

Calls in the Forest: A Comparative Approach to How Bats Find Tree Cavities

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Abstract

Although tree cavities are a particularly critical resource for forest bats, how bats search for and find new roosts is still poorly known. Building on a recent study on the sensory basis of roost finding in the noctule (Ruczynski et al. 2007), here we take a comparative approach to how bats find roosts. We tested the hypothesis that species' flight abilities and echolocation call characteristics play important roles in how well and by which cues bats find new tree roosts. We used the very manoeuvrable, faintly echolocating brown long-eared bat (*Plecotus auritus*) and the less manoeuvrable, louder Daubenton's bat (*Myotis daubentonii*) as study species. The species are sympatric in European temperate forests and both roost in tree cavities. We trained bats in short-term captivity to find entrances to tree cavities and experimentally manipulated the sensory cues available to them. In both species, cue type influenced the search time for successful cavity detection. Visual, olfactory and temperature cues did not improve the bats' performance over the performance by echolocation alone. Eavesdropping on conspecific echolocation calls played back from inside the cavity decreased search time in Daubenton's bat (*M. daubentonii*), underlining the double function of echolocation signals – orientation and communication. This was not so in the brown long-eared bat (*P. auritus*) that has low call amplitudes. The highly manoeuvrable *P. auritus* found cavities typically from flight and the less manoeuvrable *M. daubentonii* found more entrances during crawling. Comparison with the noctule data from Ruczynski et al. (2007) indicates that manoeuvrability predicts the mode of cavity search. It further highlights the importance of call amplitude for eavesdropping and cavity detection in bats.

Introduction

Although suitable tree cavities are a particularly critical resource for forest bats (Kunz & Lumsden 2003), how bats search for and find new roosts is still poorly known. The first study to explore this topic revealed that for the fast flying but not very manoeuvrable noctule (*Nyctalus noctula*), finding cavity entrances by echolocation is a difficult task

(Ruczynski et al. 2007). Additional visual, olfactory or temperature cues did not or only marginally improve the bats' performance. By contrast, conspecific echolocation calls emanating from the roost entrance clearly helped *N. noctula* in detecting and localizing tree holes. This finding underlines the double function of echolocation for echo-based orientation and communication (e.g. Barclay 1982; Fenton 2003; Siemers 2006; Jones 2008). While

many bats detect faint echoes of small insects over only a few metres (Kalko 1995; Siemers et al. 2005; Surlykke & Kalko 2008), they can hear the echolocation calls of other foraging bats 10 times this distance (Barclay 1982; Hoffmann et al. 2007; Safi & Kerth 2007).

While for the detection of small insects, echo-detection thresholds are critical, the challenge in finding a cavity entrance lies rather in discriminating a tree trunk with a hole from one without. Subsequently, bats need to choose a suitable from the many available holes (e.g. Kunz & Lumsden 2003). Although bats are able to discriminate the texture of targets in training experiments (e.g. Simmons et al. 1974; Habersetzer & Vogler 1983; Schmidt 1988), finding an entrance to a cavity within the irregularly structured surface of an extended three-dimensional object, such as a tree trunk, is a very demanding echolocation task. This applies especially to fast-flying bats with limited manoeuvrability, such as *N. noctula* (Baagøe 1987; Norberg 1987; Gebhard & Bogdanowicz 2004), which is unable to hover in order to inspect trees (Ruczyński et al. 2007).

Bat species adapted to forage close to and within vegetation such as the forest-dwelling long-eared bats (genus *Plecotus*; Swift & Racey 2002) and some *Myotis* (Siemers & Swift 2006) might therefore be less constrained in finding new tree roosts by echolocation. They are highly manoeuvrable, able to hover and to potentially inspect tree trunks in flight. Indeed, the forest-dwelling *Myotis bechsteinii* can find artificial roosts introduced into their home range within 1–4 wk (Kerth & Reckardt 2003; Kerth et al. 2006). Like many bats, this species lives in fission–fusion societies (Kerth et al. 2006). Information transfer accelerates the finding of the new roosts by colony members (Kerth & Reckardt 2003), potentially partly by eavesdropping on calls of conspecifics. The first arriving bat has to find the new roost without any social cues, however.

