Northern bats, *Eptesicus nilssonii*, use vision but not flutter-detection when searching for prey in clutter

Johan Eklöf, A. Monica Svensson and Jens Rydell

We investigated the detection cues used by the aerial-hawking bat *Eptesicus nilssonii* foraging in a cluttered environment. The bats can detect and attack rapidly moving targets within the clutter, i.e. below grass panicles, by using prey motion as a cue. Stationary objects are attacked only above the grass, but still within the clutter overlap zone. To test if the bats were guided by flutter from moth wings or by vision when searching for stationary targets, they were presented with male ghost swifts mounted on top of steel wires. There was no difference in attack frequency on live, fluttering moths compared to dead and spread ones. However, when comparing white and dark moths, we found a significantly higher attack frequency on white ones. As the attacks always were guided by echolocation calls, we hypothesize that northern bats, at least in the initial search phase, use visual cues as a complement to detect stationary ghost swifts.

J. Eklöf, A. M. Svensson and J. Rydell, Zoology Dept, Göteborg Univ., Box 463, SE-405 30 Göteborg, Sweden (johan.eklof@zool.gu.se).

When searching for insects in the vicinity of vegetation, echolocating bats have to separate the relatively weak echoes of the prey (target) from the massive echoes of the acoustically more complicated background (clutter). This task is fundamental for bats, but, nevertheless, detection of prey in clutter seems to be a serious problem for those catching airborne prey (aerial-hawking) (Kalko and Schnitzler 1993, Rydell 1998), as well as those catching prey from substrates like the ground or leaves (gleaning) (Arlettaz et al. 2001).

Bats of the families Rhinolophidae, Hipposideridae and Mormoopidae detect prey by using constant-frequency (CF) echolocation pulses, which are Doppler shifted against fluttering targets such as flying insects. The Doppler shifts allow separation of prey and clutter echoes in the frequency domain by means of specializations in the inner ear and the brain (Schnitzler 1987, Neuweiler 1990). This detection system is considered an adaptation that allows efficient detection of prey in clutter (Fenton et al. 1995). In contrast, most insectivorous bats, including those of the family Vespertilionidae, use only frequency-modulated (FM) echolocation pulses and they also lack the apparent auditory specializations for detection of Doppler shifted echoes. Nevertheless, laboratory experiments have suggested that some of these bats, i.e. *Pipistrellus stenopterus* and *Eptesicus fuscus*, also can detect Doppler shifted echoes from fluttering targets (Sum and Menne 1988, Roverud et al. 1991), presumably by means of a different, largely unknown, technique.

The visual sensitivity in some echolocating bats (e.g. *Eptesicus fuscus*) remains good in low illumination, indicating that they are able to use vision during the night (Ellins and Masterson 1974). However, it is not known if and how visual cues are used for prey detection, except in a few cases. The gleaning bat *Macrotus californicus* (Phyllostomidae) locates prey on the ground by vision (Bell 1985), while *Nyctophilus gouldi* and *N. geoffroyi* (Vespertilionidae) that employ both gleaning and aerial-hawking tactics, use vision only

---

when pursuing flying prey (Grant 1991). It has also been suggested that other aerial-hawking bats, such as *Craseonycteris thonglongyai* (Craseonycteridae) and *Taphozous georgianus* (Emballonuridae), use vision when foraging, by making use of the bright sky at dusk, against which insects are seen as silhouettes (Pettigrew 1980).

The purpose of this study was to examine whether aerial-hawking vespertilionid bats use supplementary cues consisting of a) flutter-detection and b) vision when searching for prey in clutter. We made use of a natural foraging situation, which has been studied and described in detail earlier (Andersson et al. 1998, Rydell 1998, Jensen et al. 2001). In short, it consists of a group of male ghost swifts *Hepialus humuli* (Lepidoptera: Hepialidae) that swarm in stationary display flight over and among grass (a hayfield) at dusk. These moths are large (wingspan ca 6 cm), silvery white, and, because they lack ultrasonic hearing, cannot detect bats at a distance (Rydell 1998). They are intensively exploited by aerial-hawking bats, usually groups of *Eptesicus nilssonii* (Vespertilionidae), patrolling over the field.

