 2000; Ruczyński and Bogdanowicz, 2005) (reviewed in Gebhard and Bogdanowicz, 2004). Depending on the sensory task, noctules emit frequency modulated (FM) or quasi-constant frequency (QCF) echolocation signals with peak frequencies of approximately 20 kHz in flight (Russo and Jones, 2002; Obrist et al., 2004). In spring, females from Central Europe migrate northeast (e.g. to northern Poland) to raise their young (e.g. Strelkov, 1969; Petit and Mayer, 2000; Strelkov, 2000). In autumn, while returning they may fly hundreds of kilometres in search of profitable feeding areas (Gaisler et al., 1979) (reviewed by Gebhard and Bogdanowicz, 2004). We used 11 adult bats (five males, six females) for our behavioural experiments and recorded the calls of another adult female for the playback experiments.

Husbandry

Bats were housed and used in behavioural tests at the Białowieża Mammal Research Institute for a maximum of 20 days. After testing, all bats were released at the site of capture. We scheduled netting of new bats and the release of tested bats both spatially and temporally to exclude the possibility of recaptures.

All protocols were conducted under licence from the Polish Ministry of the Environment (DOPog-4201-04A-4/05/al, DOPogiz-4200/IV.D-02/8438/05/aj) and with formal approval from the Local Ethical Commission (Białystok). Bats were housed in individual cages in a separate room at 22°C ambient temperature. They had access to water *ad libitum* and, in addition, were given water from a syringe after each training or testing session. Bats were fed mealworms (larvae of *Tenebrio molitor*), which they received as rewards during training and testing. We weighed bats daily to ensure that they remained within 90% of their initial mass and hand-fed them until they were approximately 1 g above capture mass just prior to release.

Flight room

Experiments were conducted in a 5.3×6.9 m flight room with a ceiling height of 3.4 m (Fig. 1). The walls and ceiling were covered by smooth black foil to prevent bats from hanging on the walls (Siemers and Page, 2007). In the centre of the flight room we erected a large alder log (*Alnus glutinosa*; height 174 cm, diameter 22 cm) on which we placed the experimental log. Close to one wall of the room we provided a wooden plank as a starting perch for the bats. The experimental log was 3.2 m from the perch.

The bats' behaviour in the flight room was filmed using three infrared-sensitive cameras (NVC-130BH, Novus, Taiwan). The room was illuminated by two infrared panels (LED YK-8800, Yoko Technology Corp., Taiwan). One camera, equipped with a wide-angle lens (NVL 358D, Novus, Korea), filmed an

overview of the flight room, while the other two (zoom lens NVL 550D, Novus, Korea) provided close-up images that covered the entire circumference of the experimental log. The video signal was recorded onto a personal computer hard disc via a PCI card (NVB-050/4A, Novus, Korea) and the software DVR System provided by Novus. Signals from the two close-up cameras were recorded at 10 frames s^{-1} , and signals from the overview camera at 22 frames s^{-1} . The computer was in a separate room, while a monitor used to observe the bats' behaviour was located in one corner of the flight room. The monitor and the experimenter were covered by a large, dark blanket and thus the flight room was completely dark during experimental trials. We monitored echolocation activity using a Petterson D-230 bat detector (Petterson Electronics, Uppsala, Sweden), the heterodyne output of which was recorded onto the video sound track.

Experimental logs and manipulation of available cues

We used a total of 700 experimental logs. Each log was 40 cm high, had a diameter of 19–23 cm and was cut from an alder trunk (*Alnus glutinosa*) bought at a local sawmill. Alders are used by noctule bats for roosting (Ruczyński, 2003). We drilled an artificial cavity 11 cm in diameter and about 35 cm deep into each log from above and added an entrance hole of 4.5 cm in diameter either 6.5 cm from the upper or lower edge of the experimental log. The entrance hole was located in one of eight possible positions (Fig. 1). The diameter of the artificial logs slightly exceeded the minimum diameter of trees at the level of the cavity used by noctules in Białowieża Primeval Forest. The diameter of the artificial entrances was in the range of naturally preferred entrance sizes (Ruczyński and Bogdanowicz, 2005).