In this study, we took a comparative approach to the sensory basis of roost finding in forest bats. We tested the hypothesis that species' flight abilities and echolocation characteristics play key roles in how well and by which cues bats find new tree roosts. In order to enable valid comparison with the data on roost finding in *N. noctula* gathered by Ruczyński et al. (2007), we used the same experimental procedure. While *N. noctula* have rather low flight manoeuvrability, here we chose one species of intermediate (*Myotis daubentonii*) and another of very high (*Plecotus auritus*) manoeuvrability (Baagøe 1987; Norberg & Rayner 1987). Daubenton's bat (*M. daub-*

entonii Kuhl, 1817) typically forages over rivers and lakes, capturing prey close to and scooping or gaffing it from the water surface; calls are broadband, especially when flying in cluttered situations (Jones & Rayner 1988; Kalko & Schnitzler 1989; Siemers et al. 2001a,b). The brown long-eared bat (*P. auritus* Linnaeus, 1758) is a slowly flying, hovering species with large ears that help it in detecting and localizing sounds of prey, with which it then typically gleans from vegetation (Swift & Racey 2002). It emits broadband, multiharmonic echolocation calls, typically at amplitudes much below *N. noctula* and *M. daubentonii* (Waters & Jones 1995; Swift & Racey 2002). The study bats were captured in the Białowieża Primeval Forest (Eastern Poland), where all the three bat species roost almost exclusively in trees during summer (Ruprecht 1976).

Following Ruczyński et al. (2007), we trained bats to find the entrance to a tree cavity in a flight room and manipulated the sensory cues available to them. They had only echo-information or one additional cue, either visual, temperature-related, olfactory or acoustic (i.e. conspecific echolocation calls). We tested the following hypotheses and predictions. (1) Search time for successful cavity detection will depend on the cues provided and differ between species. Specifically, eavesdropping on conspecific calls should decrease the search time for both species. As *P. auritus* calls are very faint (Waters & Jones 1995), we expected the eavesdropping effect to be more pronounced in *M. daubentonii*. *Plecotus auritus* has relatively large eyes and can use vision for finding prey under favourable conditions (Eklöf & Jones 2003). We therefore expected it to show increased cavity-detection performance with visual cues available. Finally, we predicted that *M. daubentonii* and *P. auritus* should find the entrance hole faster than *N. noctula* (Ruczyński et al. 2007) by echolocation alone, because slower flight should result in a more detailed echo image for the bats. (2) The more manoeuvrable a species, the more likely it is to detect the cavity entrance from flight. We expected a higher proportion of in-flight-detections in the very manoeuvrable *P. auritus* when compared with *M. daubentonii*.

Material and Methods

As stated above, we followed the experimental protocol established by Ruczyński et al. (2007) for *N. noctula* in order to allow for a valid comparison between this and the present study. Therefore, we have provided a relatively brief description of

methods here and refer the reader to Ruczyński et al. (2007) for details.

Study Animals

We captured individual *P. auritus* and *M. daubentonii* in the Białowieża Forest (North-eastern Poland) with mistnets (2 × 6 m and 2.5 × 4 m, 2 × 12 m, Ecotone, Gdańsk, Poland) set across small rivers (Narewka – four sites, Hwoźna – one site, Braszcza – one site), at a pond located at the border of the Białowieża National Park, and on roads inside the forest, between July and Sept. 2006 and 2007. We used six adult *P. auritus* (four males and two females) and nine adult *M. daubentonii* (six males and three females) for our behavioural experiments and recorded the calls of another adult female each of *P. auritus* and *M. daubentonii* for the playback experiments. After testing, all bats were released at the site of capture. Capture, husbandry and testing 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).

Husbandry

Bats were kept at the Białowieża Mammal Research Institute for a maximum of 22 d. They were housed in individual cages at 22°C ambient temperature with *ad libitum* access to water. Bats were fed mealworms (larvae of *Tenebrio molitor*) given as rewards during training and testing. We weighed bats daily to ensure that they remained within 90% of their initial mass.

Flight Room

Experiments were conducted in a 5.3 m × 6.9 m flight room with a ceiling height of 3.4 m. A large alder log (*Alnus glutinosa*, height 174 cm, diameter 22 cm) in its centre supported the experimental log. At 3.2 m from the log, a starting perch (wooden plank) was provided for the bats. The bats' behaviour in the flight room was filmed for off-line analysis under infrared-sensitive illumination (one overview and two close-up cameras). The flight room was completely dark during experimental trials. We monitored echolocation activity using a Petterson D-230 bat detector, 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 (40 cm height, 19–23 cm diameter) was cut from an alder trunk (*Alnus glutinosa*) and had an artificial cavity (11 cm diameter, approx. 35 cm depth) drilled into it from above with an entrance hole (4.5 cm diameter, either 6.5 cm from the upper or lower edge of the log) in one of eight possible positions. Diameter and entrance of the logs were within the range of roost trees used by bats in Białowieża Primeval Forest (Ruczyński & Bogdanowicz 2005; I. Ruczyński, unpublished data).

