

Finding prey by associative learning in gleaning bats: experiments with a Natterer's bat *Myotis nattereri*

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I show that a Natterer's bat (*Myotis nattereri*) was operantly conditioned to echo cues from a large object; in this case a round bowl full of mealworms. In a subsequent choice experiment the bat preferred the empty, round bowl over an unknown, quadratic bowl filled with prey. I suggest that the quick but transient learning of cues indicating prey rich habitat patches might be adaptive for bats hunting in cluttered environments, where they can often not directly detect prey using echolocation. Therefore, it might be an additional foraging strategy of some gleaning bats to search for specific structural cues indicating a high probability of prey being present.

Key words: *Myotis nattereri*, prey perception, echolocation, learning, operant conditioning, gleaning, foraging

INTRODUCTION

Bats may have difficulty using echolocation to find prey on surfaces such as vegetation, because echoes from prey will be masked by echoes reflecting from the vegetation (e.g., Schnitzler and Kalko, 2001). Insectivorous bats that hunt in such situations often appear to rely on passive listening for insect sounds to detect prey (reviewed in Schnitzler and Kalko, 2001, but see also Schmidt *et al.*, 2000). Wing morphometry, fecal analyses, field observations and behavioral experiments indicate that Natterer's bat, *Myotis nattereri* (Kuhl, 1817) — family Vespertilionidae, forages close to vegetation (Norberg, 1981; Gregor and Bauerova, 1987; Shiel *et al.*, 1991; Beck, 1995; Arlettaz, 1996; Swift, 1997; Siemers *et al.*, 1999; Siemers and Schnitzler, 2000). Behavioral experiments

show that *M. nattereri* uses echolocation rather than passive listening for detecting prey close to the substrate (Siemers and Schnitzler, 2000; Swift and Racey, 2001). Siemers and Schnitzler (2000) reported that these bats could find prey very close to, but not directly on vegetation when echoes from prey were probably completely overlapped and hence masked by those from vegetation. Swift and Racey (2001) clearly showed that *M. nattereri* is able to glean prey from vegetation.

Here I report the observation of the accidental operant conditioning of a Natterer's bat to a 'prey specific situation' and details of some experiments I conducted to explore this conditioning. My findings suggest that gleaning bats might in some cases use an additional strategy for detecting prey: they might search for specific structural cues indicating a high probability of prey being

present at a given site, i.e. the bats might detect prey indirectly by associative learning. My observations are very preliminary because they are of only one individual. However, they are noteworthy because they emphasize the importance of echolocation for prey detection in this bat species and suggest that learning to recognize structural cues for rich prey patches might be important when hunting in clutter.

MATERIALS AND METHODS

At the end of August 1998 four *M. nattereri* (three non-lactating females and one juvenile male) were taken from roosts under license from the regional environmental authority (Regierungspräsidium Tübingen). During the experiments the bats flew freely in a flight tent measuring $7.5 \times 3.5 \times 2.5$ m. All four bats captured tethered mealworms close to a clutter screen (Siemers, 2000). By chance, one of the bats was conditioned to a 'prey specific situation' and accidentally learned to glean mealworms from a bowl. Here I report data on the operant conditioning of this one animal. All bats were released at the site of capture at the end of the experiments.

Echolocation calls were recorded using a time expansion system (custom-made; Department of Animal Physiology, University of Tübingen) and analyzed with a color spectrograph (SonaPC; B. Waldmann, University of Tübingen; FFT 256 points, Hanning-window). For a detailed description of recording and analysis procedure and equipment see Siemers and Schnitzler (2000). The behavior of the bat was video-taped using a CCD video camera (Sanyo, VC 1950; 50 half-frames/s), an Orion Combi 600 LCD recorder and infrared stroboscopic illumination (custom-made; Department of Animal Physiology, University of Tübingen).

I presented mealworms to the bats in two plastic bowls, a round, white one (12 cm diameter, 5 cm high) and an orange, square one (11 × 11 cm, 8 cm high). After the initial operant conditioning, bowls and mealworms were placed on a smooth cardboard surface (22 × 30 cm) about 50 cm in front of an artificial clutter-screen (polypropylene carpet covered with 5 mm diameter latex/chalk half-spheres spaced approx. 12 mm apart). The area surrounding the flight tent was dimly lit.