Materials and methods

Study sites

We conducted the tests at three known ghost swift leks in southern Sweden (province of Västergötland, 57°N) from 30 May to 8 June 2000 and 18 June to 28 June 2001. The three sites consisted of 1–3 ha open hayfields, surrounded by farmland and forest patches (Andersson et al. 1998, Rydell 1998, Jensen et al. 2001). Grass (mainly *Phleum pratense*) and herbs (e.g. *Trifolium* spp. and *Ranunculus* spp.) at a height of approximately 0.5–1.0 m dominated the vegetation in the hayfields.

Observation techniques

We observed the bats (*E. nilssonii*) both visually and with bat detectors (Pettersson D-200 and D-960, Pettersson Elektronik AB, Uppsala, Sweden; Ahlén 1981) from dusk until midnight (i.e. 2300–0100 Central European Summer Time). The bats could be observed almost constantly, as they circled over the field. However, we focussed our observations on the experimental area, and we did not attempt to follow individual bats for extended periods. As far as we could observe, neither the bats nor the naturally flying moths were disturbed by our presence, presumably because we consistently avoided using artificial lights. The bats were not individually marked and had not been captured by us.

Experiment with rapidly moving targets

To imitate insects moving rapidly among the clutter, we used a homemade catapult to fire 30 mm diameter paper marbles. The marbles were fired horizontally ca 5 m in front of patrolling bats. Because there were many bats hunting over the field, we assume that several bats were involved in the experiment. To test if the bats use visual cues when searching for moving targets, we presented white and black marbles in random order. The marbles were also shot at different heights (ca 0.1 and 1.0 m above the vegetation, respectively). Both heights were within the bats' clutter overlap zone, the extent of which depends on the pulse duration, and typically extends up to 1.5 m above the vegetation in this particular foraging situation (Jensen et al. 2001).

From video-taped sequences of fired marbles, we calculated that they were potentially detectable to the bat (i.e. remaining above the vegetation) for 0.5–0.8 s when shot from the higher level and about half of this time when shot from the lower level. The longer durations are comparable to the time that naturally flying *H. humuli* males spend above the grass panicles during vertical display "jumps", when they are most often captured by the bats, and it thus attempts to imitate the natural foraging situation (Rydell 1998, Jensen et al. 2001). We counted the number of capture attempts on black and white marbles, respectively.

Experiments with stationary targets

To test if the bats were guided by flutter from moth wings or by vision, when searching for stationary targets, they were presented with dead or live male ghost swifts, mounted, using a small drop of cyanoacrylate glue, on top of 5 mm steel wires, which were bent and blunted at the end (to avoid hurting the bats). We made pairwise presentations of mounted moths in hayfields, where natural *H. humuli* leks occurred, so that the bats flying over the field had access to both mounted and naturally flying prey. For the flutter detection experiment we used a live, fluttering moth presented beside a dried, spread one, i.e. one that did not flutter, but which had the same size and colour as the live one. For the vision experiment, we used two dead and spread moths, one of which was mounted with the white (dorsal) side up, and the other with the dark grey (ventral) side up, assuming that the acoustic image of either side was the same to the echolocating bats.

We presented the moths 1–2 m apart, and we usually also presented an empty wire as a control. We shifted the positions of the targets ca 1 m in random directions, following each attack from a bat or after 5 min, if no attack had occurred by then, so that the bats were prevented from memorizing the exact position of the

targets. As in the experiment with paper marbles, we presented the moths at two different heights relative to the vegetation; a) within 0.1 m of the grass panicles, and b) 0.7–1.2 m above the grass panicles. Throughout we observed which of the two moths (or the control) was attacked.

Results

Between two and ten *E. nilssonii* were regularly searching for lekking *H. humuli*, of which there were hundreds at each locality. The bats typically patrolled above the leks at a height of 3–5 m attacking the moths by diving almost vertically towards the ground, as described in previous papers (Andersson et al. 1998, Rydell 1998, Jensen et al. 2001). The attacks were always associated with distinct "feeding buzzes", i.e. a clear increase in the echolocation pulse repetition rate (Griffin et al. 1960).