In behavioural experiments, bats were given 6 min to detect the entrance to the artificial roost. If they did not react to it by either crawling or flying towards it, we scored the trial as a negative response. We performed five types of trials in which we manipulated sensory cues available to bats for finding the entrance. In the control condition, which was conducted in

complete darkness, only echo-acoustic information was available (E – 'echolocation' task).

In the 'vision + echolocation' task (VE), the bats were provided with visual cues by dimly lighting the flight room. For this purpose we used a neon light (CF-36W, Pila, Poland) located on the ceiling, directly over the experimental log. The light was covered by duct tape and emitted light ranging from 240 lux close to the lamp to 5.4–13 lux in the vicinity of the experimental log (Minolta Auto Meter IV, Japan; sensor directed towards the light; resolution 0.4–10 lux). The light intensity close to the trunk was slightly lower than the light intensity we measured when noctules could first be observed hunting during the early evening at Białowieża (I.R. and B.M.S., unpublished).

In the 'temperature-related cue + echolocation' task (TE), we heated the artificial tree cavities to $6.8 \pm 1.4^\circ\text{C}$ (mean \pm s.e.m.; range $3\text{--}11^\circ\text{C}$, $N=12$) above ambient temperature. Under field conditions, the temperature in noctule roosts at night is on average 7.1°C above ambient temperature (Ruczyński, 2006). Heating was achieved by placing a 1-litre jar containing ~350 ml hot water into the cavity 20–90 min before the trial started and removing it just before the experiment. This volume of water allowed for the desired temperature to be maintained for up to 1.5 h. The bats could potentially sense the warmth by thermosensation. However, detection of air-flow caused by emanating warmth with mechanosensors is conceivable, as is also simply smelling more intense wood odour from inside the cavity as a result of heating. Because our approach did not discriminate between these options, we use the term 'temperature-related cues' instead of temperature cues.

In the 'passive acoustic cue + echolocation' task (AE), passive acoustic cues were experimentally provided by playbacks of echolocation calls from inside the tree cavity. To reduce variation associated with possible information about individual identity that might be coded in echolocation calls (Fenton, 2003) (but see Siemers and Kerth, 2006), we used only calls recorded from one adult lactating female who was not included in the other experiments. The echolocation calls of this individual were recorded while it sat in the entrance hole of an experimental trunk and broadcasted outwards.

To record calls, we aimed an Avisoft condenser microphone (CM16, Avisoft, Berlin, Germany) at the trunk entrance from 1 m distance and recorded the signal onto a laptop hard drive through Avisoft UltraSoundGate and running Avisoft-Recorder software (sampling rate 384 kHz, 16 bit; Avisoft). The recorded signal was filtered (high-pass filter, 10 kHz, SasLab Pro, Avisoft), digitally amplified and played back with Avisoft-Recorder software through a National Instruments D/A conversion PCMCIA card (DAQCard-6062E, National Instruments, Hungary), Avisoft Bioacoustics ultrasound power amplifier (USPA/19) and a broadband loudspeaker (Ultrasonic Speaker ScanSpeak, Avisoft).

Calibration of the recording and playback setup against a $\frac{1}{4}$ " measuring microphone (BF 40, G.R.A.S., Holte, Denmark) showed that the frequency response of the combined system was flat ± 6 dB between 10 and 115 kHz and ± 4 dB between 22 and 60 kHz. Noctule calls fall within this range and hence no further filtering was required to ensure natural playbacks. The calls we used were 1–2 ms FM sweeps from 60 to 23 kHz (1st harmonic,

