



Det här verket är upphovrättskyddat enligt *Lagen (1960:729) om upphovsrätt till litterära och konstnärliga verk*. Det har digitaliserats med stöd av Kap. 1, 16 § första stycket p 1, för forskningsändamål, och får inte spridas vidare till allmänheten utan upphovsrättsinnehavarens medgivande.

Alla tryckta texter är OCR-tolkade till maskinläsbar text. Det betyder att du kan söka och kopiera texten från dokumentet. Vissa äldre dokument med dåligt tryck kan vara svåra att OCR-tolka korrekt vilket medför att den OCR-tolkade texten kan innehålla fel och därför bör man visuellt jämföra med verkets bilder för att avgöra vad som är riktigt.

This work is protected by Swedish Copyright Law (*Lagen (1960:729) om upphovsrätt till litterära och konstnärliga verk*). It has been digitized with support of Kap. 1, 16 § första stycket p 1, for scientific purpose, and may no be disseminated to the public without consent of the copyright holder.

All printed texts have been OCR-processed and converted to machine readable text. This means that you can search and copy text from the document. Some early printed books are hard to OCR-process correctly and the text may contain errors, so one should always visually compare it with the images to determine what is correct.



# Vision in echolocating bats

Johan Eklöf





# Vision in echolocating bats

Johan Eklöf

Dissertation



Göteborg University

Department of Zoology

Box 463

SE-405 30 Göteborg

Sweden

Avhandling för filosofie doktorsexamen i zoomorfologi, som enligt Naturvetenskapliga fakultetens beslut kommer att offentligens försvaras onsdagen den 28 maj 2003, kl 10:00 i föreläsningssalen, Zoologiska institutionen, Medicinaregatan 18, Göteborg. Fakultetsopponent är Professor Paul Racey, University of Aberdeen.

## Bat - Bats

<b>bat</b> (b <sup>ǎ</sup> t)	<i>n.</i> A binge; a spree
	<i>n.</i> A stout wooden stick; a cudgel
	<i>n.</i> Any of various nocturnal flying mammals of the order Chiroptera, having membranous wings that extend from the forelimbs to the hind limbs or tail and anatomical adaptations for echolocation, by which they navigate and hunt prey
	<i>v.</i> To hit
	<i>v.</i> To wander about aimlessly
	<i>v.</i> To discuss or consider at length
<b>bats</b>	<i>adj.</i> Crazy; insane
<b>bat out</b>	To produce in a hurried or informal manner
<b>off the bat</b>	Without hesitation; immediately
<b>go to bat for</b>	To give assistance to; defend
<b>not bat an eye</b>	To show no emotion; appear unaffected
<b>have bats in (one's) belfry</b>	To behave in an eccentric, bizarre manner

*A doctoral thesis at a university in Sweden is produced either as a monograph or as a collection of papers. In the latter case, the introductory part constitutes the formal thesis, which summarises the accompanying papers. They have already been published or are manuscripts at various stages (in press, submitted or in ms).*



Illustrations by Olof Helje



## Eklöf, J. Vision in echolocating bats

Zoology Department, Göteborg University

**Key words:** acoustic clutter, foraging tactics, Microchiroptera, perception, sensory ecology, ultrasound, visual acuity

### ABSTRACT

The use of ultrasonic echolocation (sonar) in air is seriously constrained by the attenuation of high frequency sounds and unwanted echoes from the background (called clutter). Therefore, in many situations, echolocating bats have to rely on other sensory cues. The aim of this thesis is to investigate the use of vision by echolocating bats.

Bat eyes are generally small, especially among aerial hawking insectivores, with the exception of members of the family Emballonuridae. In gleaning, and in frugivorous species, however, the eyes tend to be larger and more prominent. The eyes of all bats are well adapted to low illumination, having mainly rod-based retinas, large corneal surfaces and lenses, and generally large receptor fields. Bats can easily detect small differences in brightness on clear nights, and the visual acuity remains relatively good in dim illuminations. The visual resolving power (as obtained from counts of retinal ganglion cells or by optomotor response tests) varies considerably among the different species of bats, from less than  $0.06^\circ$  of arc in *Macrotus californicus* (Phyllostomidae) to almost  $5^\circ$  in aerial hawking *Myotis* species (Vespertilionidae). Generally, the visual acuity is similar to that of rats and mice, suggesting that cm-sized object can be discriminated at ranges less than a few metres. Studies on pattern discrimination have yielded highly variable results. Fruit and nectar eating species respond to patterns to a larger extent than aerial insectivores.

One of the most fundamental roles of the eyes is to register the amount of ambient light, in order to establish photoperiodic cycles. Some tropical bats avoid too bright conditions, i.e. moonlit nights probably due to increased predation risk, a behaviour not found in high latitude species.

As sonar only works well at short ranges, vision is primarily used for detection of landmarks and to avoid objects when moving over long distances, for example during seasonal migration and when commuting between feeding sites. In these situations, there seems



to be precedence of vision over sonar. At short range, within that of echolocation, bats may defer to visual cues in addition to sonar and spatial memory to solve different tasks of orientation, especially when there is conflicting information. Light conditions and time of the day may determine the behaviour of the bats and thus which sensory cues will be used.

There is an increasing amount of data suggesting that vision might be of importance in some situations and some aspects of foraging, especially for frugivorous and nectarivorous bats, which can make use of differences in brightness and spectral composition, to find different food items. But even in species traditionally considered to rely heavily on echolocation, such as most insectivorous bats, vision seems to play a more important role than has been recognised previously. The gleaning brown long-eared bat (*Plecotus auritus*, Vespertilionidae), known to forage mostly by using passive listening, detects prey more readily by using vision than by using sonar, and the aerial hawking northern bat (*Eptesicus nilssonii*, Vespertilionidae), use visual information in addition to sonar to find large stationary prey in clutter.

Although echolocation is the key innovation that have made it possible for bats to fly at night, vision is retained as an important complement; and indeed bats use an array of different sensory inputs to solve the different tasks of life.