I defined an 'attack' of the bat to a bowl as the bat touching the bowl with its uropatagium. The bat often continuously hovered above and around a bowl while

repeatedly 'attacking' it; a behavioral sequence I termed 'hover-and-attack-bout'.

RESULTS

When landing on a cage where its conspecifics were housed, a female *M. nattereri* lost its balance and slid into a white round bowl next to the cage. The bowl contained about 250 mealworms. The bat grabbed a mealworm and flew off. The bat returned in a few seconds and approached the bowl, striking its uropatagium against the rim of the bowl. The bat repeated the approach flight three times, retrieving one or two more mealworms. I then moved the bowl in the flight tent and started video-taping the bat's behavior. When the bat flew by the bowl at the new position, it hovered around it for 240 s without touching it. Over the next 60 min, the bat spent 650 s in eight 30 to 150 s long hover-and-attack-bouts above and around the bowl. The bat 'attacked' the bowl 101 times by touching the inner or outer side of the rim with its uropatagium. When the bat touched the inner side of the bowl, it sometimes successfully caught a mealworm in the uropatagium. The bat transferred the mealworm from the uropatagium to the mouth and flew away chewing. During each of these sessions the bat continuously emitted short, broadband echolocation signals and, prior to touching the bowl, emitted a terminal buzz. It never landed in the bowl nor did it take mealworms directly with its mouth.

I then removed the bowl and put three alive and moving mealworms onto the smooth cardboard surface where the bowl had been. The bat inspected the site for 100 s without landing or touching the surface or catching any mealworms. When I placed the round bowl (now without mealworms) back onto the cardboard, the bat 'attacked' the empty bowl (13 times in 120 s). I filled the bowl again with meal-

worms and the bat ‘attacked’ the bowl another 28 times (three hover-and-attack-bouts with total duration of 180 s). Subsequently I initiated a choice experiment whereby at the opposite edges of the cardboard surface, the round bowl (empty) was presented simultaneously with the square one, new to the bat but filled with about 250 live mealworms. The rustling mealworms were clearly audible at least to my human ear from where the bat hovered over the experimental set up. The bat was tested during two hover-and-attack-bouts in this choice experiment (duration of bouts 110 s and 130 s, respectively). The position of the bowls was exchanged between the two bouts. While 20 ‘attacks’ were directed at the round, empty bowl, only two (unsuccessful) ‘attacks’ occurred at the quadratic one with mealworms (Fig. 1). The bat significantly preferred the empty bowl as a target over the square one ($\chi^2 = 14.7$, $d.f. = 1$, $P < 0.001$).

In the next night, I again presented the round, empty bowl on the cardboard. The bat ‘attacked’ three times in one 20 s hover-and-attack-bout and then lost interest at which point I concluded the experiment.

DISCUSSION

After one accidental experience, an experimental bat learned to associate the round bowl with prey. The bat never attacked mealworms on the cardboard where the round bowl had been, and rarely did it look for mealworms in the square bowl that was unfamiliar to it as a feeding site. But the bat readily and repeatedly tried to retrieve prey from the round bowl, making attempts to take prey even when the bowl was empty. The evidence suggests that the bat was not perceiving the mealworms themselves but was operantly conditioned to the bowl as an indication of prey. This interpretation is supported by the fact

that the bat sometimes touched the bowl’s outer side where no mealworms were attainable. I hypothesize that the bat specifically recognized the bowl but then ‘attacked’ it randomly, being successful in some instances only. The recognition of the bowl appeared to be independent of its location. The site where the bowl had been did not trigger ‘attacks’, even when prey was present. That is, the bat was not conditioned to a spatial location. Passive acoustic, olfactory or visual cues did not appear to be sufficient to elicit an attack by the bat. I hypothesize that the bat was conditioned to echo-cues encoding the round bowl. However, the use of visual information cannot be completely ruled out. My findings support the hypothesis that echo-information plays a key role for prey perception in *M. nattereri* whereas passive cues seem to be less important (Siemers and Schnitzler, 2000; Swift and Racey, 2001).

