

Cave-dwelling bats do not avoid TMT and 2-PT – components of predator odour that induce fear in other small mammals

Tess Driessens^{1,2} and Björn M. Siemers^{1,*}

¹Max-Planck Institute for Ornithology, Sensory Ecology Group, Eberhard-Gwinner-Straße, 82319 Seewiesen, Germany and

²Vrije Universiteit Brussel, Department of Biology, Pleinlaan, 1050 Brussels, Belgium

*Author for correspondence (siemers@orn.mpg.de)

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SUMMARY

Recognition and avoidance of predators is fundamental for the survival of prey animals. Here we conducted the first study assessing chemosensory predator recognition in cave-dwelling bats. We used a Y-maze approach to test the reaction of greater mouse-eared bats (*Myotis myotis*) to two synthetically derived components of predator odour (2,4,5-trimethyl-3-thiazoline, TMT, a component of fox faeces scent; and 2-propylthietane, 2-PT, a component of mustelid scent) and to the natural scent of the least weasel (*Mustela nivalis*). It is well documented that rodents and several other small mammals show strong and at least partly innate fear reactions when confronted with these odorants. By contrast, the bats did not show any avoidance or fear reaction, despite the fact that relatively high odorant concentrations were presented. Furthermore, they did not react differently towards predator scent and towards acrid but otherwise neutral odours (basil or goat). The number of entries into the Y-maze arm with the odour source and the time spent in this arm as well as the bats' overall exploratory activity and several other behavioural variables were not affected by the odour treatments. Generally, the sense of smell is well developed in bats and plays an important role in bat behavioural ecology. It is thus somewhat surprising that the bats did not show any avoidance reaction to predator scent, even though direct contact with a mustelid or fox would result in death. We discuss ecological explanations that might have prevented bats from evolving olfactory predatory recognition and avoidance.

Key words: predator recognition, olfaction, scent, TMT, 2-PT, least weasel, bats, *Myotis myotis*.

INTRODUCTION

Recognition and avoidance of predators is fundamental for the survival of individual prey. Therefore, many prey organisms are capable of assessing and responding to cues signalling the presence of a predator. Depending on the environment and adaptations of the prey, these cues may be of a visual (McGowan and Woolfenden, 1989), auditory (Berger, 1999) or chemosensory nature (Weldon, 1990). Chemosensory predator detection has been reported for a variety of taxa (Kats and Dill, 1998), including invertebrates (Thomas et al., 2008), fish (Chivers and Smith, 1994), amphibians (Sih and Kats, 1994), reptiles (VanDamme and Castilla, 1996), birds (Amo et al., 2008; Roth et al., 2008) and, importantly, many mammals (Apfelbach et al., 2005). Eisenberg suggested that olfactory cues were crucial for predator detection already in early mammals, as these were probably night active (Eisenberg, 1983).

A series of field and laboratory studies has shown that predator chemical cues trigger distinctive behavioural responses, including stimulus avoidance, defensive behaviour, increased defecation rates (Punzo, 2005), reduced overall activity and the suppression of non-defensive behaviours (e.g. foraging, feeding, grooming or mating) (for reviews, see Kats and Dill, 1998; Apfelbach et al., 2005). In some of these studies the test animals have been exposed to the natural odour of predator skin and fur, while others used predator urine, faeces or anal gland secretions (reviewed in Apfelbach et al., 2005). More recently, many studies have focused on synthetically derived components of predator anal gland secretions or faeces as unconditioned fear stimuli (e.g. Wallace and Rosen, 2000; Dielenberg and McGregor, 2001; Blanchard et al., 2003; Apfelbach et al., 2005; Fendt et al., 2005; Fendt and Endres, 2008). In contrast

to natural predator odours, synthetic compounds allow the use of standardised and comparable concentrations and to eliminate possible confounding factors, such as effects of recent diet of the odour donor (Berton et al., 1998). 2,4,5-trimethyl-3-thiazoline (TMT) is a synthetically derived component of faeces of the red fox (*Vulpes vulpes*) and induces fear in rodents (Vernetmaury et al., 1984). The innate behavioural reactions of rats to TMT exposure are similar to those caused by natural predators odours, e.g. freezing and other species-specific defence reactions (Wallace and Rosen, 2000; Fendt et al., 2005; Fendt and Endres, 2008). In some cases, however, no fear or anti-predator behaviours were observed in response to TMT (Burwash et al., 1998; McGregor et al., 2002). Another synthetic compound of predator odour, 2-propylthietane (2-PT), is derived from the odour bouquet of the anal gland of stoats (*Mustela erminea*). Heale et al. reported an attenuated feeding behaviour in rats when their food was scented by 2-PT (Heale and Vanderwolf, 1994). Other studies have shown avoidance responses in voles, pocket gophers and brushtail possums when exposed to synthetic substances from mustelid anal gland secretions, including 2-PT (Sullivan et al., 1988a; Sullivan et al., 1988b; Sullivan et al., 1990; Woolhouse and Morgan, 1995).