## Eklöf, J. Syn hos ekolokaliserande fladdermöss

Zoologiska institutionen, Göteborgs universitet

### SAMMANFATTNING

Fladdermöss av underordningen Microchiroptera använder sig av ekolokalisation (sonar; SOund Navigation And Ranging) för att orientera och för att finna byten i mörker. Sonar ersätter således till viss del den funktion som synen har hos många andra djur. På grund av uttunnningen av ljudvågor i luft och så kallat "klotter" är dock räckvidden vanligen begränsad till ett fåtal meter. Fladdermöss måste därför använda sig av andra sinnesintryck för att komplettera den ibland begränsade information som sonar ger. I denna avhandling belyser jag synens roll i fladdermössens liv.

Fladdermössens ögon är vanligen små och kan verka obetydliga, men variationen är stor. Hos arter som plockar byten från underlag (gleaners) och bland fruktätare finner man de största ögonen. Alla fladdermusögon är dock anpassade för svagt ljus, med stora linser och breda receptorfält. Fladdermöss är relativt bra på att upptäcka små skillnader i belysning och deras synskärpa försämras inte nämnvärt i ljusförhållanden vi skulle uppfatta som totalt mörker. Synskärpa eller upplösningsförmåga varierar dock mycket mellan olika arter. Man kan mäta upplösningsförmåga antingen teoretiskt genom att räkna ganglieceller i ögat, eller genom beteendestudier, i vilka fladdermössen presenteras med roterande linjemönster av olika storlek. Vissa av våra svenska *Myotis*-arter ser inte mycket bättre än att de kan separera objekt med  $5^\circ$  mellanrum, medan den amerikanska *Macrotus californicus* kan separera objekt med mindre än  $0.06^\circ$ , vilket ungefär motsvarar upplösningsförmågan hos en hund. Huruvida fladdermöss kan skilja ut olika former och mönster med hjälp av synen verkar också variera betydligt mellan olika arter, men generellt verkar frukt- och nektarätare vara bättre på detta än sina insektsätande släktingar.

En av de mest grundläggande av ögats funktioner är att registrera mängden ljus i omgivningen och på så vis kalibrera den inre klockan. Vissa tropiska fladdermöss undviker att flyga ut om natten är för ljus, till exempel då det är fullmåne, ett beteende vi inte finner i någon högre utsträckning bland fladdermössen på våra breddgrader. Eftersom sonar endast fungerar tillfredsställande på korta avstånd, används synen främst på längre håll, för att till exempel finna landmärken

och för att undvika hinder på väg till och från födoplatser, eller under migration. I sådana situationer verkar det som om synintryck är viktigare än information från sonar. Även inom räckvidden för sonar kan man ibland se att fladdermöss förlitar sig till synen, särskilt om sonar- och synintryck står i konflikt. Mängden ljus och tiden på dygnet kan också avgöra vilket av sinnena som har företräde.

Frukt- och nektarätande fladdermöss har generellt sett bättre syn än insektsätare och kan förmodas utnyttja synen i relativt stor utsträckning då de söker efter föda. Men även insektsätare tar hjälp av syninformation då det behövs. Långörad fladdermus *Plecotus auritus* plockar ofta stillasittande insekter från blad och använder då framför allt sin känsliga hörsel för att lokalisera ljud som bytena själva åstadkommer. Den använder dock synintryck hellre än ekolokalisation som komplement till den passiva hörseln. Nordisk fladdermus *Eptesicus nilssonii* använder sig delvis av syn för att finna stora stillastående byten bland växtlighet, byten som är svåra att urskilja med hjälp av sonar. Detta trots att de har en relativt begränsad visuell upplösningsförmåga, ca 1°, vilket är ungefär 60 gånger sämre än en människas.

Ekolokalisationen är utan tvekan det som gjort fladdermössen till en av de mest framgångsrika och mångskiftande däggdjursgrupperna på jorden. De har dock behållit ett funktionellt synsinne som ett viktigt komplement. De, liksom vi använder sig av så många olika sinnesintryck som möjligt för att lösa livets uppgifter.

## CONTENTS

INTRODUCTION.....	10
VISION IN ECHOLOCATING BATS	
The microchiropteran eye.....	12
The brain and the retinal pathways.....	15
What bats can see.....	17
Vision in orientation and navigation.....	24
Vision in foraging and prey detection.....	27
Predator surveillance and social behaviour.....	33
Multimodality – vision and echolocation.....	34
ACKNOWLEDGEMENTS.....	38
REFERENCES.....	39
PAPER I. <b>Eklöf, J.</b> & Jones, G. 2003. Use of vision in prey detection by brown long-eared bats <i>Plecotus auritus</i> . - Animal Behaviour (In Press).....	48
PAPER II. <b>Eklöf, J.</b> , Svensson, A. M. & Rydell, J. 2002. Northern bats ( <i>Eptesicus nilssonii</i> ) use vision but not flutter-detection when searching for prey in clutter. - Oikos 99, 347-351.....	62
PAPER III. <b>Rydell, J.</b> & <b>Eklöf, J.</b> 2003. Vision complements echolocation in the aerial hawking northern bat ( <i>Eptesicus nilssonii</i> ) - Submitted manuscript.....	70
PAPER IV. <b>Eklöf, J.</b> 2003. Visual acuity and eye size in insectivorous bats. - Manuscript.....	80
PAPER V. <b>Eklöf, J.</b> , Tranefors, T. & Vázquez, L-B. 2002. Precedence of visual cues in the emballonurid bat <i>Balantiopteryx plicata</i> . - Mammalian Biology 67, 42-46.....	92
PAPER VI.    Karlsson, B-L., <b>Eklöf, J.</b> & Rydell, J. 2002. No lunar phobia in swarming insectivorous bats (family Vespertilionidae). - Journal of Zoology London 256, 473-477.....	100