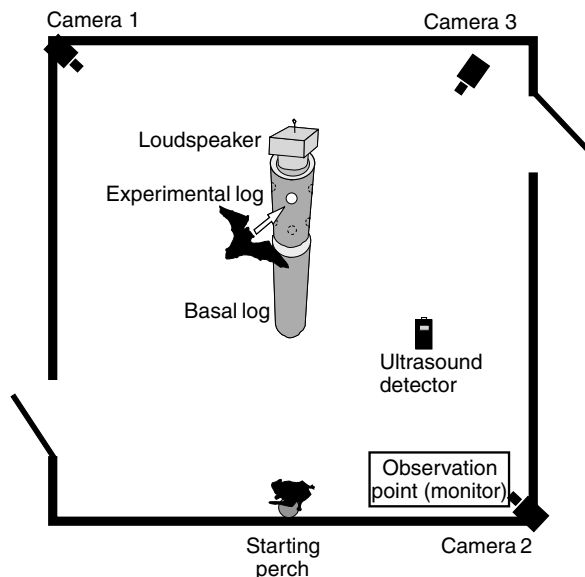


Fig. 1. Schematic diagram of the flight room setup.

which had the most energy; often the second and parts of a third harmonic were visible). Amplitudes of the calls recorded from the bat sitting at the entrance corresponded to ~60–70 dB SPL at 1 m in front of the cavity. We adjusted playbacks so that roughly 40 dB SPL could be detected 1 m from the cavity entrance; i.e. we acoustically mimicked a noctule sitting and calling from inside the roost. The playback sequence was 50 s in duration and a loop file was played until the end of the trial. The loudspeaker, housed in a metal box and acoustically isolated with cork to direct the playback signal only into the artificial trunk, was installed on top of the experimental log (Fig. 1). In order to keep the echo-acoustic appearance of the experimental logs equal in all experiments, the loudspeaker was mounted on top of the log in the trials without playbacks as well.

In the 'olfaction + echolocation' task (OE), we tested for the role of olfaction. Bats are known to discriminate individuals from their own *versus* other colonies based on olfactory cues and exhibit strikingly different behavioural responses (Safi and Kerth, 2003). Given that we could not determine colony membership of the wild-caught bats, we used each individual's own odour instead of that of a different bat to exclude ambiguities in data interpretation. A piece of cloth (3×8 cm) was exposed in the cage of the bat to be tested for 24–48 h. Four to five hours before the experimental trial, the cloth and some of the test bat's faeces were put into the experimental log, which was then tightly closed and opened shortly before the trial to allow the odour to flow out from the roost entrance. To provide an appropriate control, a piece of cloth of the same size and material, but without bat odour, was put into all logs in non-olfaction trials. In OE trials, the cork tube and the loudspeaker were covered with thin plastic foil to prevent odour contamination of the loudspeaker.

After a single use, each log was ventilated outside the building for at least 20 days before potential reuse. The flight room was ventilated by opening two doors in opposite corners before and after each bat's daily session, as well as briefly after the fifth trial of each session.

Training and testing

The experiment was conducted in two stages: (1) a training phase and (2) a testing phase. All training and testing was performed with only one bat in the flight room. Each day started with a 'warm-up' phase of 5–10 min free flight in the flight room without exposure to experimental logs. In the first part of training, a log with eight similar-sized entrances was offered to the bats in the middle of the flight room. The large number of entrances was chosen to enhance the chance that bats would successfully find at least one of them. The bats were trained to begin hole-finding flights from a wooden starting perch. After finding an entrance and crawling into the log, bats were rewarded with mealworms. Depending on training progress, we consecutively reduced the number of available entrances. Finally, only one entrance was left in one out of eight possible locations (two heights, four directions; Fig. 1) to minimise the use of spatial memory between trials. To facilitate training, the light was switched on. Our criterion for successful training was that the bats found entrances in at least nine out of 10 trials in less than 5 min. Training of each individual took 5–14 days (with a mean \pm s.e.m. of 10.3 \pm 3.5), 1–2 h per day.