In contrast to rodents, our current understanding of chemosensory predator recognition in bats is very poor. When bats inspect potential new roosts such as tree cavities, caves and rock crevices, olfaction appears to be the ideal sensory modality for assessing predation risk from 'smelly' mammalian predators. This is because, firstly, vision is of little use in dark roosts and echolocation is not well suited to distinguish motionless predators from other objects or the roost wall (T.D. and B.M.S., unpublished data). Secondly,

smell would yield information beyond revealing whether a predator is currently inside the roost. Even in the predator's absence, a bat could potentially use the sustained presence of olfactory cues to assess whether a roost is regularly visited by a predator. Generally, the sense of smell is well developed in bats and it plays a crucial role in bat behavioural ecology (Bloss, 1999). Olfaction is important for mother–infant, colony mate and species recognition (Gustin and McCracken, 1987; Defanis and Jones, 1995; Bloss et al., 2002; Caspers et al., 2009), for sex recognition and courting rituals (Voigt and von Helversen, 1999; Bouchard, 2001) and, in some bat species, also for locating and identifying food (Rieger and Jakob, 1988; Neuweiler, 2000; von Helversen et al., 2000; Luft et al., 2003). However, so far only a single study investigated the role of olfaction for assessing predation risk in bats. Boyles and Storm found that North American tree- and attic-roosting big brown bats (*Eptesicus fuscus*) do not avoid odour cues from raccoon (*Procyon lotor*) urine and black rat snakes (*Elaphe obsoleta*) (Boyles and Storm, 2007).

In the present study, we assessed for the first time olfactory predator recognition in a cave-dwelling bat species, the greater mouse-eared bat (*Myotis myotis*). Both foxes and several species of mustelids can be regularly encountered close to and in the bats' caves in our study area in northern Bulgaria (I. Borissov, personal communication). While mustelids may reach some places of the cave wall where bats could roost, and do predate on bats (Goodpaster and Hoffmeister, 1950; Mumford, 1969; Bekker, 1988; Tryjanowski, 1997; Sparks et al., 2000), foxes typically do not climb and will only impose a predatory threat to pups and weak bats that fall down from the ceiling.

The aim of this study was to test the hypothesis that cave-dwelling greater mouse-eared bats recognise potential roost predators by olfactory cues. We presented freshly caught bats in a Y-maze with TMT, 2-PT or the natural predator odour of a least weasel *versus* an unscented blank control. In separate experiments, the bats were exposed to the smell of basil or goat, serving as an acrid but otherwise neutral baseline control. We predicted that the bats would show an avoidance response and/or reduced locomotor and exploration activity when confronted with both synthetic and natural predator odours. We further predicted that they would not exhibit these responses towards the non-predator control odours and unscented blank controls.

MATERIALS AND METHODS

Animals

For this study, a total of 58 freshly caught, adult female greater mouse-eared bats (*Myotis myotis* Borkhausen 1797) were tested. All females were captured in August 2009 at the entrance of their roost cave in the district of Ruse, Northern Bulgaria. A harp trap was used to catch the bats in front of the roost entrance when they returned from foraging between 04:30 h and 06:00 h. Only non- and post-lactating adult females were chosen. The bats were put in separate cotton bags (15 cm × 20 cm) with an identification number and transferred to a keeping room at the Tabachka Bat Research Station of the Sensory Ecology Group (MPI Seewiesen, Germany), run in cooperation with the Directorate of the Rusenski Lom Nature Park. In the keeping room, both humidity and dark–light regime (dark phase from 21:00 h to 08:00 h) were set to mimic natural conditions. Bats were kept in the labelled cotton bags until experiments were performed the following night (approximately 15 h after catching). Before each experiment, the bats were provided with water and two mealworms (larvae of *Tenebrio molitor* Linnaeus 1758). All bats were released at the place of capture directly after the experiments were finished (approximately 20 h after capture).

Capture, housing and behavioural testing had no detectable impact on the bats' health and were conducted under license of the Ministerstvo na Okolnata Sreda i Vodita, Sofia and the RIOSV Ruse (license numbers 57/18.04.2006, 100/04.07.2007, 193/01.04.2009 and 205/29.05.2009).

