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Vision complements echolocation in an aerial-hawking bat

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Abstract The northern bat *Eptesicus nilssonii* normally hunts flying insects in the air using frequency-modulated echolocation calls. It is also known to detect and catch visually conspicuous prey (white moths) hovering low among grass stalks. To overcome the problem with acoustic clutter from the grass, which interferes with target echo detection, the bats make use of visual cues in addition to those of echolocation. We therefore investigated the minimum size of prey that the bats could distinguish by using vision, by presenting the bats with different sized dead and spread moths. We found that vision increased the chance of detection only when the moths had a wingspan of at least 5 cm. Smaller targets were detected using echolocation alone. The mean detection range was 3.5 m, suggesting that the bats need a visual acuity of 49' of arc to detect the prey. This is consistent with results of optomotor response tests and counts of retinal ganglion cells in closely related species. Our results suggest that the visual acuity of *Eptesicus* bats may not be adequate for prey detection under normal conditions, but that the bats can use vision when the prey is unusually large and conspicuous. The northern bats display a flexibility in prey detection techniques not previously recognised among aerial-hawking bats and they are able to use their full visual capacity in the field.

Introduction

The functions normally served by vision in most vertebrates have been taken over by echolocation in insectivorous bats. In particular, the detection and tracking of flying insects is usually believed to be entirely acoustic (Kalko and Schnitzler 1993). Echolocation allows the

detection of very small targets, but its practical range is normally limited to a few metres, which is due to severe atmospheric attenuation and spreading loss of high-frequency sound and the poor reflective power of targets as small as insects (Lawrence and Simmons 1982; Kick 1982). On the other hand, although the eyes of insectivorous bats are small, they generally have effective light-gathering capacity and a great depth of focus (Suthers 1970; Suthers and Wallis 1970). Vision can therefore be assumed to provide important cues, particularly at ranges beyond that of echolocation, and is presumably useful for orientation and navigation at night.

However, adaptation of the visual system for nocturnal conditions occurs partly at the expense of acuity, the ability to resolve details, and this presumably limits the use of vision for some short-range purposes such as finding prey (Suthers 1970). Nevertheless, at least some bat species, particularly those that glean prey from surfaces and for which acoustic clutter (background echoes) makes echolocation less useful (Arlettaz et al. 2001), have a visual acuity that is good enough for detection of insects and other objects at close range (Bell 1985; Joermann et al. 1988; Eklöf and Jones 2003).

We recently discovered that vision also plays a role in prey detection by the northern bat *Eptesicus nilssonii* (Family Vespertilionidae), an aerial-hawking species (Eklöf et al. 2002). However, because aerial-hawking bats generally seem to have poor visual acuity (Suthers 1970), this can be expected to impose a lower limit on the size of insects that can be detected by vision. The aim of this study was to estimate the visual acuity, and to investigate the minimum size of prey that can be detected visually by northern bats in a field situation.

Materials and methods

To determine the minimum size of prey visually detectable, and to estimate the visual acuity for *E. nilssonii* foraging under practical conditions in the field, we took advantage of a natural situation where bats regularly exploit groups of male ghost swift moths *Hepialus humuli* (Hepialidae) appearing over hayfields during

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midsummer evenings in southern Sweden (57°N). These moths are silvery white and highly reflective on the dorsal side and dark grey on the ventral side, and display visually in hovering flight among the grass panicles in order to attract females (Andersson et al. 1998). Hepialids are unusual among larger moths in that they are earless and do not show any evasive response to bat echolocation calls, whether these are natural or synthetic (Rydell 1998).

At two different moth display sites, each regularly patrolled simultaneously by up to ten northern bats (which were not marked), we added dead and spread individuals to the naturally displaying moth population. The dead moths were glued to the top of steel wires and presented in pairs about 2 m apart and 0.5–0.7 m above the grass in various parts of the fields. We deliberately presented the moths at a height where separation of prey echoes from background clutter would be difficult (i.e. within the “clutter overlap zone”), thereby encouraging the bats to use other cues in addition to echolocation. The depth of the clutter overlap zone is determined by the duration of the echolocation signal by the bat ($0.5 \times \text{speed of sound} \times \text{signal duration}$), which in this case means 0.6–1.2 m above the grass (Jensen et al. 2001).

One moth in each pair had its white dorsal side facing upwards and the other had its dark grey ventral side facing upwards towards the patrolling bats. We assumed that the two were equally detectable by echolocation but that the white dorsal surface was more detectable by vision. This assumption was based on a previous experiment, showing that the moths’ silvery white dorsal coloration, which also contains a UV component, contrasts strongly against the background of green grass during the moths’ natural display time just after sunset (Andersson et al. 1998). We thus expected that the moths with their white dorsal side up and moths with their dark ventral side up would be attacked with equal frequency if bats use echolocation alone but with unequal frequency if they also use visual cues. To determine the minimum size of moths detectable by vision, we presented pairs of moths (one with the white surface showing and one with the dark surface showing) which were either intact (about 6 cm wingspan; Eklöf et al. 2002) or where both had the wingtips cut to give a total wingspan of either 5, 4 or 3 cm. Hence, size differed between the pairs of moths but the white and the dark aspects of the moths that formed a pair were always of the same size. The moths were replaced when destroyed by the bats, but were otherwise reused for as long as possible.