**B**ats (Order: Chiroptera) are among the most diverse and abundant mammals on earth and the thousand or so species comprise about one fourth of all mammalians. Bats occur throughout the world, except the Polar Regions, and show a remarkable wide range of habitat use, behaviour, morphology, and diet. Most bats feed on insects but there are also bats that feed on fruit, nectar, fish, small vertebrates, and blood. Bats are the only mammals that have evolved active flight, and they can navigate through complete darkness by using echolocation or sonar (SOund Navigation And Ranging). Bats live almost everywhere, in tropical jungles as well as in cities; they inhabit caves, trees, houses, churches, bridges, coiled banana leaves, bamboo canes, and some species even build their own tents by using large leaves. Bats have a remarkable spatial memory and are quick learners. They can form colonies of up to 20 million individuals, eat hundreds or thousands of insects every night and migrate across continents. Many bats hibernate through a cold winter and some can reach more than 40 years of age. Despite this, bats are seldom people's number one choice of favourite animal. Instead, bats have become symbols of darkness, doom and occultism in the western world. They often appear in not so flattering contexts, such as in myths, scary movies, heavy metal lyrics, and are often one of the most important ingredients in witches' brews. Being called an old bat is not a compliment, and having a bat in one's belfry is not very often socially accepted. In the eastern world, however, bats are considered as symbols of fortune and a long, prosperous life. Nevertheless, the bats' leathery wings and their ability to navigate through the night are presumably two reasons behind their often somewhat scary reputation, as well as the two main reasons behind their success as a group. But how do they perceive the world; or as Thomas Nagel (1974) put it in his classic paper: what is it like to be a bat?

All information about the surrounding world is filtered through our senses and processed in our brains in order to give us just the right kind and amount of information to help us make proper decisions. This is true for all animals, although the senses receiving the information and the brains that process it differ across the animal kingdom. The type and amount of information that is needed obviously varies considerably depending on life style. What humans cannot perceive tend to be called ultra-, infra-, or extra-something. We do not know what ultraviolet light looks like, only that it gives us a nice tan. We cannot hear infrasounds although elephants can, which is why we and not the elephants invented

the telephone. Many animals live entirely in the world of ultra-, or infra-, making it hard for us to relate to their every day life, or as Thomas Carlyle (1837) elegantly put it: “In every object there is inexhaustible meaning; the eye sees in it what the eye brings means of seeing. To Newton and to Newton’s dog Diamond, what a different pair of universes.” Bat echolocation is different from any of the senses that we are familiar with, and therefore, we cannot know or even imagine how they experience the world; or as in the words of Thomas Nagel (1974): “Anyone who has spent some time in an enclosed space with an excited bat knows what it is to encounter a fundamentally alien form of life.” With this in mind, it may seem impossible to study sensory ecology, and still, we try. We accept that there is information outside our perception range, although we will never be able to fully understand those things. We may perhaps be able to understand how a bat collects and uses information from the environment, but never what this really is like for the bat. We may however, from a human point of view, describe behaviour and reactions of animals under defined conditions. For example, when studying bats flying, and recording and describing echolocation calls, we can tell that sonar is a high precision tool, as good as vision for perceiving and identifying objects, only entirely different. But we begin to understand that echolocation alone is not enough to fully experience the world as a bat. As high frequency sounds attenuate rapidly in air, the effective range of echolocation is limited to a few metres in practice. Background echoes, known as clutter, also impose severe constraints on the use of sonar, and for a bat to perceive distant objects or objects hidden in vegetation, other senses must be used. One of these senses is vision. However, looking at a typical bat eye gives little hope of any breathtaking visual adventures. The eyes are often small and inconspicuous, especially compared to the more fanciful ears and nose-leafs of many bats, and considering our own sensory limits and the fact that bats fly at night, it is not hard to imagine why an expression like “as blind as a bat” exists. But still, bats do have eyes and perhaps “as blind as we would be if we had bat eyes” would be a more suitable expression. As I will discuss in this thesis, bats do have eyes that function for bats. In the same way humans have a sense of smell that function for humans, although a dog, or a bat for that matter, probably would not be impressed!

The aim of this introductory chapter is to put my work into perspective by summarizing current knowledge of the role of vision in the lives of the echolocating bats.

# VISION IN ECHOLOCATING BATS

## The microchiropteran eye

The eyes of Microchiroptera<sup>1</sup> rank among the smallest in mammals (Tab 1), although there are considerable differences in both eye size and morphology across species, reflecting a great ecological diversity (Chase 1972; Hope & Bhatnagar 1979a; b; Marks 1980; Suthers & Bradford 1980; Bell & Fenton 1986; **Paper IV**). In general, the eyes of frugivorous and nectarivorous Microchiroptera are larger than those of insectivorous species. Bats roosting in relatively exposed sites, and those that sometimes are active in dusk- and daylight conditions such as many members of the family Emballonuridae also have relatively large eyes. Hence eye size seems to reflect how much bats are exposed to light in their daily life.

Footnote 1. The Microchiroptera includes ca 800 species of echolocating bats but excludes the generally non-echolocating Megachiroptera or flying foxes, which are not considered in this thesis.

Tab 1 - Eye size in Microchiroptera in relation to taxonomic affinity and general feeding behaviour.

Family & Species	Eye ball axial length (mm)	Lens axial diameter (mm)	Lens radial diameter (mm)	Eye-weight (mg)	Mean body-weight (g)
<b>Vespertilionidae</b> gleaning insectivores					
<i>Plecotus auritus</i>	---	---	1.65 <sup>7</sup>	---	7 <sup>6</sup>
<i>Myotis myotis</i>	3.1 <sup>2</sup>	1.3 <sup>2</sup>	1.6 <sup>2</sup>	---	26 <sup>6</sup>
<b>Vespertilionidae</b> aerial-hawking insectivores					
<i>Eptesicus fuscus</i>	---	0.77 <sup>9</sup>	0.91 <sup>9</sup>	6 <sup>4</sup>	14 <sup>4</sup>
<i>Myotis sodalis</i>	1.68 <sup>1</sup>	0.6 <sup>1</sup>	0.94 <sup>1</sup>	---	7.3 <sup>8</sup>
<i>Myotis lucifugus</i>	---	---	---	4.4 <sup>4</sup>	10 <sup>4</sup>
<i>Nyctophilus gouldi</i>	1.9 <sup>5</sup>	---	---	---	10.5 <sup>11</sup>
<i>Myotis mystacinus</i>	---	---	0.95 <sup>7</sup>	---	5 <sup>6</sup>
<i>Myotis daubentonii</i>	---	---	1.25 <sup>7</sup>	---	10 <sup>10</sup>
<i>Nyctalus noctula</i>	1.7 <sup>2</sup>	1.03 <sup>2</sup>	1.43 <sup>2</sup>	---	27 <sup>6</sup>
<b>Emballonuridae</b> aerial-hawking insectivores					
<i>Saccopteryx bilineata</i>	2.6 <sup>9</sup>	1.5 <sup>9</sup>	1.8 <sup>9</sup>	10.4 <sup>9</sup>	7 <sup>9</sup>
<i>Saccopteryx leptura</i>	---	1.1 <sup>9</sup>	1.4 <sup>9</sup>	7.4 <sup>9</sup>	4 <sup>9</sup>
<i>Rhynchonycteris naso</i>	---	---	---	4.6 <sup>9</sup>	3 <sup>9</sup>