Olfactory stimuli

As predator olfactory cues, we used TMT (2,4,5-trimethyl-3-thiazoline, PheroTec, Delta, Canada), 2-PT (2-propylthietane, PheroTec), and the natural odour of the least weasel (*Mustela nivalis* Linnaeus 1766). Synthetic basil (Basilikum bio DEMETER, Primavera life GmbH, Sulzberg, Germany) and the natural odour of domestic goat (*Capra aegagrus hircus* Linnaeus 1758) were used as acrid non-predator olfactory cues to control for a general response against pungent odours. We used DEP (diethylphthalate, Sigma-Aldrich, Steinheim, Germany) as a solvent for the dilutions of all odorants. Pure DEP served as blank control in the Y-maze arms without odour treatment. For both synthetic compounds, TMT and 2-PT, relatively high concentrations (TMT $1.8 \times 10^{-2} \text{ mol l}^{-1}$ and 2-PT $1.8 \times 10^{-4} \text{ mol l}^{-1}$) were presented to mimic the intense natural smell of fox or stoat, which is often found in bat caves. The olfactory detection threshold for TMT in rats is in the order of $10^{-15} \text{ mol l}^{-1}$, while several primate species, including humans, have TMT detection thresholds of 10^{-12} – $10^{-10} \text{ mol l}^{-1}$ (Laska et al., 2005). Given that bats' olfactory thresholds for short-chain alcohols, aldehydes and acids are about the same as that of humans (Neuweiler, 2000), we consider it very likely that the bats can detect the TMT concentration we used, which was 8 to 10 orders of magnitude above primate threshold. For the basil control odour, we tried to achieve the same subjective smell intensity (for a human observer) as for the synthetic predator compounds. This was best achieved by a 1:32 dilution (1 µl ethereal basil oil *versus* 32 µl DEP). Despite the high concentrations and strong intensities of the described synthetic olfactory cues, the odours were still limited to the treatment arm (for airflow generation, see below) and were not perceivable in the other maze arm to any of five non-smoking humans used as a reference. For all the synthetic compounds and the pure DEP control, 25 µl of the odorant solutions were pipetted on odourless cotton pads (diameter: ca. 2.5 cm; weight: ca. 0.22 g), serving as odour source.

For the natural predator odour, we sampled the scent of a freshly road-killed male least weasel by storing odourless cotton pads in a cotton bag together with the weasel. After 3 h, the weasel was removed and the cotton bag together with the scented cotton pads were stored at a temperature of -15°C for approximately 14 days. Domestic goat was chosen as a non-predator control species because of its pungent odour and its high abundance in the study region. Cotton pads were rubbed over the head, flanks and genital area of an individual male goat and afterwards also stored at -15°C . As blank control, we used unscented cotton pads, which had been stored in the same way as the weasel and goat olfactory cues. During all procedures involving the handling of olfactory cues and blank controls, sterile latex gloves were used.

Experimental set-up

All experiments were performed in a Y-maze, constructed from polyvinyl chloride (custom version of the Y Maze Arena 'Maus', Bioobserve, Bonn, Germany). The Y-maze had three symmetrical arms with dimensions 40 cm × 7 cm × 6 cm (arm length × arm width × wall height) and was covered with a Plexiglas lid (Fig. 1A). The starting arm had an inlet to put bats into the Y-maze. Each of the two choice arms had a terminal compartment (10 cm × 6.8 cm × 6 cm) that contained the odour source (scented or unscented cotton

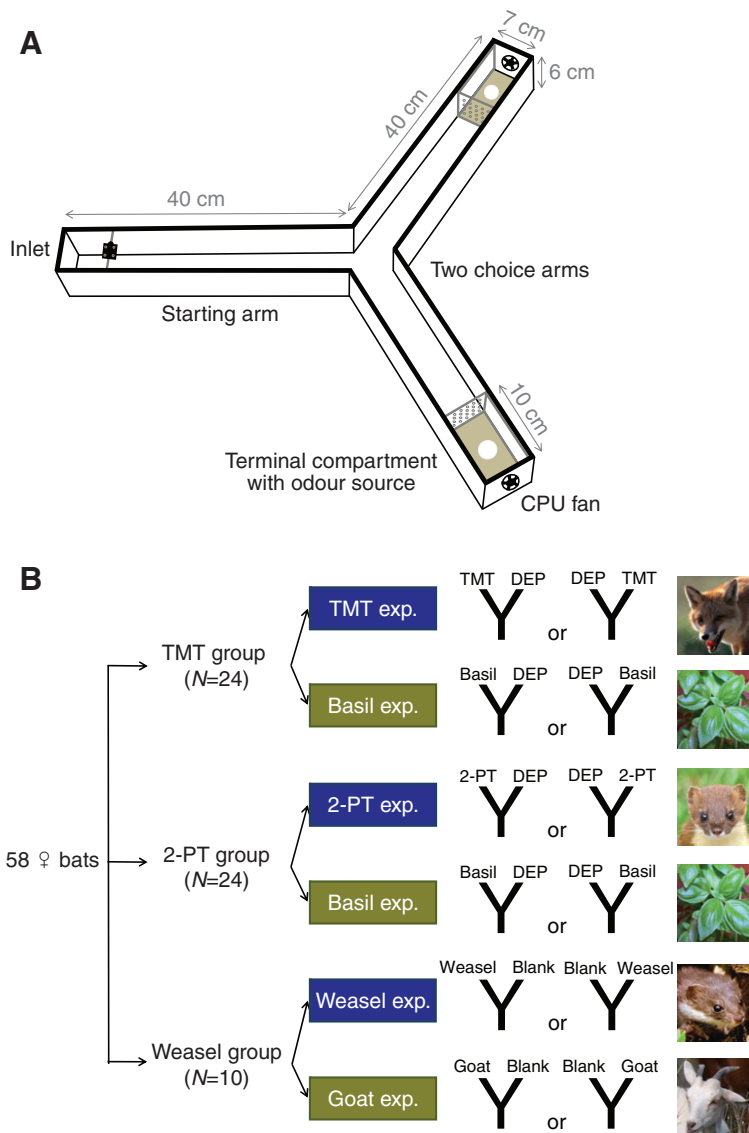


Fig. 1. Experimental set-up and design. (A) Schematic representation of the Y-maze. The starting arm had a valve to introduce bats into the maze (inlet). At the end of both choice arms, a scented (treatment) or unscented (control) cotton pad was presented in the terminal compartment. Two CPU fans provided a controlled airflow to carry odour into the choice arms.