In behavioural experiments, bats were given a 6-min time-window to detect the entrance to the artificial roost and their performance scored. We performed five types of trials. In the control condition, which was conducted in complete darkness, only echo-acoustic information was available (E – echolocation task). In the vision + echolocation (VE) task, the bats were provided with visual cues by dimly lighting the flight room. Light intensity close to the trunk (5.4–13 lux; Minolta Auto Meter IV, Japan) was slightly lower than in the field when the first bats started hunting at Białowieża (I. Ruczyński and B. M. Siemers, unpublished data). In the temperature-related cue + echolocation (TE) task, we used a jar with warm water to heat the artificial tree cavities to 6.8°C ± 1.4 SEM (n = 12) above ambient temperature. This corresponds to the temperature of bat roosts in the Białowieża forest at night with an average of 7.1°C above ambient temperature (Ruczyński 2006). Because our approach did not discriminate between thermal and olfactory cues (warm wood), we use the term 'temperature-related cues' instead of temperature cues. In the olfaction + echolocation (OE) task, we put a piece of cloth (3 × 8 cm) from the home cage (at least 24 h exposure) and some of the test bat's faeces into the experimental log 4 h prior to the trial. We closed the cavity tightly and opened it shortly before the trial to allow the odour to escape from the roost entrance. Bats are known to discriminate individuals from their own vs. other colonies based on olfactory cues and exhibit strikingly different behavioural responses (Safi & Kerth 2003). Given that we could not determine colony membership of the wild-caught bats, we used each individual's own odour. As a control, a piece of cloth of the same size and material, but without bat odour, was placed in 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 d before potential reuse.

In the passive acoustic cue + echolocation (AE) task, passive acoustic cues were experimentally provided by playbacks of echolocation calls from inside the tree cavity (Ultrasonic Speaker ScanSpeak, USPA/19 amplifier, Avisoft; NI DAQCard-6062E, Berlin, Germany). To reduce the variation associated with possible information about individual identity in the calls (Fenton 2003; but see also Siemers et al. 2005; Siemers & Kerth 2006, Kazial et al. 2008); we used only calls recorded from one adult female per species that was not included in the experiments. The echolocation calls were recorded while the individuals sat in the entrance hole of an experimental trunk and broadcasted outward (CM16 Avisoft condenser microphone, Avisoft UltraSoundGate; SR 384 kHz). The combined recording and playback set-up showed a flat frequency response of ± 6 dB between 10 and 115 kHz (for more details see Ruczyński et al. 2007). The main energy of both *P. auritus* (Waters & Jones 1995) and *M. daubentonii* echolocation calls falls within this range (Jones & Rayner 1988; Kalko & Schnitzler 1989) and hence no further filtering was required to ensure natural playbacks. The calls consisted of 0.5–2 ms FM (Frequency Modulated) sweeps with the first harmonics ranging from approx. 85 to 35 kHz in *M. daubentonii* and 55 to 33 kHz in *P. auritus*. A prominent second and parts of a third harmonic were present in most calls. In *P. auritus*, the second harmonic typically had most energy; upper cut-off frequency was approx. 100 kHz. Amplitudes of the *P. auritus* calls recorded from the bat sitting at the entrance corresponded to 50 dB SPL (Sound Pressure Level) or below at 1 m in front of the cavity. For *M. daubentonii*, the calls were at approx. 60 dB SPL. We adjusted playbacks so that roughly these same amplitudes were reached 1 m in front of the playback speaker. As the speaker was mounted on top of the cavity and broadcasted into it, we thereby acoustically mimicked a bat sitting and calling from *inside* the roost. The cavity itself acted as a low-pass filter. Amplitudes outside the log at 10 cm from the entrance hole were approx. 40 dB SPL for *P. auritus* (peak frequency approx. 70 kHz) and approx. 55 dB SPL for *M. daubentonii* (peak frequency approx. 47 kHz). The playback sequences (*P. auritus* 24 s; *M. daubentonii*: 14 s) were played looped 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. 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.

Training and Testing

In a first stage, the bats were trained to begin hole-finding flights from a wooden starting perch and to enter the experimental log through an entrance hole for a food reward. To aid the experimenter, dim light was switched on as in the VE condition during training. To facilitate training, we used a trunk with eight entrances (initially 16 for *P. auritus* in a smaller room, $2.9 \times 3.9 \times 2.2$ m) and then consecutively reduced the number of entrances. Our criterion for successful training was that the bats found entrances in at least nine out of 10 trials in <5 min. Training of each individual took 4–17 d (with an $\bar{x} = 11.1 \pm 3.4$ SEM), 1–2 h per day.

