

Visual acuity and eye size in five European bat species in relation to foraging and migration strategies

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Abstract

Optomotor response tests provided visual acuity thresholds in five species of north European insectivorous bats of the family Vespertilionidae. Individuals of three species of predominantly aerial-hawking and trawling *Myotis* (*M. brandtii*, *M. mystacinus* and *M. daubentonii*) responded only to a stripe pattern equivalent to 5 degrees of arc, whereas the long-distance migrant *Pipistrellus nathusii*, another aerial-hawking species, responded to 1 degree. In contrast, *Plecotus auritus*, which is a gleaner and capable of detecting prey using vision alone, responded to a pattern equivalent to 0.5 degrees. The visual acuity was positively correlated with eye diameter, which varied from 0.9 mm in *M. mystacinus* to 1.7 mm in *P. auritus*. The results are consistent with earlier findings on related species in other parts of the world. The variation in eye size and visual acuity among insectivorous bats reflect differences in foraging techniques and perhaps also in migrating behavior, thus illustrating how vision is used as a complement to ultrasonic echolocation in various navigation and foraging situations.

Key words: Chiroptera; optomotor response; orientation; navigation; night vision; spatial resolution.

Introduction

The eyes of insectivorous bats are adapted to nocturnal conditions, and, although they are small, they have relatively large corneal surfaces and lenses and large receptor fields, which provide good light gathering capacity. However, this partly occurs at the expense of acuity, the ability to resolve fine spatial detail (Suthers 1970; Suthers, Wallis 1970). Generally, bat eyes are best suited for long-range operation, and considering the short effective range of ultrasonic echolocation (Lawrence, Simmons 1982), vision is probably of major importance in guidance over longer distances (Griffin 1970; Boonman et al. 2013).

Nevertheless, some bats use vision over short distances as well, such as during escape and obstacle avoidance experiments (Chase 1981; Chase, Suthers 1969; Bradbury, Nottebohm 1969). Bats may even use vision to find prey under some conditions, a task that requires relatively fine detail discrimination at a very short range (Bell 1985; Grant 1991; Vaughan, Vaughan 1986; Surlykke et al. 1993; Eklöf et al. 2002a; Eklöf, Jones 2003). Vision and hearing are closely integrated in bats (Horowitz et al. 2004; Boonman et al. 2013), as in other animals, but visual information usually takes precedence over echolocation in situations when sufficient light is available (Eklöf et al. 2002b; Orbach, Fenton 2010). In view of the relatively recent findings

that bats possess color vision (Wang et al. 2004; Müller, Peichl 2005; Zhao et al. 2009), including sensitivity for UV (Winter et al. 2003; Müller et al. 2009; Xuan et al. 2012) and specializations for dim light vision (Shen et al. 2010), bat eyes are clearly much more complicated and versatile than previously anticipated.

The potential visual acuity can be estimated theoretically, based on counts of retinal ganglion cells, and this has been done in several species of bats (Marks 1980; Pettigrew et al. 1988; Heffner et al. 2001). Estimates based on this technique show a large range of variation, from 16 minutes of arc in the gleaner and partly carnivorous *Macroderma gigas* and *Megaderma lyra* (Megadermatidae), two species with unusually large eyes, to 1.4 degrees in the strictly insectivorous flutter-detector *Rhinolophus rouxii* (Rhinolophidae), which has very small eyes (Pettigrew et al. 1988). Behavioural observations such as optomotor response tests, where the visual acuity is tested directly, generally agree with the theoretical predictions, and confirm that the visual acuity varies considerably from species to species and to some extent is related to behavioral characters such as the typical foraging technique (Suthers 1966; Manske, Schmidt 1976; Bell, Fenton 1986).

Generally, gleaners, species able to detect and catch non-flying insects and other animals, seem to have better visual capacity than other bats, i.e. aerial-hawking species,

those that normally detect and catch insects in the air. This is probably because the search for food is to some extent guided by vision in gleaners, maintaining strong natural selection on this trait (Bell, Fenton 1986; Eklöf, Jones 2003).

It also seems possible that bats that perform long-distance migrations may require relatively sharp vision, assuming that orientation and navigation partly rely on visual cues on the night sky such as single bright stars or stellar constellations (Childs, Buchler 1981; Buchler, Childs 1982) or perhaps the moon. This has not been examined as far as we know.