(B) Experimental procedure. The 58 experimental subjects were divided into three groups. Each group was tested in one predator experiment (dark blue) and in one non-predator experiment (green). The assignment of treatment and control to the two choice arms as well as the order in which bats were exposed to predator and non-predator experiment were determined with a balanced, randomised test protocol. exp. = experiment; 2-PT = 2-propylthietane; DEP = diethylphthalate; TMT = 2,4,5-trimethyl-3-thiazoline. Predator photos courtesy of Dietmar Nill (red fox, *Vulpes vulpes*), Rollin Verlinde (stoat, *Mustela erminea*) and Karol Zub (least weasel, *Mustela nivalis*).

pads). The cotton pads were placed on odourless filter paper to prevent direct contact of the odour compounds with the Y-maze material, to avoid olfactory contamination. At the end of each choice arm, a CPU fan (MFB40H-12 SEPA brushless fan, SEPA Europe, Freiburg, Germany) was built in to provide a low-noise controlled airflow of approximately 281 min^{-1} , measured in the middle of each choice arm (air velocity meter TA410, TSATM, High Wycombe, UK). An array of holes in the division between terminal compartment and choice arm allowed the airflow to carry odour to the bats but prevented them from direct access to the odour source.

Experimental procedure

All experiments were performed during the natural activity period of the bats (at night between 22:00h and 04:00h). A maximum of six bats were tested per night. Each bat was exposed to two odour experiments (Fig. 1B), a 'predator experiment' (predator odour *versus* blank control) and a 'non-predator experiment' (neutral but acrid odour – basil or goat – *versus* blank control). The non-predator experiment served to assess a general baseline reaction to acrid but otherwise neutral odours. We ran the following three combinations of predator and non-predator experiments. (1) A group of 24 bats

got TMT *versus* pure DEP during the predator experiment and basil *versus* DEP during the non-predator experiment. This group of experimental subjects is referred to as the TMT group. (2) A second group of 24 bats were exposed to 2-PT *versus* pure DEP and again basil *versus* DEP. This is the 2-PT group. (3) A group of 10 bats was presented with natural weasel odour *versus* a blank cotton pad and with goat odour *versus* a blank cotton pad. This is the weasel group. Within groups, we labelled the experiments according to the applied olfactory cues (Fig. 1B). The choice arms with the olfactory cue will be referred to as 'treatment arm' and the other choice arm, with the blank control, as 'control arm'. We followed a balanced, randomised test protocol to determine the treatment arm for each trial and to define the order in which bats were tested in the predator and the non-predator experiment.

As stated above, each bat was provided with two mealworms and water prior to the beginning of each experiment. This served to ensure a standardised level of activity and motivation in the bats. Half a minute after putting the odour sources into the Y-maze, the bat was placed into the starting arm. The experiment started once the inlet was closed and lasted for 8 min thereafter. The six bats were tested in the same order in both odour experiments with a

break of approximately 90 min for each bat. After each trial, the Y-maze was cleaned with 70% alcohol and dried to remove all odour residues.

Data acquisition and behavioural analysis

Behavioural trials were filmed for online display and recorded for off-line analysis using an infrared (IR)-sensitive camera (DCR-TRV80E, Sony, Berlin, Germany). An IR lamp (IR spotlight IP65, Conrad, Hirschau, Germany) was positioned at approximately 3 m above the cross point of the Y-maze (point where two choice arms converge) to provide extra illumination for the camera. IR light is not visible for bats (Mistry and McCracken, 1990) and could therefore not have influenced the bats' behaviour.

All video data were analysed off-line and scored with event-recorder software (custom made by Andreas Bernauer and given to us by Markus Fendt of the University of Tübingen) by an observer who was not aware of the respective test conditions. Our aim was to score avoidance responses and/or reduced locomotor and exploration activity, as these behaviours are well-documented, adaptive anti-predator strategies (Kats and Dill, 1998; Apfelbach et al., 2005; Caro, 2005). We quantified the number of entries into and the total time spent in each maze arm. For the latter, we discriminated between time spent with passive and active behaviour. Passive behaviour encompassed sitting (with body movements such as head turning), self-grooming (characterised by licking) and motionless behaviour (immobile, crouched posture). Active behaviour included crawling and biting the holes in the division between terminal compartment and choice arms. In addition, we scored which of the two choice arms the bats entered first (first entry choice). We also noted the presence of faeces in different maze arms, as predatory stress in rodents is related to an increased number of faecal boli (Avanzi et al., 1998; Antoniadis and McDonald, 1999; Castilho and Brandao, 2001; Punzo, 2005). During the 8 min trials, all bats left the starting arm and entered at least one of the two choice arms.