After successful training, we started the testing phase, during which we measured bats' performance at finding the cavity entrance for each of the five different tasks described above. For every individual, we conducted eight trials for each of the five tasks (E, VE, TE, AE, OE), resulting in a total of 40 trials per bat. We conducted 10 trials per bat per night. This ensured continued motivation because they were still hungry after the 10th trial and habitually ate another 5–10 mealworms before being returned to their cage. The testing phase took four nights for each individual. Each of the eight entrance hole positions (Fig. 1) was used once per task. The sequence of available cues and positions of the entrance hole were selected according to a pseudo-random test protocol. Each task type was run twice per night and bat. Furthermore, each entrance position was used once, and two positions twice per night.

Bats were placed by hand onto the starting perch. The trial started when they first took flight. They were given a 6-min period to search for the cavity entrance. When the bat did not find the entrance within this time, the trial was ended and scored as 'entrance not detected'. When bats successfully entered a cavity, they were handfed a mealworm and then returned to their home cage while the next trial was prepared.

Video analysis

We classified the circumstances of cavity detection into two categories: (1) 'from flight' – when a bat either landed at or nearby (up to 1.5×body length) the entrance *and* walked immediately (in <1 s) and in a straight line from its landing position towards the entrance or (2) 'from crawling' – when a bat clearly detected the entrance while crawling on the experimental log. We further extracted the following time parameters: (1) search time – total time from when the bat took flight from the starting perch until it entered the cavity entrance; (2) crawling time – total time of quadrupedal searching on the experimental log. Resting bouts and activity outside the experimental log were not considered.

Statistical analysis

The time values obtained from the eight trials per bat for each task type (in two cases seven due to missing data) were pooled into a single datum to avoid pseudo-replication by using the medians of search time and crawling time for statistical testing. We computed repeated-measures ANOVAs with 'task type' as the within-subject factor and 'sex' as the between-subject factor. Performance in the echolocation-only task was compared to performance in each of the other four tasks by using *post-hoc* paired *t*-tests.

To analyse the proportion of trials in which the bats detected the cavity entrance from flight, we also used one datum per bat and task type to avoid pseudo-replication. We used proportion data (X in-flight-detections out of n trials per bat and task type), which formed a binomial distribution, and transformed them into data that were close to a normal distribution [p. 280, eqn 13.8 in (Zar, 1999)].

$$p' = \frac{1}{2} \left(\arcsin \sqrt{\frac{X}{n+1}} + \arcsin \sqrt{\frac{X+1}{n+1}} \right),$$

where X is the number of in-flight-detections and n is the

number of trials performed. We computed a repeated-measures ANOVA and *post-hoc* paired *t*-tests on the transformed data.

To account for multiple comparisons in *post-hoc* tests, we used manual Bonferroni correction (p -values \times number of comparisons). As the application of the Bonferroni correction is currently debated and comes at the risk of making more type II errors, i.e. not recognising a true effect as significant (e.g. Verhoeven et al., 2005), we report both corrected and uncorrected P -values, when the test made a difference.

Statistics were computed using SPSS 14.0 (SPSS Inc., Chicago, IL, USA), JMP 4.0.4 (SAS Institute, Cary, NC, USA) and Microsoft Excel 2002.

Results

All 11 bats were successful in finding a cavity within 6 min, with only two negative responses during 348 total trials. Search time was significantly affected by task type (Fig. 2), while there was no influence of the bats' sex on search time (repeated-measures ANOVA; task type as within-subject factor, $F_{4,36}=3.48$, $P=0.017$; sex as between-subject factor, $F_{1,9}=0.18$, $P=0.683$; interaction task type \times sex, $F_{4,36}=1.28$, $P=0.296$). In *post-hoc* comparisons, only search time in the acoustics + echolocation task differed significantly from the echolocation-only task (paired *t*-tests, $t_{10}=3.24$, $P=0.009$, $P_{\text{Bonferroni}}=0.036$) in contrast to the other three tasks (paired *t*-tests, $t_s<2.1$, $P_{\text{Bonferroni}}>0.28$). The bats found the tree holes faster in the presence of conspecific echolocation calls than in the trials without.