Hence, the main purpose of this study was to test the hypothesis that visual acuity varies across bat species according to their foraging and migration strategies, and that gleaner species show better visual acuity than aerial hawking ones. We also investigated the possibility that migrating bats apply stellar or possibly lunar navigation, and perhaps show better visual acuity than stationary (non-migratory) species. Long-term data on migration flight activity of Nathusius' pipistrelle *Pipistrellus nathusii*, a known long-distance migrant (Hutterer et al. 2005), were analyzed, testing the hypothesis that migration intensity increases on clear as compared to cloudy nights, i.e. with and without stellar (and lunar) cues, respectively.

Materials and methods

The behavioural experiments were made at (a) the old magnetite mine at Taberg, 13 km south of Jönköping in south-central Sweden (57°41'N, 14°05'E), and (b) Pape Ornithological Station at the Baltic coast in southernmost Latvia (56°10'N, 21°01'E). For descriptions of these localities in some detail, we refer to Karlsson et al. (2002), Pētersons (2004) and Šuba et al. (2012), respectively. At Taberg, bats (eight *Plecotus auritus*, three *Myotis mystacinus*, two *M. brandtii* and three *M. daubentonii*) were caught in mist nets outside one of the mine entrances, while at Pape the bats (21 *Pipistrellus nathusii*, of which 13 were tested) were captured in a large Helgoland-type funnel trap placed near the shoreline, as described previously (Pētersons 2004). At Taberg the tests were made in the evening from August to November 2002 and from March to April 2003. The tests at Pape were made in August and September 2011 and 2012, while bats were on migration.

The bats were tested for optomotor responses immediately after capture or as soon as they had come to rest. To achieve the responses, we used two devices (one at each site) similar to those used by Suthers (1966) and Bell and Fenton (1986). Each of the devices consisted of a 30 cm high and 60 cm diameter revolving drum with a 20 cm high and 10 cm diameter plexiglass cylinder in the centre with the experimental bat inside. The drum could be rotated freely and independently of the cylinder by hand in both directions. Inside the drum and visible from its center, we attached a paper with a sinusoidal grating

pattern of varying fineness. A sinusoidal pattern means that the luminance varied continuously from black to white. We used sinusoidal pattern instead of discrete black and white stripes to reduce the risk of optical illusions, which could otherwise elicit responses from the bats and thus make the results harder to interpret (as suggested by D. Nilsson and E. Warrant at Lund University, Sweden). Six gratings with different width (distance from white to white) were used; 2.84, 1.42, 0.57, 0.43, 0.28 and 0.14 cm, respectively, equivalent to subtending angles of 5, 2.5, 1, 0.75, 0.5 and 0.25 degrees of arc, as seen from the bat's point of view (i.e. from the center of the plexiglass cylinder). When a response was recorded the grating was switched to a finer pattern until no response was recorded, indicating that the bat could no longer resolve the pattern. At this point a wider pattern was reintroduced, to make sure that the bat still responded to the moving stripes. This also served as a control for responses to stimuli other than the stripes, such as, for example, noise originating from the drum and our own movements. Of the bats captured at Taberg, two *M. mystacinus* individuals and one *M. daubentonii* individual did not respond to the widest pattern (5 degrees) and they were therefore released and not tested further. These individuals are not included in the results table (Table 1).

Natural light was usually insufficient for direct unaided observation of the bats' responses. Therefore, dim artificial light conditions were maintained during the experiments. At Taberg, the study setup was placed outdoors ca 5 m from a 40 W light bulb that permanently illuminated the entrance to a building (the "Mining Office"). This measure provided us with sufficient light to see what happened inside the cylinder. The light intensity inside the drum was thus 0.1 to 0.7 lux (Photometer IL 1400A, International Light Inc., USA). At Pape, the tests were made inside a small lab facility and the light intensity inside the drum was 3 to 7 lux (Lutron YK-2001 TM with a YK-200PLX light meter probe; Lutron Electronics Enterprise Co. Ltd., USA).

At Taberg, the faces of the bats were photographed after testing the optomotor responses, using a high quality macro lens and a flash, to achieve an estimate of the eye diameter. We held the bats by hand so that the face of the bat was perpendicular to the lens (bat seen in profile) with a ruler next to the bat, providing a cm scale. At Pape, photos from other individuals than those tested for optomotor response were used. The eye sizes of individual bats were later estimated on a computer screen, using only bats that had eyes fully open and where the bat and the ruler were in focus. The bats were released at the site of capture immediately after the experiments and the photographs.