To prevent the bats from learning the exact positions of the moths, the pairs were moved at least a few metres following each attack by a bat. Hence each pair of moths was attacked only once while in each position.

Moths and bats were observed visually and also acoustically with a Petterson D-940 bat detector from a distance of 2–10 m. The visual observations were facilitated by the relatively good light conditions prevailing at 57°N around midsummer (June 2002), which always made it possible to see what happened in sufficient detail. The experiments were performed only as long as moths were displaying naturally nearby, which occurred for about 30 min each evening (Andersson et al. 1998). We determined the height at which the bats patrolled over the field, by using a measured and marked lamppost at the edge of the field as a reference. We counted the number of attacks on moths with white dorsal side up and moths with dark grey ventral side up, and compared the results for each moth size using one-tailed χ^2 statistics.

Results

Neither bats nor moths showed any obvious response to our presence. The bats seemed to forage normally, possibly because they had become habituated to our presence over several seasons. The bats typically patrolled in large circles over the field at a height of 3–4 m (mean 3.5 m), and they always emitted echolocation calls during the search as well as throughout the attacks on the

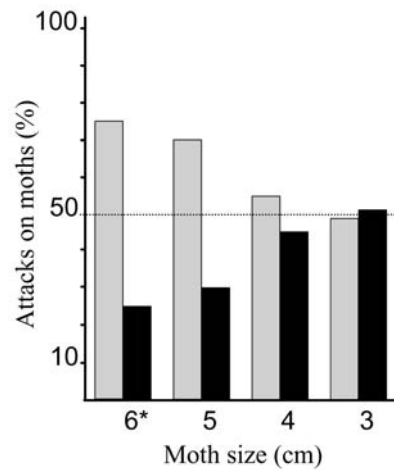


Fig. 1 Frequency of attacks by northern bats (*Eptesicus nilssonii*) on dead and spread *Hepialus humuli* moths mounted on top of wires and presented to foraging bats in a field among naturally occurring moths. Moths were cut to different wingspan sizes and displayed in pairs, one showing its white dorsal side upwards and the other the dark grey ventral side. The greater frequency of attacks on moths showing the white dorsal surface (white bars) than on those with dark ventral side upwards (dark bars) indicates that the bats detected the moths using visual cues. The asterisk indicates that the 6 cm moths had not been cut, but were presented at their natural size (mean 6 cm)

moths. An attacking bat typically performed a rapid and more or less vertical dive towards the grass while switching from search-phase echolocation calls to a typical “feeding-buzz”, i.e. short pulses and high pulse repetition rate.

Attacks on moths with white dorsal surface upwards were more frequent than on moths with dark grey surface upwards only when the moths were 5 cm ($\chi^2_1=8.64$, $P<0.01$, $n=56$) or larger ($\chi^2_1=14.52$, $P<0.001$, $n=62$), suggesting that the detection was facilitated by vision in these cases. The detection of 4 cm ($\chi^2_1=0.49$, $P>0.05$, $n=51$) and 3 cm ($\chi^2_1=0.02$, $P>0.05$, $n=45$) moths was apparently not facilitated by vision and therefore must have been guided entirely by echolocation (Fig. 1). We expected the total number of attacks on large moths to be more frequent than on smaller moths, because the larger size presumably increased the chance of detection. Although this appeared to be the case, the absolute attack frequency (the number of attacks per bat) was difficult to measure because the number of bats searching for moths over the field was constantly changing.

Discussion

Assuming that the bats detected a moth visually before initiating an attack, the moths in this study were detected at a range of 3.5 m, which was the mean patrolling height. At this distance, a 5 cm moth represents 49' of arc. This agrees well with theoretical estimates of visual acuity based on counts of retinal ganglion cells, suggesting 40'

of arc (Pettigrew et al. 1998; Koay et al. 1988) and behavioural tests of the optomotor response, suggesting at least 1° of arc, in the closely related species *Eptesicus fuscus* from North America (Bell and Fenton 1986). Unpublished optomotor response tests of other *Eptesicus* species, namely *E. capensis* and *E. zuluensis* from southern Africa, suggest that these species have a visual acuity of at least 54' of arc (M.B. Fenton and C.V. Portfors, personal communication). Our experiment is the first estimate of the visual acuity of *E. nilssonii*.

The visual acuity of *Eptesicus* spp. appears to be intermediate among bats. It is much better than in many other aerial-hawking insectivores, e.g. *Myotis* spp. (3–5°) (Suthers 1966), but not as good as that of some gleaning insectivores, e.g. *Macrotus californicus* and *Antrozous pallidus* (4' and 15', respectively) (Bell and Fenton 1986). It is comparable to that of vampires and frugivores of the family Phyllostomidae (16–42') and insectivores of the family Emballonuridae (23–42') (Pettigrew et al. 1998; Suthers 1966; Manske and Schmidt 1976). The reason why the visual acuity differs so much among species and genera of bats is not clear.