Bats detected the cavity entrance in flight in about 12.2% of trials (range 7–22%). In the remaining cases, they found the entrance while crawling on the experimental log. The proportion of trials in which the bats detected the cavity entrance from flight was significantly influenced by task type (Fig. 3; repeated-measures ANOVA on the transformed proportion data for in-flight-detections; task type as within-subject factor, $F_{4,36}=4.96$, $P=0.003$) but was unaffected by the bats' sex (sex as between-subject factor, $F_{1,9}=0.14$, $P=0.713$; interaction task

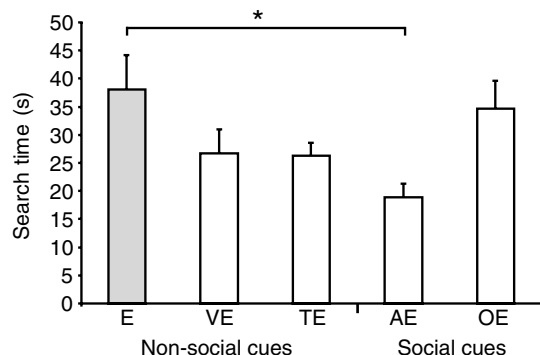


Fig. 2. Search time. Bars represent means \pm s.e.m. of individual medians ($N=11$ bats). Tasks are abbreviated as follows: E, echolocation; VE, vision + echolocation; TE, temperature + echolocation; AE, acoustic cues + echolocation; OE, olfaction + echolocation. Significant results from *post-hoc* comparisons of bats' performance in the echolocation task (grey bar) with all the other four tasks are indicated (paired *t*-tests, Bonferroni corrected P -values: $*P<0.05$). For further statistics, see text.

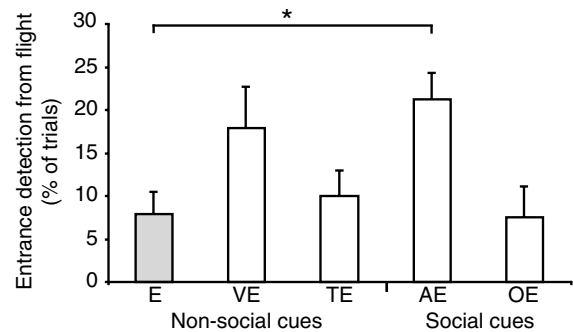


Fig. 3. Proportion of trials in which the bats detected the cavity entrance while in flight. Bars represent means \pm s.e.m. of individual medians ($N=11$ bats). Tasks are abbreviated as follows: E, echolocation; VE, vision + echolocation; TE, temperature + echolocation; AE, acoustic cues + echolocation; OE, olfaction + echolocation. Significant results from *post-hoc* comparisons of bats' performance in the echolocation task (grey bar) with all the other four tasks are indicated (paired *t*-tests, Bonferroni corrected P -values: $*P<0.05$). For further statistics, see text.

type \times sex, $F_{4,36}=0.998$, $P=0.421$). *Post-hoc* comparisons indicated that bats found the entrance from flight significantly more often in the acoustics + echolocation task compared with the echolocation-only condition (paired *t*-tests, $t_{10}=-3.41$, $P=0.007$, $P_{\text{Bonferroni}}=0.028$). Search time in the other three tasks did not differ from the echolocation-only task (paired *t*-tests, $t_s=-1.5, -0.2, 0.9$, $P_{\text{Bonferroni}}>0.6$).

We then restricted our analysis to the subset of trials in which the bats detected the entrance while crawling. In this subset, task type had a significant effect on crawling time (Fig. 4), while there was again no influence of sex (repeated-measures ANOVA; task type as within-subject factor, $F_{4,36}=3.80$, $P=0.011$; sex as between-subject factor, $F_{1,9}=0.347$, $P=0.570$;