To test whether the intensity of *P. nathusii* autumn migration increases on clear nights, assuming that a clear sky provides the best conditions for stellar and/or lunar navigation, we used data from a long term census of migrating bats at Pape Ornithological Station, collected from 10 August to 10 September 2003 – 2012 by one of

us (GP). At this site, bats migrate in large numbers at low altitude along the coast of the Baltic Sea (Petersons 2004; Šuba et al. 2012). Passes of migrating bats were counted manually in 15-min intervals during the first two hours after sunset ($n = 300$), aided by an ultrasound detector (model D-200 or D-240X, Pettersson Elektronik AB, Uppsala, Sweden). Relative cloud cover was assessed on a four-class scale: clear sky, some clouds (< 50% cloud cover), cloudy (50 to 80% cloud cover) and overcast (> 80% cloud cover). Other factors, such as ambient temperature, wind speed and wind direction were also recorded and included in the analysis. Records that contained fog, rain or strong wind ($> 6 \text{ m s}^{-1}$; $n = 122$) were not included in the analysis, because much fewer bats migrate in such conditions (Petersons, unpublished data). A multi-way analysis of covariance (ANCOVA) was used to test for the impact of cloud cover, wind direction and wind speed on the number of bat passes, using ambient temperature as covariate. The data on bat passes were log transformed to fit the normal distribution. The analysis was made using R version 2.13.0 (R Foundation for Statistical Computing, Vienna, Austria).

Results

When put in the cylinder the bats typically moved about for a few minutes and they sometimes continued to do so during the test. However, most of them unambiguously responded to the rotating pattern by moving their heads in a snappy, stereotyped manner, either following the direction of the rotating drum or in the opposite direction, as described earlier by others (Suthers 1966; Bell, Fenton 1986).

The results (Table 1) were consistent within a species and genus but differed considerably and consistently between the genera. Individuals of the three species of *Myotis* were similar in performance and responded only to the largest pattern, equivalent to 5° of arc. In the brown long-eared bat *Plecotus auritus* all individuals except one responded down to the pattern equivalent to $1 - 0.5^\circ$. Nathusius' pipistrelle *Pipistrellus nathusii* was intermediate, individuals of this species usually responded down to 1° (Table 1).

The eye size varied with visual capacity as expected (Table 1). The *Myotis* spp. had the smallest eyes (ca. 1 mm

diameter) and *P. auritus* the largest (ca. 1.7 mm). *P. nathusii* was intermediate (ca. 1.3 mm).

The migration intensity of *P. nathusii* at Pape varied considerably in relation to cloud cover (Fig. 1). On average, more passes were registered under a clear sky, and the effect of cloudiness was statistically significant. However, considerable migration activity still occurred on cloudy nights. Wind direction and ambient temperature also had significant impacts on migration intensity (Table 2). On average most bat passes were recorded when the wind blew from the east and from the southwest (headwind).

Discussion

Visual acuity differs considerably among bats in general and this is also the case within the Vespertilionidae, the family to which the species tested here belong. The variation presumably reflects the extent to which the bats make use of vision and what they do with it. As expected, the relatively big eyed gleaner *Plecotus auritus* did much better than the three predominantly aerial-hawking and trawling *Myotis* species that we tested, and which also had much smaller eyes (Fig. 2).

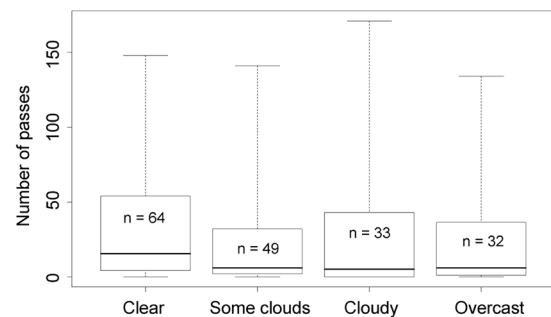


Fig. 1. Box-whisker plots of the number of passes of migrating *P. nathusii* in relation to the cloud cover. Passes were recorded during 15-minute intervals at Pape Ornithological Station during autumn migration (10 August to 10 September 2003 – 2012). Stripes indicate the medians, whiskers indicate the maximum and minimum numbers and the boxes show the inter quartiles; n is the number of observations in each class.