The repertoire of detection techniques used by northern bats searching for insects is relatively large. *E. nilssonii* usually feeds on swarming insects in open air (Rydell 1989), where echolocation is relatively straightforward and insects or swarms of insects can be detected through single echoes; so-called “glints”. Insects that move rapidly near vegetation, so that acoustic clutter masks the echoes from the insects, are detected through their shift in position relative to the background. This technique obviously requires comparison of the echoes containing both the target and the background between several successive pulses (Jensen et al. 2001). When the insects stay among clutter and do not move relative to the background, as in the present case, few echolocation cues are available and the bats apparently employ vision to enhance the detection. We have shown previously that *E. nilssonii* do not make use of the Doppler effects induced by the wing movements of the hovering moths (Eklöf et al. 2002). Nevertheless, the bats always emitted echolocation calls during the search as well as throughout the attacks on the moths, which suggests that the attacks were consistently guided by echolocation.

Whether vision is useful or not in a particular foraging situation depends not only on the size of the target and the range, but presumably also on the contrast between the target and the background and the prevailing light conditions (Andersson et al. 1998; Ellins and Masterson 1974). In our case, the prey insects were much larger than most other prey eaten by this species (Rydell 1989) and they also displayed an unusually high contrast against the background (Andersson et al. 1998). Hence, the use of vision for prey detection is probably unusual in this species, and we can therefore assume that it normally relies on echolocation alone for this purpose. Nevertheless, our study shows that echolocating bats are flexible and ready to use whatever information is available to find

food, and, assuming that the visual acuity of *E. nilssonii* is similar to that of *E. fuscus*, we find that these bats are able to use their full visual capacity in the field.

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References

- Andersson S, Rydell J, Svensson MGE (1998) Light, predation and the lekking behaviour of the ghost swift *Hepialus humuli* (L.) (Lepidoptera: Hepialidae). *Proc R Soc Lond B* 265:1345–1351
- Arlettaz R, Jones G, Racey PA (2001) Effect of acoustic clutter on prey detection by bats. *Nature* 414:742–745
- Bell GP (1985) The sensory basis of prey location by the California leaf-nosed bat *Macrotus californicus* (Chiroptera: Phyllostomidae). *Behav Ecol Sociobiol* 16:343–348
- Bell GP, Fenton MB (1986) Visual acuity, sensitivity and binocularity in a gleaning insectivorous bat, *Macrotus californicus* (Chiroptera: Phyllostomidae). *Anim Behav* 34:409–414
- Eklöf J, Jones G (2003) Use of vision in prey detection by brown long-eared bats *Plecotus auritus*. *Anim Behav* 66 (in press)
- Eklöf J, Svensson AM, Rydell J (2002) Northern bats (*Eptesicus nilssonii*) use vision but not flutter-detection when searching for prey in clutter. *Oikos* 99:347–351
- Ellins SR, Masterson FA (1974) Brightness discrimination thresholds in the bat, *Eptesicus fuscus*. *Brain Behav Evol* 9:248–263
- Jensen ME, Miller LA, Rydell J (2001) Detection of prey in clutter by the northern bat, *Eptesicus nilssonii*. *J Exp Biol* 204:199–208
- Joermann G, Schmidt U, Schmidt C (1988) The mode of orientation during flight and approach to landing in two Phyllostomid bats. *Ethology* 78:332–340
- Kalko EKV, Schnitzler HU (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
- Kick S (1982) Target-detection by the echolocating bat, *Eptesicus fuscus*. *J Comp Physiol A* 145:432–435
- Koay G, Kearns D, Heffner HE, Heffner RS (1998) Passive sound-localization ability of the big brown bat (*Eptesicus fuscus*). *Hearing Res* 119:37–48
- Lawrence BD, Simmons JA (1982) Measurements of atmospheric attenuation at ultrasonic frequencies and the significance for echolocation by bats. *J Acoust Soc Am* 71:585–590
- Manske U, Schmidt U (1976) Untersuchungen zur optischen Musterunterscheidung bei der Vampirfledermaus, *Desmodus rotundus*. *Z Tierpsychol* 49:120
- Pettigrew JD, Dreher B, Hopkins CS, McCall MJ, Brown M (1988) Peak density and distribution of ganglion cells in the retinae of microchiropteran bats: implications for visual acuity. *Brain Behav Evol* 32:39–56
- Rydell J (1989) Food habits of northern (*Eptesicus nilssonii*) and brown long-eared bats (*Plecotus auritus*) in Sweden. *Holarct Ecol* 12:16–20
- Rydell J (1998) Bat defence in lekking ghost swift (*Hepialus humuli*), a moth without ultrasonic hearing. *Proc R Soc Lond B* 265:1373–1376
- Suthers RA (1966) Optomotor responses by echolocating bats. *Science* 152:1102–1104
- Suthers RA (1970) Vision, olfaction and taste. In: Wimsatt WA (ed) *Biology of bats*, vol II. Academic Press, New York, pp 265–281
- Suthers RA, Wallis NE (1970) Optics of the eyes of echolocating bats. *J Vision Res* 10:1165–1173