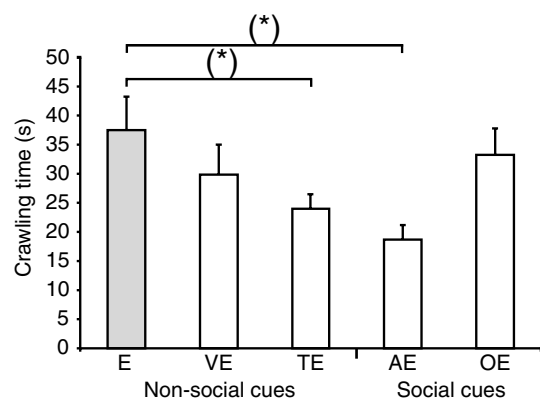


Fig. 4. Crawling time. Data are only from trials in which we scored the detection to have occurred 'from crawling'. Bars represent means \pm s.e.m. of individual medians ($N=11$ bats). Tasks are abbreviated as follows: E, echolocation; VE, vision + echolocation; TE, temperature + echolocation; AE, acoustic cues + echolocation; OE, olfaction + echolocation. Significant results from *post-hoc* comparisons of bats' performance in the echolocation task (grey bar) compared with the other four tasks are indicated in the graph [paired *t*-tests, Bonferroni corrected P -values: (*), significance lost when Bonferroni correction was applied; uncorrected $P<0.05$]. For further statistics, see text.

interaction task type \times sex, $F_{4,36}=1.94$, $P=0.124$). In *post-hoc* comparisons, both crawling time in the acoustics + echolocation task and in the temperature + echolocation task was shorter than in the echolocation-only task (paired *t*-tests, E *versus* AE, $t_{10}=2.94$, $P=0.015$, $P_{\text{Bonferroni}}=0.06$; E *versus* TE, $t_{10}=2.44$, $P=0.035$, $P_{\text{Bonferroni}}=0.14$; note that significances vanish when Bonferroni correction is applied). Crawling time in the other two tasks did not differ significantly from the echolocation-only task (paired *t*-tests, E *versus* LE and SE; $t_8<1$, $P_{\text{Bonferroni}}=1$). Bats always echolocated when crawling.

Discussion

The aim of our study was to determine which sensory cues are used by forest-dwelling noctule bats to detect new tree roosts. Given that standardised observation of this behaviour, let alone experimental manipulation of available cues, is extremely difficult in the field, we set up an experiment with captive bats that mimicked the natural situation. Our data show that conspecific echolocation calls (AE) clearly increased detection performance. The evidence for this comes from the higher proportion of detections from flight and also when bats were crawling. The other cues we presented had no, or at best weak, effects. In the following, we refer to long-range detection as a detection over at least one or typically several metres, i.e. from flight. The term 'short-range detection' is used for detection over (much) less than 1 m, i.e. typically while walking on the trunk.

The fact that the bats generally landed on the trunk and searched for cavity entrances by prolonged crawling suggests that the entrance was not easily detectable using echolocation or any other modality while the bats approached the log or circled around it. This indicates that finding new cavities is generally difficult for noctules. Spontaneous landing and subsequent crawling of naive bats on experimental logs occurred from the beginning of training. This was in stark contrast to three brown long-eared bats (*Plecotus auritus*) tested using a similar setup; these bats are very manoeuvrable, can hover and detected cavities mostly from flight (I.R., E.K.V.K. and B.M.S., unpublished data). Although noctule roost entrances in Białowieża Primeval Forest are typically surrounded by several metres of free airspace (Ruczyński and Bogdanowicz, 2005), roost entrances are sometimes obscured by numerous branches and leaves, which excludes the possibility of detection from flight. Taken together, our results suggest that crawling behaviour during searching for new roosts might be species specific and associated with agile, but not manoeuvrable, bats such as noctules.