Table 1. Eye diameter and optomotor responses to patterns of different fineness in five European bat species. The n-values under the minimum separable angle refer to the number of individuals showing the modal value and the number of responding individuals, respectively

Species	Eye diameter (mm)	Ambient light (lux)	Minimum separable angle	
			Modal value	Range
<i>Plecotus auritus</i>	1.7 ± 0.1 ($n = 4$)	0.1 – 0.7	$45'$ ($n = 3$)	$30' - 2.5^\circ$ ($n = 8$)
<i>Myotis mystacinus</i>	1.0 and 0.9 ($n = 2$)	0.1 – 0.6	5° ($n = 1$)	
<i>Myotis brandtii</i>	Not measured	0.1 – 0.6	5° ($n = 2$)	
<i>Myotis daubentonii</i>	1.2 and 1.3 ($n = 2$)	0.1 – 0.3	5° ($n = 2$)	
<i>Pipistrellus nathusii</i>	1.3 ± 0.1 ($n = 21$)	3 – 7	1° ($n = 7$)	$45' - 5^\circ$ ($n = 13$)

Table 2. A multi-way ANCOVA table showing the number of passes of migrating *P. nathusii* at Pape in Latvia in August and September 2003 to 2012 in relation to cloud cover and other weather factors (wind direction, wind speed and temperature)

Factor	Values	SS	d.f.	F	p
Cloud cover	Clear (<i>n</i> = 64)	16.0	3	3.4	0.019
	Some clouds (<i>n</i> = 49)				
	Cloudy (<i>n</i> = 33)				
	Overcast (<i>n</i> = 32)				
Wind direction	No wind (<i>n</i> = 21)	104.2	4	16.6	< 0.001
	North (<i>n</i> = 29)				
	East (<i>n</i> = 49)				
	South (<i>n</i> = 32)				
Wind speed	West (<i>n</i> = 47)	1.6	1	1.0	0.32
	0 m s ⁻¹ (<i>n</i> = 21)				
	1–2 m s ⁻¹ (<i>n</i> = 96)				
	3–5 m s ⁻¹ (<i>n</i> = 61)				
Ambient temperature	15.5 °C (SD = 3.1)	24.5	1	15.6	< 0.001
Residuals		263.0	168		
Total	<i>n</i> = 178	409.1	177		

The response to the 5° but not to the 2.5° pattern by the *Myotis* spp. used in our tests was consistent across the three species and our result was also consistent with an earlier test of the American conspecific *M. lucifugus*, which responded down to 3 – 6° patterns (Suthers 1966). Because of this consistency, we believe that our results are robust with respect to *Myotis* spp., despite the fact that only five individuals were tested successfully. A visual acuity in this range suggests that these bats can detect a 5 to 9 cm object at 1 m at best. Therefore, it seems very unlikely that they can visually detect the insects that they eat, which are mostly chironomids and other small flies (e.g. Swift, Racey 1983). Insects must therefore be detected by echolocation alone. Nevertheless, vision may be used to detect large objects at distances beyond the range of echolocation and may therefore be important in navigation and orientation. Indeed, the loss of vision drastically reduces the homing performance in other *Myotis* species such as *M. sodalis* (Hassell 1966; Davis, Barbour 1970) and *M. austroriparius* (Layne 1967), as well as in many other bats (Hassell 1966; Williams et al. 1966; Davis, Barbour 1970; Holland 2007).

In contrast to *Myotis* spp. the brown long-eared bat *Plecotus auritus* responded to a pattern equivalent to 30' of arc, which means that this species should be able to see objects as small as 0.9 cm diameter at a distance of 1 m. Among the Vespertilionidae only the pallid bat *Anthrozous pallidus*, which also is a gleaner, has been shown to have a better resolving power, namely 15' (Bell, Fenton 1986). *P. auritus* typically feeds on relatively large prey items (Swift, Racey 1983; Rydell 1989), including many moths and beetles, and can detect at least some prey items, e.g. mealworms, by the use of vision alone (Eklöf, Jones 2003).

The visual acuity of *Nathusius*' pipistrelle *Pipistrellus nathusii* was intermediate between those of *Myotis* spp. and *Plecotus auritus*. In contrast to the other four species,

P. nathusii is a long-distance migrant (Hutterer et al. 2005), and as such it may perhaps be expected to show a visual acuity of sufficient quality for perception of stars or other objects on the night sky, cues which may possibly be used during nocturnal orientation and navigation. Its visual acuity is similar to that of some other aerial-hawking bats that typically forage in open air, such as the big brown bat *Eptesicus fuscus* in North America and the northern bat *E. nilssonii* in Europe, species considered to be non-migratory (Bell, Fenton 1986; Rydell, Eklöf 2003). Optomotor responses provided similar acuity thresholds (0.9 to 1.5°) for aerial-hawking vespertilionid bats in Africa (*Neoromicia capensis*, *N. zuluensis*, *N. nana*, *Scotophilus dinganii*, *Pipistrellus rueppelii* and *Nycticeius schlieffeni*), and also in aerial-hawking species of other families from the same area [e.g. *Miniopterus natalensis* (Miniopteridae), *Chaerophon pumila* and *Mops midas* (Molossidae); using the nomenclature in Monadjem et al. (2010); M.B. Fenton and C. Portfors, unpublished results, cited in Eklöf 2003]. Hence, the visual acuity of *P. nathusii* is by no means exceptional, but rather typical for open air foragers among aerial-hawking bats, presumably including both migratory and more stationary species.