After successful training, we started the testing phase. 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 bats were 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 (two heights, four directions) were 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; 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. When the bat did not find the entrance within the 6-min period, the trial was ended and scored as 'entrance not detected'. In this case (which occurred in only three out of 600 trials), the search time was conservatively assumed as 360 s for statistical analyses. When bats successfully entered a cavity, they were handfed a reward and then returned to their home cage while the next trial was prepared.

Video Analysis

We classified cavity detection into two categories: (1) from flight – when a bat either landed at or near (up to $1.5 \times$ body length) the entrance and started

walking immediately (<1 s) and in a straight line towards the entrance; or (2) from crawling – when a bat clearly detected the entrance while crawling on the experimental log. We further extracted (1) the search time – total time from when the bat took flight from the starting perch until it entered the cavity entrance, and (2) the crawling time – total time of quadrupedal searching on the experimental log. Resting bouts and activity outside the experimental log were not included.

Statistical Analysis

We used a GLM to analyse the influence of task type (fixed factor) on the search and crawling time. To account for the repeated-measures design, we specified individual as a random factor. Performance in the E-only task was compared with that in each of the other four tasks by using *post hoc* Dunnett tests (two-sided). Species differences were assessed by a repeated-measures ANOVA on individual means per task type.

To analyse the proportion of trials in which the bats detected the cavity entrance from flight, we used one datum per bat and task type. 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 (Zar 1999, p. 280, eqn 13.8).

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

where X is the number in-flight-detections and n the number of trials performed. We computed a

repeated-measures ANOVA and *post hoc* paired t-tests (E-only task vs. each of the other four tasks) on the transformed data. To account for multiple comparisons in *post hoc* tests, we used manual Bonferroni correction (p-values times number of comparisons). For comparison with the performance of *N. noctula*, we reanalysed the *N. noctula* data from Ruczyński et al. (2007) in the way described here. Statistics were computed using SPSS 15.0 (SPSS Inc., Chicago, IL, USA) and Microsoft Excel 2003.

Results

All bats of both species were generally successful in finding the cavity entrance within the 6-min time-window. The six *P. auritus* never failed (n = 240 trials). Of the nine *M. daubentonii*, one bat failed twice and another once in a total of 360 trials.

Search Time

Search time was significantly affected by task type (Fig. 1a, b), but it did not differ between species (repeated-measures ANOVA on the pooled data set; task type as within-subject factor: $F_{4,52} = 4.58$, $p = 0.003$; species as between-subject factor $F_{1,13} = 0.43$, $p = 0.525$; interaction task type \times species, $F_{4,52} = 1.80$, $p = 0.143$). When analysed separately for the two species, the influence of task type on search time remained significant for both species (*P. auritus*: GLM, factor task type, $F_{4,20} = 3.45$, $p = 0.018$; *M. daubentonii*: $F_{4,32} = 3.43$, $p = 0.019$; individual specified as random factor to account for repeated-measures design). In *post hoc* pairwise comparisons for *P. auritus*, search time in the E-only task did not differ signifi-

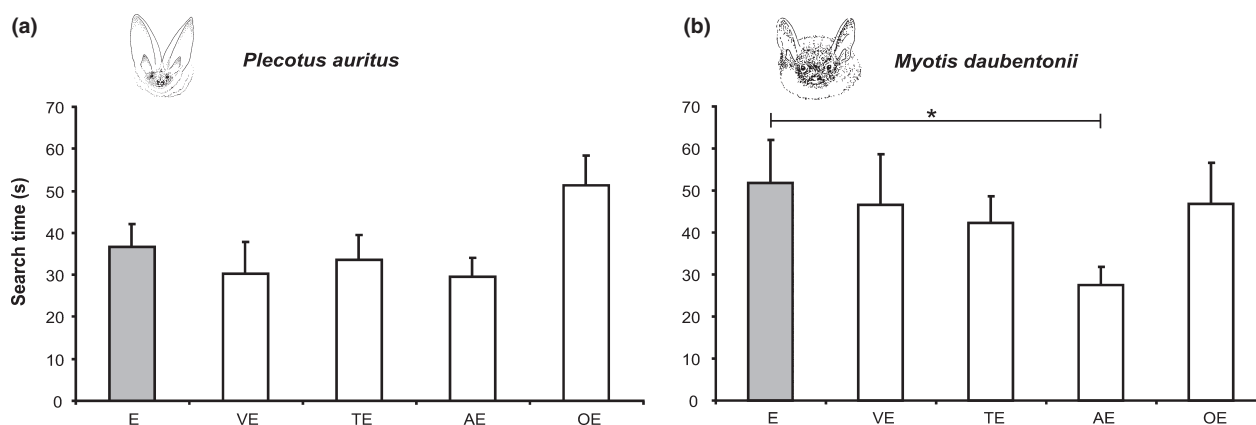


Fig. 1: Search time in *Plecotus auritus* (n = 6 bats) and *Myotis daubentonii* (n = 9 bats). Bars represent means \pm SEM of individual means. Tasks are abbreviated as follows: E, echolocation; VE, vision + echolocation; TE, temperature + echolocation; AE, acoustic cues + echolocation; OE, olfaction + echolocation. A significant result from *post-hoc* comparisons of bats' performance in the echolocation task (grey bar) with the other four tasks is indicated (Dunnett test: $*p < 0.05$). For further statistics, see text.