Non-social cues

Echolocation

Echolocation is the primary sensory modality that bats use for spatial orientation (e.g. Schnitzler et al., 2003) and, in many species, also for detection, localisation and classification of prey (Griffin et al., 1960; Griffin, 1968). Bats face difficulty when objects of interest such as prey are close to or in vegetation, as they can be acoustically masked for the bat, meaning that echoes from the object and the background strongly overlap (Schnitzler and Kalko, 2001; Siemers and Schnitzler, 2004). On one hand, detection of tree cavities by echolocation alone is difficult, because faint echoes from the cavity's entrance and possibly

from its back plane will overlap with massive echoes from the trunk surface. On the other hand, it is likely that cavities generate characteristic echo-acoustic patterns, such as spectral notches due to interference by multiple wavefronts from the trunk surface and cavity back plane. In contrast to evaluating echoes of an artificial, regularly structured hole plate (Habersetzer and Vogler, 1983; Mogdans and Schnitzler, 1990), the task of finding a single entrance within the irregularly structured surface of an extended three-dimensional object (e.g. a tree trunk) is much more challenging from an echo-acoustical viewpoint.

To obtain sufficient information on the exact position of a hole, a bat must likely sample multiple echoes from slow hovering flight to reliably recognise such patterns. This is a difficult task for fast-flying and agile, albeit not manoeuvrable, noctules (Baagøe, 1987; Norberg, 1987) (reviewed by Gebhard and Bogdanowicz, 2004). In accordance with this, in the echolocation-only task (E), bats detected the entrance in only 7% of all cases from flight and took an average of 44 s to find it. The notion that detecting a cavity entrance by echolocation alone is difficult for a noctule is corroborated further by the fact that performance clearly improved in the presence of additional cues, namely conspecific calls.

Vision

Besides echolocation, visual and temperature-related information was available as non-social cues in our experiments. While vision in some bats can play an important role in prey detection (Bell, 1985; Eklöf et al., 2002a; Eklöf and Jones, 2003; Rydell and Eklöf, 2003), long-distance orientation (Griffin, 1970) and obstacle avoidance (Bradbury and Nottebohm, 1969), it did not significantly improve the time required for cavity detection from a distance in our study, even though bats were in a large, unobstructed flight cage with the logs clearly exposed.

At short range, visual cues did not result in faster detection of the entrance as compared to the echolocation-only task although we provided light levels similar to those encountered by emerging noctules in Białowieża Primeval Forest (I.R. and B.M.S., unpublished). For visual prey detection, the degree of contrast between prey and background is important (Eklöf et al., 2002a; Eklöf and Jones, 2003). As contrast between cavity entrances and the surrounding tree bark is usually low in the forest under twilight conditions and at night, this does not provide substantial visual cues. Our results suggest that visual information is not important for the detection of new cavity entrances, because even with dusk-like light levels, there was no significant enhancement of performance.

Temperature-related cues

Temperature-related (TE) cues had no influence on long-range detection of cavities, but they reduced crawling time (although significance vanished when Bonferroni correction was applied). Preliminary recordings in the study area during summer 2005 using a thermo-camera capable of measuring absolute temperatures (Jenoptik, Jena, Germany) revealed that cavity entrances were at least 1–2°C warmer than the surrounding bark. This might result from different thermal conductance, capacitance and, above all, the warmer internal

temperature of tree cavities in comparison with external night temperatures (Ruczyński, 2006). Our aim was to mimic this natural situation. While the bats might indeed have sensed the temperature gradient by thermosensation, they could alternatively have detected emanating warm air-flow with mechanosensors or else have simply smelt more intense wood odour from inside the cavity as a result of heating. Although not of help at long range, temperature-related cues may be useful for detecting entrance holes at close range and potentially also for selecting parts of trees for an intensified search where there is a greater chance of finding suitable cavities (e.g. warm trunks or branches). For forest-dwelling bats, warm cavities are probably crucial for juvenile development (Racey, 1973; Sano, 2000; Sedgeley, 2001; Ruczyński, 2006). A recent study suggests that the presence of conspecifics and social thermoregulation exerts more influence than microclimate on tree roost preferences in at least one species of cavity-dwelling bats (Willis and Brigham, 2007).