It is intriguing that the bat gave up ‘attacking’ the empty bowl quite quickly in the second night, after persistently ‘attacking’ it in the first night. Possibly the association between bowl echo cues and prey was

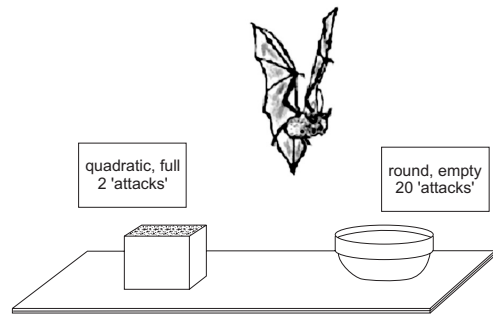


FIG 1. In a choice experiment a Natterer’s bat was presented with a round bowl it had been operantly conditioned to and with an unfamiliar, quadratic bowl. In the experiment, the round bowl was empty and the new, quadratic one was full of mealworms providing passive acoustic (rustling), and possibly olfactory and visual cues. The bat preferred the previously rewarded round bowl over the new, quadratic bowl filled with prey ($\chi^2 = 14.7$, $d.f. = 1$, $P < 0.001$; $n = 22$)

weakened over the day and then dropped, because the reinforcement, i.e., prey, was missing. I suggest that the quick but transient learning about prey rich patches might be adaptive for bats hunting in cluttered environments, where they can often not directly detect prey using echolocation. In a bat's foraging area, e.g., a certain plant species might be ephemerally infested by phytophagous insects or be a preferred night roost to certain arthropods. If prey density is high, random 'attacks' might be rewarding even when these arthropods are not directly detectable for the bats. Operant conditioning to specific plant's foliage or bark structure might trigger such random 'attacks'. The echo cues of these structural targets then would serve as indirect cues to prey. It is possible that tactile information transduced by the hairs fringing the outer edge of the uropatagium may allow *M. nattereri* to detect prey at very close range during such random 'attacks' (Horáček and Hanák, 1984; Arlettaz, 1996).

Obviously, my very preliminary observation is only a first indication of a possibly important additional foraging strategy of some gleaning bats: searching for specific structural cues indicating a high probability of prey being present. More extensive experimental studies as well as field observations are needed to clarify whether and how frequently bats use echo cues of structural targets to find prey rich patches. It already is known for a long time that echolocating bats are able to discriminate objects of different shapes and surface-structured targets, also during flight (e.g., *Myotis lucifugus* — Griffin *et al.*, 1965; *Vampyrum spectrum* — Bradbury, 1970; *Eptesicus fuscus* — Simmons and Vernon, 1971; *Myotis myotis* — Habersetzer and Vogler, 1983). Schmidt *et al.* (2000) recently reported that the gleaning carnivorous *Megaderma lyra* even uses echolocation to directly assess prey items presented on sub-

strate. Further, it has been shown that bats learn the location of (formerly) prey rich sites and direct 'random attacks' to these locations (*Noctilio leporinus* — Schnitzler *et al.*, 1994; *Myotis bechsteinii* — Staden, 1995). There also are examples of bats habitually foraging at potentially prey rich sites and structures such as cow sheds (*Myotis emarginatus* — Krull *et al.*, 1991), street lamps (e.g., Rydell, 1992) or insect light traps (*Myotis septentrionalis* — Miller and Treat, 1993). In these cases, it is not clear, however, whether the bats have learned to associate situation or site specific cues (light, echo cues, location etc.) with a high probability of encountering prey or whether they just detect their prey directly. I suggest that indirect (echo) cues might be important especially for gleaning bats when hunting for prey in clutter. Apart from *M. nattereri*, other gleaning species, such as the European *M. emarginatus* and the Nearctic fringed myotis (*M. thysanodes*), would be promising candidates for further studies.

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