cantly from any of the four other tasks [*post hoc* Dunnett tests, $p(\text{OE}) = 0.069$; the three remaining $p > 0.65$; Fig. 1a]. For *M. daubentonii*, search time in the AE task, where they could eavesdrop on calls of conspecifics from inside the cavity, was significantly shorter than in the E-only task (*post hoc* Dunnett test, $p = 0.011$; Fig. 1b). Search time in the three other tasks did not differ from E-only (*post hoc* Dunnett tests, $p > 0.59$).

Mode of Cavity Detection

When searching for the entrance, *P. auritus* circled around the tree trunk in slow flight and frequently hovered in short distance (<50 cm) from its surface. The *P. auritus* detected the cavity entrance from flight in 94–100% of trials (Fig. 2a). By contrast, *M. daubentonii* often landed and continued searching by quadrupedal crawling; only 20–31% of detection events were scored as from flight (Fig. 2b). In the remaining 69–80% of cases, the bats found the entrance while crawling on the experimental log. Crawling was often preceded by repeated bouts of short flights and landings (maximally 46). The proportion of trials in which the bats detected the cavity entrance from flight differed highly significantly between species (repeated-measures ANOVA on the transformed proportion data for in-flight-detections; species as between-subject factor $F_{1,13} = 27.53$, $p < 0.001$). Task type also influenced the proportion of in-flight detections (task type as within-subject factor: $F_{1,7,22.7} = 7.68$, $p = 0.004$; interaction task type \times species, $F_{1,7,22.7} = 22.54$, $p < 0.001$). When data were analysed separately for the two species, the task effect remained significant for *P. auritus*

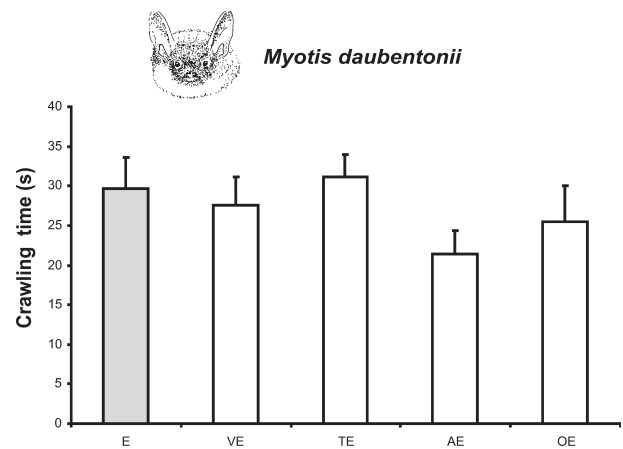
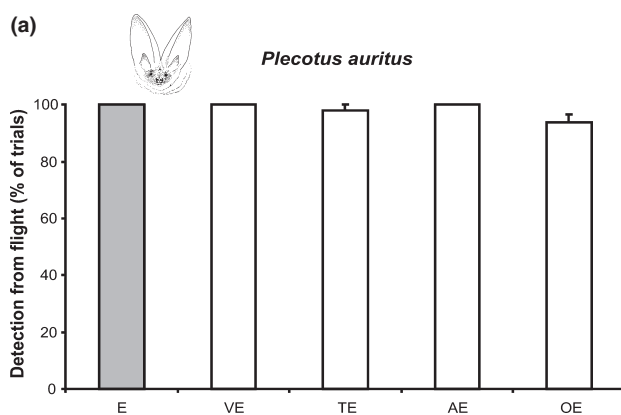


Fig. 3: Crawling time in *Myotis daubentonii*. Data are only from trials in which we scored the detection to have occurred 'from crawling'. Bars represent means \pm SEM of individual means ($n = 8$ bats; one excluded because it detected the cavity in only 7 out of 40 cases from crawling). Tasks are abbreviated as follows: E, echolocation; VE, vision + echolocation; TE, temperature + echolocation; AE, acoustic cues + echolocation; OE, olfaction + echolocation. For statistics, see text.