Rapidly moving targets (paper marbles) were frequently attacked. There were no significant differences in the attack frequency on black and white paper marbles at either of the two heights (low – close to the grass panicles, high – ca 1 m above the grass; $\chi_1^2 = 0.9$, $p > 0.05$). Hence, the results from each height were pooled. The bats occasionally attacked low moving targets (16% of shots; n = 102), but not as often as high ones (64% of shots; n = 113). Although this difference is significant ($\chi_1^2 = 28.8$, $p < 0.001$), the bats were obviously able to detect rapidly moving targets even among the clutter.

Mounted moths presented at the level of the grass panicles were never attacked (0 attacks in 95 min of observation), whereas those presented ca 1 m above the grass panicles were frequently attacked (152 attacks in 289 min of observation). This indicates that the bats were able to detect stationary prey near the edge of the clutter overlap zone, but not within the vegetation. The bats did not attack live (fluttering) moths more frequently than dead and spread ones (χ^2-test comparing fluttering and dead targets, Fig. 1a). Hence, we found no evidence that detection of stationary moths was enhanced by their wing flutter. There were occasional attacks on the control, although significantly less than on the mounted moths (Fig. 1a).

The bats attacked both white and dark mounted moths, but the white targets were attacked more frequently (χ^2-test comparing white and dark targets, Fig. 1b). Again, there were occasional, although significantly fewer, attacks on the control (Fig. 1b). The results indicate that detection of stationary prey was facilitated by visual cues in this particular situation.

Discussion

Our results show that *E. nilssonii* was able to detect and also attack rapidly moving targets (paper marbles), not only within the outer part of the clutter overlap zone, but also within the clutter itself. The fact that the bats attacked the paper marbles even among the vegetation suggests that they did not avoid the grass because of mechanical hindrance or predation risk (Jensen et al. 2001). Hence, the detection (or tracking) performance was most likely the limiting factor in our experiments with paper marbles as well as real moths. The mounted moths, which were stationary, were never attacked when presented at the level of the grass panicles, only when presented ca 1 m above the grass. This suggests that without movements, i.e. a change in position of the target between successive echoes, the bats were unable to detect and track the target among clutter. This agrees with the conclusions from an earlier experiment
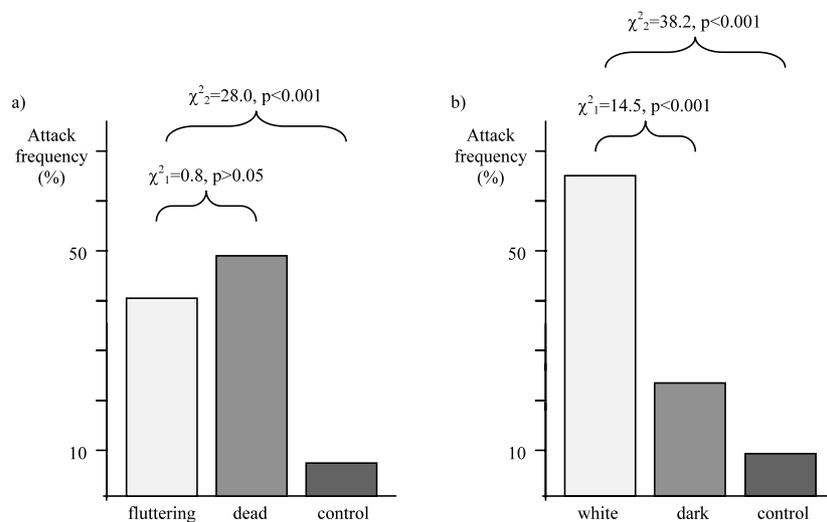

Fig. 1. Attack frequencies on different stationary prey types (*Hepialis humuli* mounted on top of wires) presented pairwise to foraging *Eptesicus nilsonii* ca 1 m above the grass, a) fluttering vs dead and spread moths (n = 86), and b) white (dorsal) side up vs dark (ventral) side up (n = 68). The control wire had no moth.

made with this predator-prey system (Jensen et al. 2001). In another experiment, captive mouse-eared bats *Myotis myotis* (Vespertilionidae) relied on auditory cues (i.e. listening for sounds produced by the prey) rather than on echolocation, when foraging among clutter (Arlettaz et al. 2001). Neither our results, nor those of Arlettaz et al. (2001), are consistent with the hypothesis that foraging bats form an acoustic image based on form and texture of target and background, using echolocation alone, as suggested for *Megaderma lyra* (Megadermatidae) (Schmidt 1988).