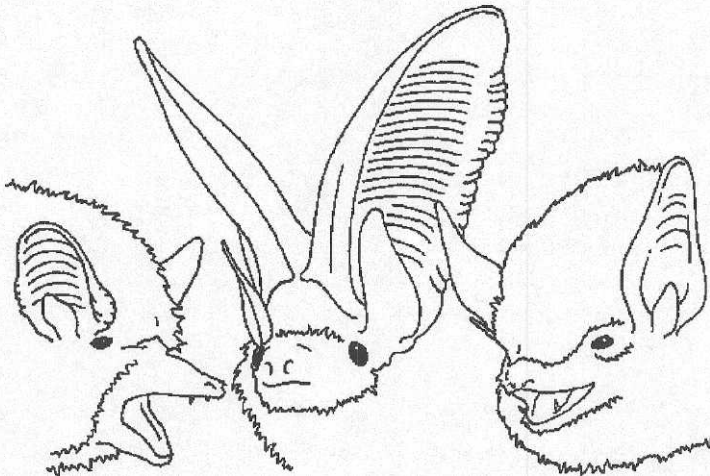
Tab 1 - cont

Species	Eye ball axial length (mm)	Lens axial diameter (mm)	Lens radial diameter (mm)	Eye-weight (mg)	mean body-weight (g)
<b>Molossidae</b>					
aerial-hawking insectivores					
<i>Molossus ater</i>	---	---	---	3.44 <sup>9</sup>	26 <sup>9</sup>
<i>Eumops perotis</i>	3.3 <sup>6</sup>	---	---	---	48 <sup>6</sup>
<b>Natalidae</b>					
aerial-hawking insectivores					
<i>Natalus tumidirostris</i>	0.66 <sup>9</sup>	---	---	0.6 <sup>9</sup>	6 <sup>9</sup>
<b>Rhinolophidae</b>					
flutter-detecting insectivores					
<i>Rhinolophus rouxi</i>	1.8 <sup>5</sup>	---	---	---	---
<i>Rhinolophus hipposideros</i>	---	0.49 <sup>9</sup>	0.68 <sup>9</sup>	---	7 <sup>12</sup>
<b>Megadermatidae</b>					
gleaning insectivores/carnivores					
<i>Macroderma gigas</i>	7.0 <sup>5</sup>	---	---	---	120 <sup>6</sup>
<b>Phyllostomidae</b>					
frugivores and nectarivores					
<i>Carollia perspicillata</i>	2.62 <sup>1</sup>	1.28 <sup>1</sup>	1.75 <sup>1</sup>	8.5 <sup>4</sup>	16 <sup>4</sup>
<i>Micronycteris megalotis</i>	3.9 <sup>9</sup>	1.9 <sup>9</sup>	2.4 <sup>9</sup>	1.04 <sup>9</sup>	6 <sup>9</sup>
<i>Phyllostomus hastatus</i>	3.94 <sup>1</sup>	1.95 <sup>1</sup>	2.44 <sup>1</sup>	40 <sup>3</sup>	77 <sup>3</sup>
<i>Glossophaga soricina</i>	2.0 <sup>9</sup>	---	---	6.22 <sup>9</sup>	9 <sup>9</sup>
<i>Anoura geoffroyi</i>	---	---	---	14 <sup>3</sup>	15 <sup>3</sup>
<i>Sturnira lilium</i>	---	2.0 <sup>9</sup>	2.3 <sup>9</sup>	11.75 <sup>9</sup>	18 <sup>9</sup>
<i>Vampyrops helleri</i>	---	---	---	24.2 <sup>9</sup>	12 <sup>9</sup>
<i>Chiroderma villosum</i>	---	1.9 <sup>9</sup>	2.2 <sup>9</sup>	70.0 <sup>9</sup>	40 <sup>9</sup>
<i>Artibeus jamaicensis</i>	4.0 <sup>6</sup>	---	---	27.4 <sup>4</sup>	38 <sup>4</sup>
<i>Artibeus lituratus</i>	---	---	---	30.4 <sup>9</sup>	61 <sup>9</sup>
<b>Phyllostomidae</b>					
sanguivores					
<i>Desmodus rotundus</i>	2.5 <sup>7</sup>	---	---	11 <sup>4</sup>	29 <sup>4</sup>
<i>Diaemus youngi</i>	---	---	---	14.1 <sup>9</sup>	40 <sup>9</sup>
<b>Noctilionidae</b>					
piscivores					
<i>Noctilio leporinus</i>	2.1 <sup>6</sup>	---	---	---	58 <sup>6</sup>
<b>Mormoopidae</b>					
aerial-hawking insectivores					
<i>Mormoops megalophylla</i>	---	---	---	1.8 <sup>9</sup>	16 <sup>9</sup>
<i>Pteronotus davyi</i>	---	0.35 <sup>9</sup>	0.7 <sup>9</sup>	1.16 <sup>9</sup>	7 <sup>9</sup>
<i>Pteronotus parnellii</i>	0.9 <sup>9</sup>	0.42 <sup>9</sup>	0.7 <sup>9</sup>	0.90 <sup>9</sup>	18 <sup>9</sup>

<sup>1</sup> Suthers & Wallis 1970, <sup>2</sup> Suthers 1970, <sup>3</sup> Suthers & Bradford 1980, <sup>4</sup> Marks 1980,<sup>5</sup> Pettigrew et al. 1988, <sup>6</sup> Baron et al. 1996a, <sup>7</sup> Paper IV, <sup>8</sup> Thomson 1982, <sup>9</sup> Chase 1972,<sup>10</sup> Bogdanowicz 1994, <sup>11</sup> Grant 1991, <sup>12</sup> Greenway & Hutson 1990