(repeated-measures ANOVA, $F_{1,8,8.8} = 735.36$, $p = 0.001$) and persisted as a trend only for *M. daubentonii* ($F_{1,7,13.4} = 3.14$, $p = 0.083$). *Post hoc* comparisons failed to show any significant difference between the proportion of in-flight-detections for the E-only task when compared to any of the other four tasks (paired t-tests, *P. auritus*: $p_{\text{Bonferroni}} > 0.30$; *M. daubentonii*: $p_{\text{Bonferroni}} > 0.12$).

In a final analysis, we examined the subset of trials in which the *M. daubentonii* found the entrance while crawling. One bat was excluded from this analysis, because it had detected the entrance from

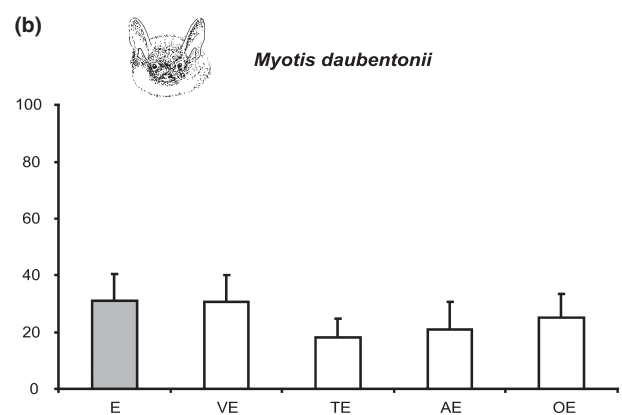


Fig. 2: Proportion of trials in which the *Plecotus auritus* ($n = 6$ bats) and *Myotis daubentonii* ($n = 9$ bats) detected the cavity entrance while in flight. Bars represent means \pm SEM of individual proportions. Tasks are abbreviated as follows: E, echolocation; VE, vision + echolocation; TE, temperature + echolocation; AE, acoustic cues + echolocation; OE, olfaction + echolocation.

crawling in only seven out of 40 cases. In this subset, task type had no significant effect on crawling time (Fig. 3; GLM, $F_{4,30.4} = 1.40$, $p = 0.258$; individual specified as random factor to account for repeated-measures design). The bats always echolocated when crawling.

Comparison with *N. noctula*

For a three-species comparison spanning from the very manoeuvrable *P. auritus* to the fast flying, but much less manoeuvrable *N. noctula*, we reanalysed data for the latter species from Ruczyński et al. (2007) in a combined data set with the present *P. auritus* and *M. daubentonii* results. For the combined data set, the effect of available sensory cues on search time remained highly significant (repeated-measures ANOVA, task type as within-subject factor: $F_{4,92} = 6.45$, $p < 0.001$). However, there was still no species difference for search time (species as between-subject factor $F_{2,23} = 0.30$, $p = 0.745$; interaction task type \times species, $F_{8,92} = 0.83$, $p = 0.581$). Also, when only comparing the search time for the E-only condition, the three species did not differ (ANOVA, $F_{2,23} = 0.72$, $p = 0.499$). By contrast, the proportion in which the bats detected the cavity entrance from flight differed among all three species (repeated-measures ANOVA; species as between-subject factor: $F_{2,23} = 44.59$, $p < 0.001$; task type as within-subject factor: $F_{2,6,58.9} = 4.80$, $p = 0.006$; interaction task type \times species: $F_{5,1,58.9} = 21.41$, $p < 0.001$; Bonferroni corrected *post hoc* test for species differences: *N. noctula*–*M. daubentonii*, $p = 0.003$; *N. noctula*–*P. auritus*, $p < 0.001$; *M. daubentonii*–*P. auritus*, $p < 0.001$). *Plecotus auritus* showed the highest proportion of in-flight-detections, *M. daubentonii* intermediate and *N. noctula* lowest.

Discussion

The aims of our study were to determine which sensory cues are used by two forest bat species, *P. auritus* and *M. daubentonii*, for detecting new tree cavities, and to test whether differences in manoeuvrability and call characteristics in these and a third species, *N. noctula* (Ruczyński et al. 2007), influence searching behaviour and detection performance.

Species Differences

Overall search time

As opposed to our prediction, the overall search time for successful cavity detection did not differ between

species, even if including the data on *N. noctula* (Ruczyński et al. 2007). By contrast, the cues available clearly affected the search time both in the present study and for the combined data set.

In-flight-detections vs. crawling

The data clearly supported our hypothesis for a correlation of manoeuvrability and the likelihood of detecting the cavity entrance from flight. The very manoeuvrable *P. auritus* showed nearly exclusively in-flight detections, while they amounted to 25% in *M. daubentonii*. In the majority of cases, *M. daubentonii* found the entrance from a crawling search on the trunk surface. This pattern was still more pronounced in the least manoeuvrable *N. noctula* that had only shown in-flight-detections in an average of 12% of trials (Ruczyński et al. 2007).