There are two observations suggesting that *E. nilssonii* does not use flutter-detection to find or track stationary prey. Firstly, mounted, fluttering moths presented at the level of the grass panicles were never attacked by the bats. Secondly, a dead and mounted moth presented beside a fluttering moth ca 1 m above the grass was attacked with the same frequency. This is inconsistent with the hypothesis that some vespertilionid bats can make use of Doppler shifted echoes from frequency-modulated echolocation calls, as suggested previously (Sum and Menne 1988, Roverud et al. 1991, Moss and Zagaeski 1994). The performance of *E. nilssonii*, and presumably also other bats that use similar echolocation calls, among clutter is thus very different from the performance of rhinolophid and hipposiderid bats. These bats use long constant-frequency pulses and auditory specializations and are therefore able to make use of the Doppler shifts generated by fluttering insect wings (Schnitzler and Flieger 1983). This permits prey detection in the immediate vicinity of vegetation.

Ghost swifts are large (wingspan 5–7 cm) moths. They also have a conspicious white dorsal side, sharply contrasting against the dark background of their natural habitat and providing an obvious cue for visually guided predators such as gulls *Larus canus* and domestic cats hunting at dusk (Andersson et al. 1998). Our results suggest that northern bats too made use of visual cues, which is also the case for two other aerial-hawking vespertilionid bats (Grant 1991). Although most insectivorous bats are mainly guided by echolocation, their visual sensitivity remains good in low illumination (Ellins and Masterson 1974) and they can be trained to respond visually to stationary objects (Suthers et al. 1969). There is also experimental and observational evidence that they make use of vision and even give precedence to visual cues in many situations, such as when selecting escape routes (Chase 1981, 1983), when commuting between feeding sites (Eklöf et al. 2002) and during migration (Griffin 1970, Timm 1989). Bats may also use vision for detection of targets. Phyllostomid bats were trained to land on a backlit grid, which they were able to detect at an early stage using vision alone. However, the actual landing performance was always under the control of echolocation (Joermann et al. 1988).

Although our results indicated that the bats were guided by visual cues, they echolocated consistently, and the attacks were always associated with feeding buzzes. This is in accordance with earlier studies, showing that *E. nilssonii* and *Myotis lucifugus* consistently use search-phase echolocation calls and feeding buzzes when detecting and pursuing insects even under midnight sun conditions in the sub-arctic (Rydell et al. 2002).

Two further lines of evidence also suggest that vision alone was not enough to detect and track the targets in our study. Firstly, black and white paper marbles were attacked with the same frequencies. Secondly, moths presented at the level of the grass panicles were not attacked at all. We therefore hypothesize that vision facilitates detection of the moths in an initial search phase, although it may not necessarily be involved in the terminal attack.

References

Ahlén, I. 1981. Identification of Scandinavian bats by their sounds. – Report 6. Swed. Univ. Agric. Sci., Uppsala.

Andersson, S., Rydell, J. and Svensson, M. G. E. 1998. Light, predation and the lekking behaviour of the ghost swift *Hepialus humuli* (L.) (Lepidoptera: Hepialidae). – Proc. R. Soc. Lond. B 264: 1345–1351.

Arlettaz, R., Jones, G. and Racey, P. A. 2001. Effect of acoustic clutter on prey detection by bats. – Nature 414: 742–745.

Bell, G. P. 1985. The sensory basis of prey location by the California leaf-nosed bat *Macrotus californicus* (Chiroptera: Phyllostomidae). – Behav. Ecol. Sociobiol. 16: 343–347.

Chase, J. 1981. Visually guided escape responses of microchiropteran bats. – Anim. Behav. 29: 708–713.