The microchiropteran eyes are shaped for nocturnal conditions in that they have large corneal surfaces and lenses relative to the size of the eye. They also have relatively large receptor fields, which give them good light gathering power at the expense of acuity, i.e. the ability to resolve fine spatial details (Suthers 1970; Suthers & Wallis 1970). The bat retina, which is relatively thin (91-126  $\mu\text{m}$ ) compared to that of voles (178  $\mu\text{m}$ ) and rats (198  $\mu\text{m}$ ), for example, consists mainly of rods, which are arranged loosely in visual streaks (Chase 1972; Marks 1980; Pettigrew et al. 1988). However, cones or at least cone like structures (receptor cells with pedicles) are present at least in the fruit-eating bats *Artibeus lituratus* and *Phyllostomus hastatus* (Phyllostomidae) and the aerial hawking insectivorous *Saccopteryx bilineata*, *Saccopteryx leptura* and *Rhynconycteris naso* (Emballonuridae) (Suthers 1970; Chase 1972).

Suthers and Wallis (1970) studied the eyes of two species of Vespertilionidae (*Myotis sodalis* and *Pipistrellus subflavus*) and four species of Phyllostomidae (the vampire bat *Desmodus rotundus*, and the fruit-eating *Carollia perspicillata*, *Anoura geoffroyi* and *Phyllostomus hastatus*), and concluded that the visual capabilities of all the species tested would allow the bats to see well at ranges beyond that of echolocation. Due to the more or less spherical lenses (small species tend to have more asymmetric lenses; Chase 1972), it also follows that most Microchiroptera have a short focal distance and hence a great depth of focus (Suthers & Wallis 1970). In fact, microchiropteran bats seem to be farsighted, indicating that vision is used predominantly at long ranges, which is where echolocation does not work so well.



The eye size and visual performance vary considerably between different species of Vespertilionidae. The northern bat *Eptesicus nilssonii* (left) has a visual acuity of ca 0.8° arc, the brown long eared-bat *Plecotus auritus* (middle), ca 0.5° arc, and *Myotis* spp. (right), 3 - 6° arc (Paper III, Paper IV).

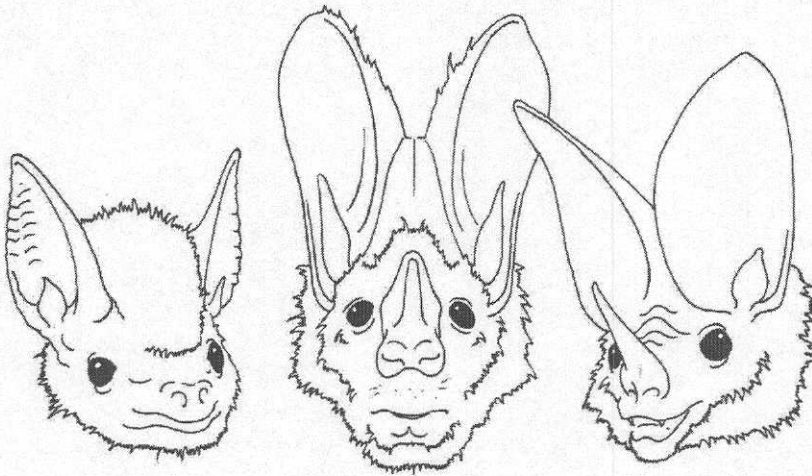
## The brain and the retinal pathways

The relative size of the internal brain structures of bats differs between insectivorous, sanguivorous and carnivorous species on one hand and frugivorous and nectarivorous species on the other (Jolicœur & Baron 1980; Barton et al. 1995; Barton & Harvey 2000). Whereas insect eating bats have enlarged echo-acoustic brain structures, fruit eating species have relatively large olfactory- and visual bulbs, clearly reflecting the different feeding strategies in the various species.

The size and lamination of the main targets of retinal projections in the brain: the superior colliculus (which transmits visual information and controls head- and eye movements) and the lateral geniculate body (a processing station on the way from the retina to the visual centre, which e.g. serves to enhance contrasts) have been studied in *Artibeus*, *Eptesicus* (Cotter 1985), *Myotis* (Cotter & Pentney 1979; Crowle 1980) and *Pteronotus* (Covey et al. 1987). Megadermatids and fruit eating phyllostomids show the thickest and most developed layers in the superior colliculus, at least in the superficial ones, which receive exclusively visual input. Also gleaning species tend to have relatively large superior colliculi. Open-air insectivorous species on the other hand, seem to have superior colliculi consisting almost entirely of the deeper layers, which receive a variety of different sensory inputs (including visual stimuli). However, some insectivorous bats, like the Emballonuridae (especially *Saccopteryx* and *Cyttarops*) have relatively large superior colliculi and resemble frugivores in this respect, although their total brain volume is smaller than in most other microchiropteran families (Baron et al. 1996b). This may perhaps reflect the fact that most emballonurid species roost in exposed sites and therefore live in bright light conditions. However, considering that the Emballonuridae form a basal clade in the phylogenetic tree, it may just as well suggest that bat ancestors had a well-developed visual system. (Simmons & Geisler 1998). The projections to the superior colliculus are similar to those of most mammals, in that they have no binocular overlap, and thus the left superior colliculus receives input only from the right eye and vice versa (Pettigrew 1986; Neuweiler 2000). In Megachiroptera and in primates, both superior colliculi receive input from both eyes, and hence these animals have better stereoscopic vision than Microchiroptera. (Interestingly the microchiropteran family Rhinolophidae, which contain highly specialized echolocators, show similarities to Megachiroptera in this respect (Reimer 1989). This may reflect phylogenetic relationship rather than visual adaptation, however (e.g. Springer et al. 2001)).