Statistical analysis

For graphic display, the first three of the following parameters were expressed as percentages: (1) proportion of entries into the treatment arm *versus* the control arm (number of entries into both choice arms was set as 100%), (2) time spent in the treatment arm (again time in both choice arms was 100%) and (3) time spent showing active *versus* passive behaviours in the choice arms (here, active and passive behaviour in both choice arms add up to 100%). For definition of active and passive behaviours, see above. (4) As a measure of the bats' general locomotor and exploration activity, we counted the total amount of transitions between the different maze arms.

For statistical analysis, percentage data were transformed by applying an arcsine transformation to approximate normal distribution [$p' = \arcsin \sqrt{p}$, where p is a proportion (Zar, 1999)]. If the transformed data still deviated from normal distribution (Kolmogorov–Smirnov one-sample test: $P < 0.05$), non-parametric tests were applied on the rough percentage data. To test for avoidance behaviour with respect to odour treatment, we analysed whether the proportion of entries and of time spent in the treatment arm deviated significantly from the 50% chance level that resulted from the two choice arms [one-sample t -test; chance level $\arcsin(0.5)$]. Within each test group, we used paired t -tests to compare the bats' reactions from the respective predator and non-predator experiment.

Statistical tests were run in Systat 11 (Systat Software, Inc., Richmond, CA, USA) and SPSS 16.0 for Windows (SPSS, Inc.,

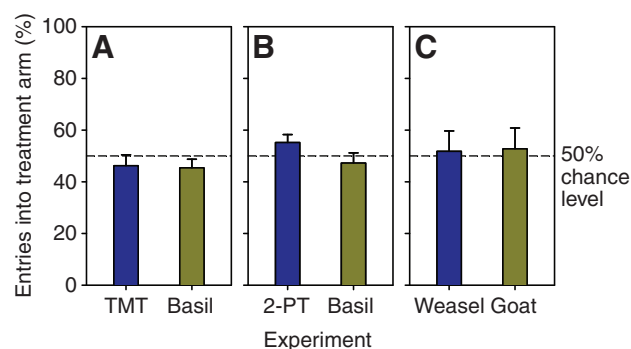


Fig. 2. Proportion of choice arm entries that were aimed at the treatment arm during predator experiments (dark blue bars; means + s.e.m.) and non-predator experiments (green bars). Chance level was 50% (dashed line). (A) Data for the 2,4,5-trimethyl-3-thiazoline (TMT) group ($N=24$) that was tested in the TMT experiment (TMT *versus* control) and in the basil experiment (basil *versus* control). (B) 2-Propylthietane (2-PT) group ($N=24$) with data for the 2-PT and the basil experiment. (C) Weasel group ($N=10$) with data for the weasel experiment and the goat experiment. The proportion of entries into the treatment arm did not differ from chance level for any of the test groups and experiments (one-sample t -test, all $P > 0.1$; for details, see text).

Chicago, IL, USA), and a probability of $P < 0.05$ was taken as significance level. Means are displayed in all graphs and error bars represent standard errors of the mean (s.e.m.).

RESULTS

In Figs 2–4, panel A always displays the results obtained from the TMT group, panel B the results for the 2-PT group and panel C the results from the weasel group. Within each panel, the dark blue bars represent the bats' reaction in the predator experiments (TMT, 2-PT or weasel, respectively) whereas the green bars represent the reactions of the same individuals in the non-predator experiments (basil or goat).

Neither the predator smell nor the non-predator olfactory cues had a significant effect on the bats' propensity to enter the treatment arms (Fig. 2). This is evidenced by the fact that the proportion of entries into the treatment arm *versus* the control arm did not deviate from a 50% chance level for any of the six experiments (one-sample t -tests, all $P > 0.1$). Within each experimental group, the proportion of entries into the treatment arm did not differ between the predator experiment and the non-predator experiment (paired t -test: all $P > 0.2$). As an example, the TMT-group bats (Fig. 2A) entered the treatment arm as frequently in the TMT experiment (blue bar) as they did in the basil experiment (green bar). Similar results were obtained for the time spent in the treatment arms (Fig. 3). Again, time allocation to the treatment arm did not deviate from the 50% chance level in any of the six experiments (one-sample t -test, all $P > 0.3$), and did not differ for predator and non-predator experiments for any of the three test groups (paired t -tests, all $P > 0.3$).

The type of olfactory cues had also no significant effect on the general locomotor and exploration activity of the bats, which we measured as the total number of transitions between all three maze arms (Fig. 4). In all six experiments, most bats crawled back and forth between the three different maze arms repeatedly within each 8 min trial. Per trial, the number of transitions between arms averaged to 20.28 ± 1.63 (second order mean \pm s.d.) overall. For all three test groups there was no difference in the number of arm transitions between predator and non-predator experiments (Fig. 4,