Chase, J. 1983. Differential responses to visual and acoustic cues during escape in the bat *Anoura geoffroyi*: cue preferences and behaviour. – Anim. Behav. 31: 526–531.

Eklöf, J., Tranefors, T. and Vazquez, L. B. 2002. Precedence of visual cues in the emballonurid bat *Balantiopteryx plicata*. – Mammal Biol. 67: 42–46.

Ellins, S. R. and Masterson, F. A. 1974. Brightness discrimination thresholds in the bat, *Eptesicus fuscus*. – Brain, Behav. Evol. 9: 248–263.

Fenton, M. B., Audet, D., Obrist, M. K. and Rydell, J. 1995. Signal strength, timing, and self-deafening: the evolution of echolocation in bats. – Paleobiology 21: 229–242.

Grant, J. D. A. 1991. Prey location by two Australian long-eared bats, *Nyctophilus gouldi* and *N. geoffroyi*. – Aust. J. Zool. 39: 45–56.

Griffin, D. R. 1970. Migration and homing of bats. – In: Wimsatt, W. A (ed.), Biology of bats. Vol. II. Academic Press, pp. 233–264.

Griffin, D. R., Webster, F. A. and Michael, C. R. 1960. The echolocation of flying insects by bats. – Anim. Behav. 8: 141–154.

Jensen, M. E., Miller, L. A. and Rydell, J. 2001. Detection of prey in clutter by the northern bat, *Eptesicus nilssonii*. – J. Exp. Biol. 204: 199–208.

Joermann, G., Schmidt, U. and Schmidt, C. 1988. The mode of orientation during flight and approach to landing in two Phyllostomid bats. – Ethology 78: 332–340.

Kalko, E. K. V. and Schnitzler, H.-U. 1993. Plasticity of echolocation signals of European pipistrelle bats in search flight: implications for habitat use and prey detection. – Behav. Ecol. Sociobiol. 33: 415–428.

Moss, C. F. and Zagaeski, M. 1994. Acoustic information available to bats using frequency-modulated sounds for the perception of insect prey. – J. Acoust. Soc. Am. 95: 2745–2756.

Neuweiler, G. 1990. Auditory adaptations for prey capture in echolocating bats. – Physiol. Rev. 615–641.

Pettigrew, J. D. 1980. Microbat vision and echolocation in an evolutionary context. – In: Nachtigall, P. E. and Moore, P. W. B. (eds), Animal sonar. processes and performance. Plenum Press, pp. 645–650.

Roverud, R. C., Nitsche, V. and Neuweiler, G. 1991. Discrimination of wing beat motion by bats, correlated with echolocation sound pattern. – J. Comp. Physiol. A 168: 259–263.

Rydell, J. 1998. Bat defence in lekking ghost swift (*Hepialus humuli*), a moth without ultrasonic hearing. – Proc. R. Soc. Lond. B 265: 1373–1376.

Rydell, J., Parker McNeill, D. and Eklöf, J. 2002. Capture success of little brown bats feeding on mosquitoes. – J. Zool. Lond. 256: 379–381.

Schmidt, S. 1988. Evidence for a spectral basis of texture perception in bat sonar. – Nature 331: 617–619.

Schnitzler, H. -U. 1987. Echoes of fluttering insects: information for echolocating bats. – In: Fenton, M. B., Racey, P. A. and Rayner, J. M. V. (eds), Recent advances in the study of bats. Cambridge Univ. Press, pp. 226–243.

Schnitzler, H.-U. and Flieger, E. 1983. Detection of oscillating target movements by echolocation in the Greater Horseshoe bat. – J. Comp. Physiol. 135: 385–392.

Sum, Y. W. and Menne, D. 1988. Flutter detection by the vespertilionid bat *Pipistrellus stenotus*? – J. Comp. Physiol. A 163: 349–354.

Suthers, R. A., Chase, J. and Bradford, B. 1969. Visual form discrimination by echolocating bats. – Biol. Bull. 137: 535–546.

Timm, R. M. 1989. Migration and molt patterns of red bats, *Lasiurus borealis* (Chiroptera: Vespertilionidae). – Illinois Bull. Chic. Acad. Sci. 14: 1–7.