Social cues

Conspecific echolocation calls

Once a roost site is known to any bats, picking up on social cues will reduce energetic cost of finding and selecting suitable tree cavities for others. Our experiments showed that echolocation calls emitted from inside a cavity significantly enhance roost detection by conspecifics, both at long and short range. Social calls and echolocation signals from bats swarming around a roost tree, a behaviour typical of many vespertilionid bats before entering a roost (e.g. Kunz, 1982; Siemers et al., 1999; Siemers and Schnitzler, 2000), will carry further and hence be more conspicuous. The attraction to conspecific calls in the context of roost finding can either be viewed as eavesdropping or, when intended communication is assumed, can provide a mechanism for information transfer on roost location and suitability among colony members (Kerth and Reckhardt, 2003). Eavesdropping was also reported for short-distance location of a hibernaculum by little brown bats (Avery et al., 1984).

Odour cues

The other social stimulus we had tested, odour cues (OE), had no influence on probability or speed of cavity detection. Our odour treatment probably provided a less intense smell than would emanate from a tree roost inhabited by many bats for several weeks; i.e. increased cue strength might have yielded different results. Our experiment mimicked a cavity used only for a short time, and in this case odour clearly was not important.

Acoustic social cues are apparently of critical importance for learning about the location of new roosts. Of all stimuli tested, both social and non-social, conspecific calls clearly had the strongest facilitating effect. This implies that roosts in current use are easiest to find for conspecifics. Hence, under a forest management perspective, maintenance of existing roosts should have high conservation priority.

Roost selection

Bats must not only detect a cavity but, more importantly, select a suitable roost in terms of quality from the pool of cavities they find. Trees in the Białowieża Primeval Forest

harbour a large number of hollows, holes and crevices (Walankiewicz, 1991) (W. Walankiewicz and I.R., unpublished data). Most cavities are not useful for bats (e.g. too shallow or cold) (Ruczyński, 2006; Ruczyński and Bogdanowicz, 2005). Bats could thus save time and energy if they limit their search effort to trees that may offer optimal roosts. Bats are quick to learn associatively (Siemers, 2001) and can distinguish echo roughness, which encodes tree species (Grunwald et al., 2004; Stilz, 2004). It is therefore conceivable that they learn which tree species or parts of trees provide the highest probability for finding suitable hides. Sedgeley and O'Donnell reported that *Chalinolobus tuberculatus* selected trees with the highest number of cavities (Sedgeley and O'Donnell, 1999b). It is unclear, however, whether this mirrors an *a priori* restriction of search effort to these trees or is just a statistical effect.

It is well documented that bats usually select larger and higher trees than those available (Sedgeley and O'Donnell, 1999a). In Białowieża Forest, noctules usually use characteristic large old oaks, ashes and alders and inhabit high cavities (average 19 m), often in dead branches or branches partly devoid of bark (Ruczyński, 2000; Ruczyński, 2003; Ruczyński and Bogdanowicz, 2005). It is possible that bats recognise these rather characteristic trees by echolocation or even vision and then, as suggested by our data, search for suitable cavities while crawling by use of echolocation, and possibly touch if no acoustic social cues are available. In contrast to old or primeval forest, managed forests are usually much more uniform and therefore associative learning should be less effective, which together with sensory constraints should render detection and selection of suitable roosts more difficult.

Taken together, our data indicate that noctules are likely to use a range of social and non-social cues to find new cavities. The detection of new cavities from a distance is difficult if only non-social cues (i.e. echolocation, vision, temperature) are at hand. Acoustic cues from conspecific calls clearly increased the bats' detection performance.

Our data further suggest that the bats usually localise new entrances from a short distance while crawling on the trunk. Even though bats always echolocated when crawling, they seemed to detect the entrance only from a distance as short as a few centimetres. Temperature might play an additional role, although its effect on the bats' performance in our experiments lost significance after Bonferroni correction. Once a bat has found a new roost, it might use spatial memory to relocate it (Winter et al., 2005). Other bats might learn about the new roost through eavesdropping or information transfer (Kerth and Reckhardt, 2003). Overall, sensory constraints may strongly limit the effectiveness of finding new cavities, and, as a countermeasure, promote sociality, information transfer and eavesdropping among bats.

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