The lateral geniculate body consists of two parts, the ventral lateral geniculate, which has connections with several other brain

structures, and the dorsal lateral geniculate, which connects to the visual cortex. In most Microchiroptera, a larger proportion of the nerves are projected to the ventral side of the lateral geniculate body, suggesting that vision is important for orientation rather than for cognitive tasks (Neuweiler 2000). However, the sizes of the retinal pathways vary between genera. The nerves are generally larger in frugivores (*Phyllostomus hastatus*, *Anoura geoffroyi*, Suthers & Bradford 1980; and *Artibeus jamaicensis*, Cotter 1985) than in insectivores (*Eptesicus fuscus*, Cotter 1985; and *Pteronotus parnellii*, Covey et al. 1987), although, again, insectivorous Emballonuridae and Megadermatidae are exceptions. Both have relatively large visual pathways projecting through the dorsal lateral geniculate to the visual cortex. This suggests that vision is more important in these species, and they show similarities to the visually oriented Megachiroptera in this respect (Neuweiler 2000), and may reflect phylogenetic relationship (Springer et al. 2001). For a comparison of different brain structures between all groups of Microchiroptera, see Baron et al. (1996a; b; c).



Three examples of large-eyed bats: Species of the family Emballonuridae (left) have larger eyes than other insectivorous aerial-hawkers, probably reflecting an unusual visual capacity among bats. The large eyed *Megaderma lyra* (Megadermatidae) (middle) show a flexible hunting strategy and uses vision in combination with sonar and passive hearing. *Macrotus californicus* (Phyllostomidae) (right) is the only microchiropteran bat shown to be capable of catching insects using vision alone.

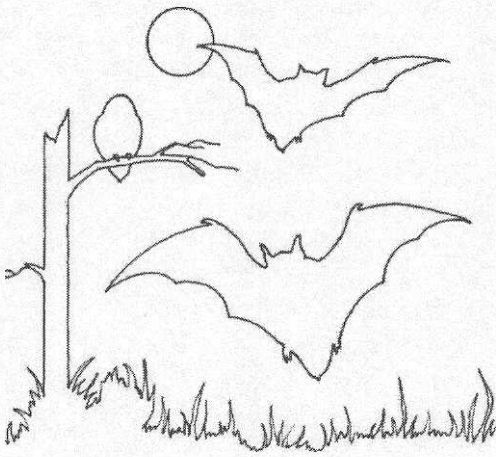
## What bats can see

### *Brightness discrimination and light sensitivity*

At the most basic level, vision is involved in the establishment of photoperiodic cycles, and serves to distinguish daylight from darkness. It was previously believed that this was the sole purpose of the microchiropteran eye (Eisentraut 1969 cited in Dietrich & Dodt 1970). The bat's activity cycle is controlled by an endogenous circadian rhythm, which is synchronized with the daylight cycle by light sampling behaviour. This means that, before they emerge from the roost to feed, the bats move from the darker areas in their roosts to lighter areas near the entrance, in order to test the outdoor light level (Erkert 1982). Cloudiness and moonlight can thus affect the time of emergence. On moonlit nights, many tropical microchiropterans typically reduce their foraging activity, presumably due to increased predation risk (Morrison 1978; Usman et al. 1980; Fleming 1988) or perhaps lower availability of food (Lang et al. 2002). In contrast, bat activity at high latitudes is not influenced by moonlight to any high extent (**Paper VI**). On twelve nights in August-September 2000, the impact of moonlight on bat swarming activity (associated with mating season) was studied at an abandoned mine in southern Sweden. Bat activity at and near the mine entrance did not vary with moon phase, or cloud cover, suggesting that moonlight had no effect on the bats' behaviour. It seems likely that insectivorous bats at high latitudes may not have been exposed to significant nocturnal predator pressure, leading to the evolution of lunar phobia, as many tropical bats. In contrast to high-latitude bats, the latter have to face specialized bat predators such as bat falcons (*Falco rufigularis*). Furthermore, high latitude bats are exposed to relatively bright light conditions throughout the summer. They do react to light, but not by decreasing their activity, instead, they fly closer to protective vegetation or sometimes high in the air (Rydell et al. 2002). This kind of behaviour is also seen in species that migrate during the day, such as the noctule, *Nyctalus noctula* (Ahlén 1997). Both types of behaviour may have the purpose of avoiding predatory birds (e.g. small hawks and falcons).

The ability of bats to detect small differences in brightness, i.e. brightness discrimination, was first studied by Eisentraut (1950), who found that *Plecotus auritus* and *Eptesicus serotinus* (Vespertilionidae) could easily distinguish black cards from white. Curtis (1952) trained the vespertilionids *Eptesicus fuscus* and *Myotis lucifugus* to search for food at the illuminated end of a box, and found that the bats' ability of brightness discrimination is similar to that of rats and mice. Brightness discrimination performance in *Eptesicus fuscus* peaks around

10 lux, which is equivalent to the light level prevailing at dusk and dawn, but remains good in illuminations as low as 0.001 lux, conditions which resembles darkness to a human eye adapted to low light intensity. As a comparison, a light level of 0.1 lux is equivalent to light levels at full moon, and on overcast nights the amount of light drops to 0.0001 lux (Ryer 1997). Based on focal distance and diameter of the dilated pupil, Dietrich and Dodt (1970) calculated that the light gathering power of *Myotis myotis* is 4-5 times that of man. This suggests that bats can readily use visual cues at dusk, when they normally emerge from their roosts, and probably also under nocturnal conditions (Ellins & Masterson 1974).



Many tropical bats minimize their activity in moonlight, presumably due to predation risk. This behaviour is not found among high latitude bats (Paper VI)

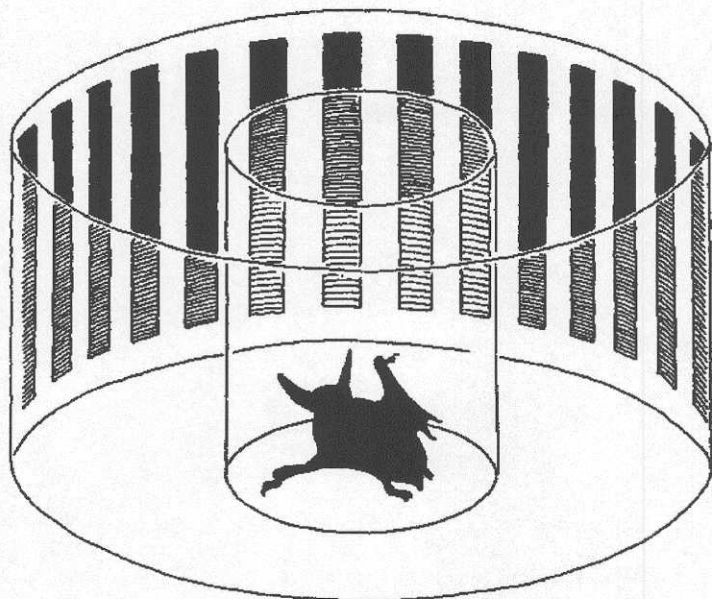
As may be expected from a retina consisting predominantly of rods, the visual sensitivity generally declines as the ambient illumination increases towards daylight (Hope & Bhatnagar 1979b). This indicates that the bat eyes work better in dim light than in bright light. This has been verified behaviourally by Bradbury & Nottebohm (1969), who found that *Myotis lucifugus* avoids obstacles better under ambient illuminations resembling dusk, than they do in bright daylight. These findings may explain why early studies, which were made in room illumination, usually failed to prove any major visual capacity in microchiropteran bats (e.g. Eisentraut 1950; Curtis 1952).