None of the three species seemed to be able to detect the cavity entrance easily from a distance. The finding that *M. daubentonii* and even more so *N. noctula* (Ruczyński et al. 2007) mostly landed on the trunk and searched for cavity entrances by crawling suggests that the entrance was not readily detectable by echolocation or any other modality while the bats approached the log or circled around it. *Plecotus auritus* typically detected the entrance while in slow or hovering flight at close distance from the trunk surface and rarely approached it in straight flight from a distance >1 m.

One could argue that all three species are actually equally capable of detecting the cavity from flight, but being more manoeuvrable, *P. auritus* may easily land closer to the desired target than *M. daubentonii* or *N. noctula*. We are sure, however, that this was not the case for the following reasons: (1) bats when crawling, often initially headed away from the entrance after landing (they clearly had not acquired knowledge on the entrance location prior to landing); (2) when acoustic cues were available, entrance detection from flight increased in *N. noctula*, i.e. sensory constraints rather than the ability to land precisely were limiting; (3) during training process, *M. daubentonii* landed on small targets such as door handles, i.e. they were well able to land precisely.

Use of Non-Social Cues

Echolocation

Despite the different search modes, search times for the E-only condition did not differ between *P. auritus*, *M. daubentonii* and *N. noctula*. Its hovering flight did not apparently allow *P. auritus* to sample the

echo scenes in more detail that would have markedly increased its search efficiency over the mostly quadrupedally searching *M. daubentonii*. Generally, all of the bats had to be at close range to find the entrance by echolocation. As opposed to detecting and locating insects in open space (Schnitzler & Kalko 2001), finding a hole in an extended surface is not a detection task, but rather a discrimination task. The bat has to tell a textured, irregular surface without a hole from one with a hole. From a distance, the sonar beam of the bat will cover a large portion of the trunk and the contribution of the hole to the overall echo will be minimal. When the bat is close, the ensonified surface will be smaller (Schmidt et al. 2000) and the relative contribution of the hole much larger. At very close range, the hole might cause a relevant drop in the echo amplitude when compared to a non-perforated surface patch. Furthermore, overlapping echoes from the entrance's sidewalls and possibly from the cavity's back wall could contribute to a distinct echo signature. For the comparable task of discriminating a textured surface without prey from one with an insect at close distance, call bandwidths predicted the performance of the tested bat species (Siemers & Schnitzler 2004). Large bandwidths are advantageous, for a detailed characterization of echolocation targets. Most bats increase call bandwidth to some degree in cluttered situations (Schnitzler & Kalko 2001). In the flight room, the two species tested here as well as *N. noctula* (Ruczyński et al. 2007) produced calls of approx. 1 octave bandwidths (first harmonic). This might further help to explain why we did not find marked performance differences in the hole finding paradigm by echolocation alone. It would thus be interesting to measure the cavity detection performance in bats than can produce extremely large call bandwidths (e.g. some *Kerivoula* and *Murina*, Kingston et al. 1999; *Myotis nattereri*, >3 octaves with the first harmonic; Siemers & Schnitzler 2000, 2004).

Vision

Vision did not significantly improve the time required for cavity detection in both studied species under experimental conditions, even though bats were in a large, unobstructed flight cage with the logs clearly exposed. Specifically, the fair visual abilities of *P. auritus* as shown in a foraging context (Eklöf & Jones 2003) did not translate into an improved ability for finding the cavity entrance. For visual prey detection, the degree of contrast between

prey and background is important (Eklöf et al. 2002; Eklöf & Jones 2003). Contrast between cavity entrances and the surrounding tree bark is usually low in the forest under twilight conditions and obviously at night. Especially for *N. noctula* that flies at relatively high light levels, it is still conceivable that vision is important for recognizing good tree candidates from a distance for subsequent in-depths hole searches by the use of echolocation, and possibly touch if no acoustic social cues are available (Ruczyński et al. 2007). Such candidate trees might include large old trees or trees with thick trunks (Ruczyński & Bogdanowicz 2008).

Temperature-related cues

Ruczyński et al. (2007) found a tendency for crawling *N. noctula* to find a cavity entrance faster when the cavity interior had been heated. By contrast, in the present study, both species did not provide any indication that temperature-related cues might help for detecting cavity entrances. Cavity temperature and microclimate is important after successful detection, however, when it comes to deciding whether the new cavity is suitable as a roost (Kerth et al. 2001; Sedgeley 2001; Ruczyński 2006).