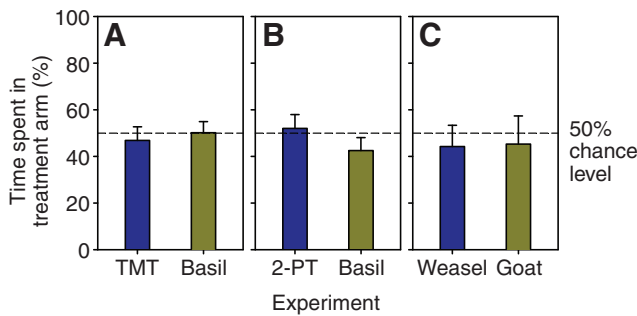


Fig. 3. Proportion of time spent in the treatment arm during predator experiments (dark blue bars; means + s.e.m.) and non-predator experiments (green bars). Chance level was 50% (dashed line). (A) Data for the 2,4,5-trimethyl-3-thiazoline (TMT) group ($N=24$) that was tested in the TMT experiment (TMT versus control) and in the basil experiment (basil versus control). (B) 2-Propylthietane (2-PT) group ($N=24$) with data for the 2-PT and the basil experiment. (C) Weasel group ($N=10$) with data for the weasel experiment and the goat experiment. The time spent in the treatment arm did not differ from chance level for any of the test groups and experiments (one-sample t -test, all $P>0.3$; for details, see text).

compare blue and green bars in each panel; Wilcoxon signed rank tests, all $P>0.4$).

The bats showed significantly more active than passive behaviour in the treatment arm during TMT and 2-PT experiments (Wilcoxon signed rank test; TMT experiment: $N=24$, $Z=-2.62$, $P=0.009$, Fig. 5A; 2-PT experiment: $N=24$, $Z=-2.06$, $P=0.040$, Fig. 5B). In the control arm, the proportions of active versus passive behaviour did not differ [Fig. 5A,B, blank control (DEP), all $P>0.07$]. These results indicate that the bats specifically increased their activity when presented with the synthetic predator olfactory cues TMT and 2-PT. However, the bats of the TMT group showed more active than passive behaviour also in the non-predator experiment, for both the treatment (basil, $N=24$, $Z=-2.37$, $P=0.018$, Fig. 5D) and the control arms (DEP, $N=24$, $Z=-2.49$, $P=0.013$, Fig. 5D). For the 2-PT group, there was no difference in the amount of active and passive

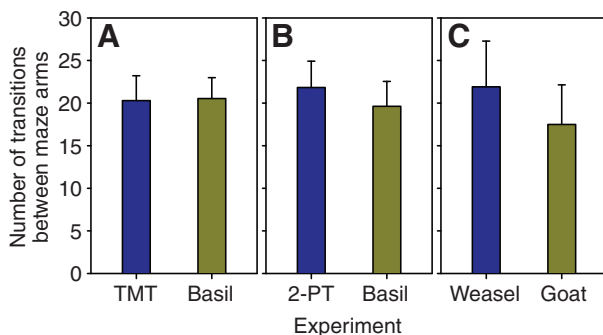


Fig. 4. Number of transitions between maze arms during predator experiments (dark blue bars; means + s.e.m.) and non-predator experiments (green bars). The number of transitions between maze arms was taken as a measure of general locomotor and exploration activity. (A) Data for the 2,4,5-trimethyl-3-thiazoline (TMT) group ($N=24$) that was tested in the TMT experiment and in the basil experiment. (B) 2-Propylthietane (2-PT) group ($N=24$) with data for the 2-PT and the basil experiment. (C) Weasel group ($N=10$) with data for the weasel experiment and the goat experiment. The number of arm transitions did not differ significantly between predator and non-predator olfactory cues (Wilcoxon signed rank test: $P>0.4$ for all three bat groups; for details, see text).

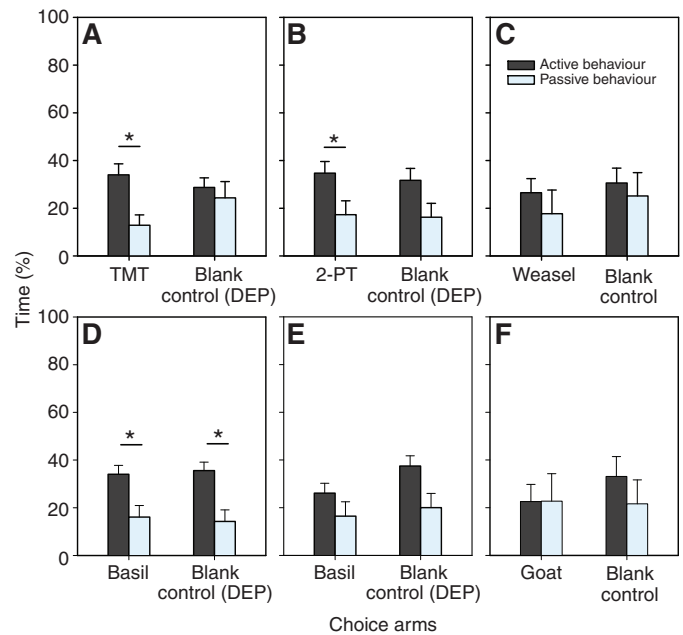


Fig. 5. Proportion of time spent in the treatment arm and the control arm showing either active behaviour (black bars; means + s.e.m.) or passive behaviour (blue bars). The first row of panels gives data for the predator experiments: (A) 2,4,5-trimethyl-3-thiazoline (TMT) experiment ($N=24$), (B) 2-propylthietane (2-PT) experiment ($N=24$), and (C) weasel experiment ($N=10$). The second row of panels shows the data for the corresponding non-predator experiments: (D) basil experiment with the TMT group, (E) basil experiment with the 2-PT group and (F) goat experiment with the weasel group. An asterisk indicates $P<0.05$ (Wilcoxon signed rank tests; for details, see text). DEP = diethylphthalate.