Light tolerance has been estimated in three species of Vespertilionidae (*Myotis myotis*, Dietrich & Dodt 1970; *Eptesicus serotinus*, Bornschein 1961; and *Eptesicus fuscus*, Hope & Bhatnagar

1979b) and three species of Phyllostomidae (*Desmodus rotundus*, *Carollia perspicillata*, and *Artibeus jamaicensis*, Hope & Bhatnagar 1979b) by measuring the luminance of light stimuli required to provoke electroretinogram responses. Among the vespertilionids, *Eptesicus fuscus* showed the highest light tolerance, and among the phyllostomids, which generally responded to lower luminance levels than the vespertilionids, *Artibeus jamaicensis* showed the highest tolerance. This presumably reflects the relative importance of vision in the different species, but perhaps more importantly the time at which these species normally emerge in the evening, and to what extent they are exposed to bright light (Hope & Bhatnagar 1979a; b). The Emballonuridae *Emballonura* spp. and *Saccopteryx* spp., some of which roost at exposed sites and often fly in daylight (Lekagul & McNeely 1977; Bradbury & Vehrencamp 1976; Kalko 1995), would thus be expected to be more light tolerant than other bats. Although, light tolerance levels have not been measured in these bats directly, the small receptive fields and the low receptor-to-ganglion ratio (ca 1:10) in *Saccopteryx* spp., compared to that of other microchiropteran species (ca 1:100), indicate a high light tolerance and good resolving power as expected. In fact they resemble diurnal mammals in this respect (Chase 1972). Nevertheless, the eyes of Microchiroptera work well under low ambient illumination, although the sensitivity to different light levels and the ability of brightness discrimination vary considerably between the different families and species.

### *Spatial resolution*

The eyes of microchiropterans are primarily adapted to function in low light levels. This carries the disadvantage of a relative poor ability to resolve fine spatial details (acuity). The ability of spatial resolution of the bat eye can be estimated either anatomically, by calculating the density of retinal ganglion cells (Marks 1980; Pettigrew et al. 1998; Heffner et al. 2001) or behaviourally, by presenting the bats with striped patterns of different fineness (Suthers 1966; Bell & Fenton 1986; Paper IV). When the visual acuity is measured with the latter method, it is often referred to as grating acuity and is expressed as degrees of arc or as cycles per degree, where one cycle is one pair of black and white stripes. The two methods give indications of the minimum separable angles, i.e. the minimum distance between two points that an animal needs in order to separate them.



The device used for the optomotor response tests (**Paper IV**), in which a bat is presented with rotating, striped patterns of different fineness. The bat responds to the revolving patterns by moving its head in a stereotype manner. The thickness of the stripes corresponds to the bats visual resolving power (acuity), measured as degrees of arc.

Comparisons between the two methods should be treated carefully because the acuity values estimated by counting retinal ganglion cells tend to be higher than those estimated from behavioural studies. This suggests that the anatomical method gives a theoretical minimum, rather than an indication of what the bats actually respond to. Nevertheless, Table 2 should give an idea of the wide range of spatial resolution ability that has been documented in different species of microchiropteran bats, from the coarse vision of the small *Myotis* spp. (Vespertilionidae) (3-5° arc, **Paper IV**) to the relatively fine visual ability of *Macrotus californicus* (Phyllostomidae) (0.06° arc, Bell & Fenton 1986). *Macrotus californicus* has by far the best resolving power found in any microchiropteran bat studied so far, and is comparable to that of a dog in this respect (Heffner & Heffner 1992). It is also the only microchiropteran known to be capable of detecting insects, using vision alone (Bell 1985).



The visual resolving power is never a fixed value, but depends on the ambient light intensity. In the common vampire bat *Desmodus rotundus*, for example, the acuity drops from 0.8° arc at a light intensity of ca 310 lux to over 2° arc in ca 0.004 lux (Manske & Schmidt 1976). Other bats, such as *Macrotus californicus* (0.06° arc) and *Antrozous pallidus* (0.25° arc) retain their visual acuity down to light levels as low as ca 0.002 lux (Bell & Fenton 1986). In comparison, species of Megachiroptera, which do not echolocate, has been shown to respond to striped patterns of 0.8° in light levels of ca 0.0005 lux, whereas humans responds only to patterns of 1.3° arc under the same conditions (Neuweiler 1967). Hence, in very dim light, bats can see better than humans.

Tab 2 - Visual acuity in Microchiroptera (expressed as degrees of arc). Behavioural acuity values (b) come from optomotor response tests, and theoretical values (t) are calculated from the number of ganglion cells per unit area of the retina. Acuity is the minimum separable angle, i.e. the best values obtained for each species. Asterisks (\*) indicate that the ambient light level was not measured (or that acuity was measured theoretically). For consistency, the values of visual acuity and light levels were sometimes converted from other units, used in the original paper.