Use of Social Cues

Odour

Odour cues had no effect on finding roost entrances in any of the species. 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. Odour potentially could play a more important role in cavity selection; e.g. to detect its previous use by predators (Boyles & Storm 2007).

Eavesdropping on conspecifics' calls

As predicted, the presence of an ultrasound signal that the experimental subject could eavesdrop on, namely conspecific echolocation calls, clearly reduced the search time in *M. daubentonii*. This corroborates the results for noctules (Ruczyński et al. 2007) and suggests that eavesdropping generally will yield a long range detection benefit for bats in search of suitable roosts (Jones 2008). Barclay (1982) had shown in the field that playbacks of echolocation calls attracted bats to unused night roost. However, in the present study, playback of conspecific calls did not decrease search time in *P. auritus*. *Plecotus* calls

are very faint (Waters & Jones 1995); especially when the bats are in a cluttered surrounding (Swift & Racey 2002). As we played back calls at naturalistic amplitudes, mimicking *P. auritus* echolocating inside a tree cavity, it is conceivable that the calls were only audible at such a close range that no significant reduction of the bats' search time resulted. Eavesdropping on 'whispering' bats such as *Plecotus* when inside a roost thus seems of limited use. It will be interesting to vary call intensity in future work to test whether the lack of a facilitating effect of acoustic cues in *P. auritus* is indeed caused by their inconspicuousness. Echolocation calls of bats swarming around a roost tree at the end of the night (e.g. Kunz 1982; Siemers & Schnitzler 2000) will carry further and be audible at a longer range. If bats intend to attract conspecifics, they can in addition use loud and more conspicuous social calls (Pfalzer & Kusch 2003; Siemers 2006). As an example, Vaughan & O'Shea (1976) described how swarming ('rallying') *Antrozous pallidus* utter conspicuous directive calls when approaching and flying about in the roosting area. *Plecotus auritus* is also known to produce conspicuous social calls in flight, but remain quiet when inside a roost (J. Furmankiewicz, pers. comm.). Clearly, conspecific calls appear to be the most important social cues for roost finding in at least some bats. It will thus be interesting to concentrate on acoustic cues in future studies. These could be designed to test for cue specificity, e.g. to compare the effect of echolocation calls vs. social call or of conspecific vs. heterospecific calls. It is known that bats can be attracted to calls of other species both in a foraging and a distress context (e.g. Barclay 1982; Russ et al. 2004) and thus is conceivable for roost location as well.

Learning and sociality

Associative learning can be useful when bats search for prey (Siemers 2001). Bats also obtain important information by 'watching' other bats (Gaudet & Fenton 1984; Page & Ryan 2006). Because finding new tree roosts is a difficult task (this study; Ruczyński et al. 2007), learning may be important for decreasing its costs. Bats may search for characteristic elements of trees, but also observe other bats when these search for or signal presence of suitable roost. Benefits connected with learning and information transfer about roosts may promote sociality (as has been suggested for foraging bats by Safi & Kerth 2007) in species frequently changing roosts or having difficulties in finding cavities.

Conclusions

Finding new tree roosts is a difficult task both for non-migratory forest bats (this study) as well as for migratory species (Ruczyński et al. 2007). Irrespective of flight, echolocation and visual abilities, bats seem to be able to detect cavity entrances only from a very close range. This implies that searching for new cavities requires detailed and time-consuming sampling of trees, especially as not every tree hole a bat finds turns out to be a suitable roost (Kunz & Lumsden 2003). Whereas *M. daubentonii* (Arnold et al. 1998; Dietz et al. 2006) forages open water and *N. noctula* in the open skies (Kronwitter 1988; Rachwald 1992), *P. auritus* habitually hunts inside the forest (Entwistle et al. 1996). It manoeuvres at close distance to foliage and tree trunks in search for noisy prey (Swift & Racey 2002). This might provide additional opportunities for detecting new tree cavities. Detailed spatial sampling of the forest interior on foraging flights might also help explain how another manoeuvrable bat, *M. bechsteinii*, likewise listening for prey sounds, but using more broadband calls (Siemers & Kerth 2006; Siemers & Swift 2006), efficiently finds new bat boxes (Kerth & Reckardt 2003; Kerth et al. 2006).

Once a tree roost is in use, individual bats can relocate it using spatial memory. Other individuals can find it considerably more effectively by eavesdropping on the echolocation calls of conspecifics, provided they come at sufficient amplitude. Besides providing spatial information to the caller, echolocation signals have a communicative function (Barclay 1982; Fenton 2003; Siemers 2006; Jones 2008). Taken together, used tree roosts are likely both salient on individual bats' mental maps and in the acoustic landscape of their forest environment. For conservation and forest management, established networks of roost trees should therefore have very high protection priority.

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