behaviour in the non-predator experiment (basil, $N=24$, $Z=-1.61$, $P=0.108$; DEP, $N=24$, $Z=-1.67$, $P=0.094$, Fig. 5E). In the weasel group, there was no difference in the amount of active and passive behaviour in any of the experiments (Fig. 5C,F, all $P>0.3$).

Finally, the type of the olfactory stimuli did not affect which maze arm the bats entered first (Pearson's χ^2 -tests, $P>0.4$ for all three experimental groups). It also did not affect the proportion of bats that deposited faecal boli, bit the maze division, showed sitting behaviour, self-grooming or motionless behaviour (data and results from Pearson's χ^2 -tests in Table 1).

DISCUSSION

In contrast to our prediction, we did not find any evidence for an avoidance response, reduced locomotor or exploration behaviour of bats that were confronted with synthetic predator odours (TMT, 2-PT) or natural weasel scent. Furthermore, first entry choice and faeces deposition were not affected by predator olfactory cues. Rather, the bats showed the same indifferent reaction as to the non-predator odours (basil and goat).

While our results, based on a total sample of 58 individuals, clearly showed no fear response of bats to mustelid and fox olfactory stimuli, many other studies found fear-inducing effects of these olfactory cues on rodents and other small mammals (reviewed in Apfelbach et al., 2005). For example, TMT, the synthetically derived component of fox faeces, innately induces avoidance, freezing behaviour and other defensive responses in rats and mice (Wallace and Rosen, 2000; Fendt et al., 2005; Fendt and Endres, 2008). The synthetic substance derived from mustelid

Table 1. Number of individual bats showing the listed specific behaviours during predator and non-predator experiments

Behaviour	N=24 (total)			N=24 (total)			N=10 (total)		
	TMT	Basil	P-value	2-PT	Basil	P-value	Weasel	Goat	P-value
Faeces deposition	10	13	0.532	9	13	0.394	1	4	–
Active behaviours									
Biting	3	5	–	5	5	1.000	3	3	–
Passive behaviours									
Sitting	16	13	0.577	18	16	0.732	9	9	1.000
Self grooming	12	11	0.835	10	10	1.000	6	6	1.000
Motionless	8	13	0.275	7	8	0.796	6	4	0.527

P-values from Pearson's χ^2 -tests are tabulated. – sample size too small for statistical testing. TMT, 2,4,5-trimethyl-3-thiazoline; 2-PT, 2-propylthietane.

anal gland secretions, 2-PT, elicited fearful behavioural responses in rats, voles, pocket gophers and brushtail possums (Sullivan et al., 1988a; Sullivan et al., 1988b; Sullivan et al., 1990; Heale and Vanderwolf, 1994; Woolhouse and Morgan, 1995). Furthermore, a variety of rodent species were affected by natural least weasel odour, including different odour sources such as faeces (Bolbroe et al., 2000; Koivisto and Pusenius, 2003), anal gland secretion (Stoddart, 1980), bedding (Fuelling and Halle, 2004), cage wash (Borowski, 2002) and a whole animal (Jedrzejewski and Jedrzejewska, 1990; Korpimaki et al., 1996; Koivisto and Pusenius, 2003). It is thus somewhat surprising that the greater mouse-eared bats did not show any fearful reaction to the same type of predator olfactory cues, even though direct contact with a mustelid or fox would result in death. Furthermore, greater mouse-eared bats fly close to the ground when foraging and even land briefly to pick up arthropods (Arlettaz, 1996). Unlike other bat species hunting in free air space or above water surfaces, they are thus potentially vulnerable to ground-based mammalian predators not only in and around roosts but even during foraging. In the following, we discuss some possible and mutually non-exclusive explanations for the fact that the bats' behaviour was not affected by the predator odours.

Firstly, we have to consider whether the bats could at all perceive the olfactory cues presented during our experiments. The TMT concentration we used was 8 to 10 orders of magnitude above primate threshold and even 13 orders of magnitude above rodent threshold (see Materials and methods) and – to a human observer – mimicked the intense natural smell of foxes that is often detectable in caves. As olfactory thresholds for several classes of chemical substances are comparable for bats and humans (Neuweiler, 2000), we are confident that the presented predator smell was way above perception threshold for the bats. Another indication comes from the fact that during TMT and 2-PT experiments, the bats displayed more active than passive behaviour in treatment arms but not in control arms. This might be a specific reaction and hence provide evidence that the bats did perceive the predator odours but did just not show avoidance or fearful behaviour in response. Yet, this interpretation requires a cautionary note, as increased active behaviour was also found in both choice arms during the non-predator experiment in the TMT group.