The big brown bat *E. fuscus* seems to use visual cues for nocturnal orientation and navigation purposes (Buchler, Childs 1982) and there is indeed experimental evidence that it can see single bright stars against the night sky (Childs, Buchler 1981). The northern bat *E. nilssonii* occasionally uses vision in prey detection under exceptional circumstances, provided that the prey is large, slow moving and visually conspicuous (Eklöf et al. 2002a). Our analysis demonstrated that the migration activity of *P. nathusii* increased considerably on clear nights, although relatively high activity was also observed on overcast nights. This suggests that *P. nathusii* may use stars and/or other

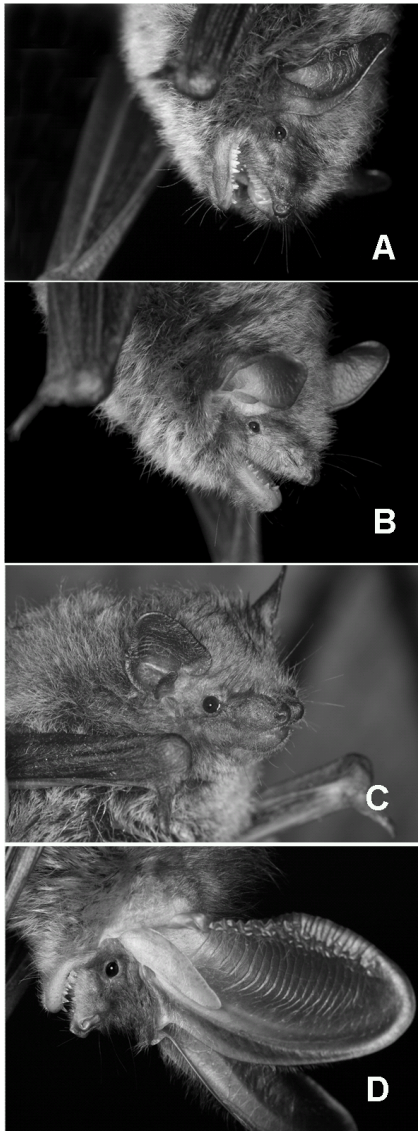


Fig. 2. Portraits of four of the species used in this study, illustrating the differences in eye size. A, *Myotis brandtii*; B, *Myotis daubentonii*; C, *Pipistrellus nathusii*; D, *Plecotus auritus*. The pictures are not exactly to scale; *M. brandtii* and *P. nathusii* are somewhat smaller than the other two species. Photo by J. Rydell.

cues on the night sky for navigation purposes, but also that such cues are by no means the only ones used. Other potential cues include, for example, the earth's magnetic field (Holland et al. 2006).

The visual acuity in bats varies with the ambient light intensity and also with the contrast between the object and the background. In the common vampire bat *Desmodus rotundus*, for example, the acuity drops from 48' at a light intensity of 31 mL (ca. 310 lux) to about 2° at 4×10^{-4} mL (ca. 0.004 lux; Manske, Schmidt 1976). Other bats, such as *Macrotus californicus* (Phyllostomidae) and *Anthrozous pallidus* (Vespertilionidae), both of which are gleaning insectivores or carnivores, retain visual acuity down to light levels as low as 2×10^{-4} mL (ca. 0.002 lux; Bell, Fenton

1986). For comparison, a light level of 0.1 lux is roughly equivalent to the light under full moon and similar to the experimental conditions in this study.

The best optomotor response does not necessarily occur at high or even moderate light intensity. Rather, bats tend to perform best in dim light (Bradbury, Nottebohm 1969). For example, individuals of *E. fuscus* respond optimally to brightness discrimination at ambient light levels of about 10 lux, a condition roughly equivalent to that prevailing at dusk and dawn, but perform well down to 0.001 lux (Ellins, Masterson 1974). As the ambient illumination increases towards daylight, the visual sensitivity generally declines, although the tolerance varies between species (Hope, Bhatnagar 1979). The ambient light level and the way it was measured differ strongly between the tests reported in the literature, sometimes making the results a bit hard to compare.

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