Secondly, relying on olfactory cues for predator recognition comes at the advantage of assessing past and current presence of a predator but at the same time provide less temporal resolution and thus less specific information about predation risk, compared with visual and auditory cues (Bouskila and Blumstein, 1992). Thus, the bats may ignore olfactory cues and rely more on vision, echolocation or audition for predator detection. The limited number of bat studies that assessed these types of predator recognition provided largely

negative or equivocal evidence, however (Fenton et al., 1994; Kalcounis and Brigham, 1994; Petrzelkova and Zukal, 2001; Petrzelkova and Zukal, 2003; Baxter et al., 2006) (T.D. and B.M.S., unpublished).

Thirdly, bats often select roosts and perches inside roost caves or trees in a way that predation risk is minimised (Ruczynski and Bogdanowicz, 2005). For instance, bats may avoid some predators by roosting high enough above the ground (Riskin and Pybus, 1998; Hutchinson and Lacki, 2000), in narrow crevices (Vonhof and Barclay, 1997; Riskin and Pybus, 1998) or in darker parts of the roost where visually oriented predators cannot operate (Riskin and Pybus, 1998). As long as such primary defences suffice to minimise the accessibility of roosting spots, bats might ignore predator olfactory cues. As mustelids, canids and felids regularly visit or even inhabit large bat caves, it might even be maladaptive not to use or to desert a cave, just because scent indicates a predator is or was somewhere in the cave. In addition to predation risk, many other factors affect roost choice in bats, e.g. food availability, social organisation, microclimate and roost structure (Medway and Marshall, 1972; Findley and Wilson, 1974; Kunz, 1982; Riskin and Fenton, 2001). These may play a more decisive role for roost assessment and choice than predation risk; especially in areas where suitable roosts are sparse.

Fourth, specific predator-recognition mechanisms might not have evolved in bats because of low actual predation pressure. Flying in relatively predator-safe airspace, coloniality and roost selection (Barclay et al., 1982; Fenton et al., 1994; Lewis, 1995; Jenkins et al., 1998; Ferrara and Leberg, 2005), clustering in large aggregations and mass emergence (Fenton et al., 1994; Jones and Rydell, 1994; Kalcounis and Brigham, 1994; Speakman et al., 1995; Petrzelkova and Zukal, 2001) and, above all, the nocturnal lifestyle of bats (Rydell and Speakman, 1995; Speakman, 1995) largely reduce the chance of any individual bat to be attacked by a predator. Moreover, bats are mainly confronted with unspecialised predators that only consume bats when opportunity exists (Fenton et al., 1994; Sparks et al., 2000). However, individual predatory birds (Ruprecht, 1979; Schmidley, 1991; Yancey et al., 1996; Estok et al., 2010) and martens (Bekker, 1988; Tryjanowski, 1997) can locally specialise in catching bats in or at roosts and hibernacula. As response to a high local predation pressure, bats may learn to associate certain predators with danger (Hanson and Coss, 1997; Griffin, 2004; Caro, 2005). Fenton et al., for example, demonstrated in a field study that bats change their behaviour in response to real attacks by predators (Fenton et al., 1994). Such an associative learning process might thus involve direct experience with a predator (Kramer and Von St. Paul, 1951) and distress calls exhibited by attacked conspecifics (Conover and Perito, 1981; Mateo and Holmes, 1997; Russ et al., 1998).

Hypothetically, colony size may influence the bats' responses towards predator odours, as larger colonies provide a better protection for the individual by 'dilution in numbers' than smaller colonies (Caro, 2005). All of our 58 test subjects stem from the same large maternity colony and thus we could not test for a colony size effect. This question might be interesting for future studies.

To the best of our knowledge, this is the first study investigating the importance of olfaction for recognising potential roost predators in a cave-dwelling bat. The synthetic substances TMT and 2-PT as well as natural least weasel odours are known to elicit fear responses in rodents, in part even innately (Apfelbach et al., 2005), but effects of these odours were never before tested on bats. The clear result that wild greater mouse-eared bats did not show any fear response towards mustelid and fox odours was unexpected. However, our results were consistent with those reported by Boyles and Storms where tree-dwelling big brown bats did not avoid olfactory cues of raccoons and black rat snakes (Boyles and Storms, 2007). Certainly, more research is needed to test for the generality of our findings across bats and across different potential roost predator species such as domestic cats (*Felis catus*), squirrels and, in the tropics, bat-eating bats. Furthermore, predator odours from the same species but from different sources, e.g. derived from fur, skin, faeces, urine or scent glands, can elicit different responses in prey animals (Apfelbach et al., 2005) and should therefore be tested too. In addition, future research is required to better understand the importance of prior experience with a predator for the reaction of bats to predator cues. Finally, comparing predator recognition between individuals from small and large colonies may provide valuable insights into the as yet poorly understood mechanisms of predator recognition in bats.

LIST OF ABBREVIATIONS

2-PT	2-propylthietane
DEP	diethylphthalate
TMT	2,4,5-trimethyl-3-thiazoline

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