Species	Light (lux)	Visual acuity	Reference	Method
<b>Vespertilionidae;</b> gleaning insectivores				
<i>Antrozous pallidus</i>	0.004	0.25°	Bell & Fenton 1986	b
<i>Plecotus auritus</i>	0.7	0.5°	<b>Paper IV</b>	b
<b>Vespertilionidae;</b> aerial-hawking insectivores				
<i>Eptesicus fuscus</i>	*	1°	Bell & Fenton 1986	b
<i>Eptesicus fuscus</i>	*	0.7°	Koay et al. 1998	t
<i>Eptesicus nilssonii</i>	1-10	0.8°	<b>Paper III</b>	-
<i>Eptesicus capensis</i>	3600-4800	0.9°	Fenton & Portfors unpubl	b
<i>Eptesicus zuluensis</i>	4400	0.9°	Fenton & Portfors unpubl	b
<i>Myotis lucifugus</i>	*	3-6°	Suthers 1966	b
<i>Nyctophilus gouldi</i>	*	0.8°	Pettigrew et al. 1988	t
<i>Myotis brandtii</i>	0.1	5°	<b>Paper IV</b>	b
<i>Myotis mystacinus</i>	0.1	5°	<b>Paper IV</b>	b
<i>Myotis daubentonii</i>	0.1-0.3	5°	<b>Paper IV</b>	b
<i>Mimiopterus schreibersii</i>	33	0.9°	Fenton & Portfors unpubl	b
<i>Pipistrellus nanus</i>	6400	0.9°	Fenton & Portfors unpubl	b
<i>Pipistrellus rueppellii</i>	3200	0.9°	Fenton & Portfors unpubl	b
<i>Scotophilus borbonicus</i>	40-5500	0.9°	Fenton & Portfors unpubl	b
<i>Nycticeius schlieffeni</i>	5000	1.5°	Fenton & Portfors unpubl	b
<b>Emballonuridae</b> aerial-hawking insectivores				
<i>Saccopteryx bilineata</i>	*	0.5°	Pettigrew et al. 1988	t
<i>Saccopteryx leptura</i>	*	0.7°	Suthers 1966	b
<i>Taphozus georgianus</i>	*	0.4°	Pettigrew et al. 1988	t

Tab 2 – cont

Species	Light (lux)	Visual acuity	Reference	Method
<b>Molossidae;</b> aerial-hawking insectivores				
<i>Molossus ater</i>	*	10°	Chase 1972	b
<i>Tadarida pumila</i>	81-5800	0.9°	Fenton & Portfors unpubl	b
<i>Tadarida midas</i>	20000	0.9°	Fenton & Portfors unpubl	b
<b>Rhinolophidae</b> flutter-detecting insectivores				
<i>Rhinolophus rouxi</i>	*	1.4°	Pettigrew et al. 1988	t
<i>Rhinolophus fumigatus</i>	160-4800	0.9°	Fenton & Portfors unpubl	b
<b>Megadermatidae</b> gleaning insectivores/carnivores				
<i>Megaderma lyra</i>	*	0.3°	Pettigrew et al. 1988	t
<i>Macroderma gigas</i>	*	0.3°	Pettigrew et al. 1988	t
<b>Phyllostomidae</b> frugivores and nectarivores				
<i>Carollia perspicillata</i>	*	0.3°	Suthers 1966	b
<i>Glossophaga soricina</i>	*	3°	Chase 1972	b
<i>Anoura geoffroyi</i>	*	0.7°	Suthers 1966	b
<i>Sturnira lilium</i>	*	0.3°	Chase 1972	b
<i>Artibeus jamaicensis</i>	*	0.5°	Heffner et al. 2001	t
<i>Artibeus cinereus</i>	*	0.4°	Pettigrew et al. 1988	t
<b>Phyllostomidae</b> sanguivores				
<i>Desmodus rotundus</i>	*	0.7°	Suthers 1966	b
<i>Desmodus rotundus</i>	3.1	0.8°	Manske & Schmidt 1976	b
<i>Desmodus rotundus</i>	0.04	2.5°	Manske & Schmidt 1976	b
<i>Diademus youngi</i>	*	3°	Chase 1972	b
<b>Phyllostomidae</b> Gleaning insectivores				
<i>Macrotus californicus</i>	0.002	0.06°	Bell & Fenton 1986	b
<b>Other mammals;</b>				
<i>Rattus</i> (rat)	*	0.3°	Heffner & Heffner 1992	t
<i>Canis</i> (dog)	*	0.06°	Heffner & Heffner 1992	t
<i>Felis</i> (cat)	*	0.045°	Hughes 1977	t
<i>Macaca</i> (macaque)	*	0.01°	Cowey & Ellis 1967	b
<i>Homo</i> (man)	*	0.009°	Hughes 1977	t
<i>Homo</i> (man)	0.0005	1.3°	Neuweiler 1967	b

### *Pattern discrimination*

Bats can visually distinguish patterns and shapes of objects. The nectarivorous *Anoura geoffroyi* (Phyllostomidae) distinguishes rectangles from solid discs of the same surface area, when trained to seek food at the discs (Suthers & Chase 1966; Suthers et al. 1969). This species is also able to distinguish outlines of erected triangles from inverted ones, as long as the baselines of the triangles are intact. However, when the bats were presented with two sides of a triangle, i.e. an outline of a triangle without a base, the shape was no longer distinguished from other shapes. This indicates that *Anoura geoffroyi* does not possess a concept of form, but rather perceive the relative position of horizontal lines. Similar conclusions were drawn from studies of common vampire bats *Desmodus rotundus* (Phyllostomidae). This species is able to separate vertical stripes but not horizontal stripes from circles of the same area (Schmidt & Manske 1978; Manske & Schmidt 1979). In contrast, the insectivorous species *Vespertilio superans* (Vespertilionidae) cannot distinguish objects of different shapes but equal size, and responds only to the size of the surface areas (Chung et al. 1990). The only bat that has been shown unambiguously to respond to shapes alone is the frugivorous phyllostomid *Carollia perspicillata*. This species can discriminate squares from circles, even if the squares are rotated (Suthers et al. 1969).

In conclusion, studies on pattern discrimination have yielded highly variable results, but in general it seems as if fruit- and nectar-eating microchiropterans respond to patterns and shapes more readily than insectivorous species. This may perhaps reflect that plants are more easily detected by vision, and less detectable by sonar than insects, and that frugivores therefore may use a different search image when foraging.

### *Perception of colour*

Given that microchiropteran bats are all more or less nocturnal, true colour vision seems unlikely to occur in these animals, as it would probably be of minor importance. Nevertheless, cones occur in the retinas of some species, although most authors report only rods (reviewed by Suthers 1970; Chase 1972). Nevertheless, there is evidence that at least two different photo pigments occur in the eyes of Microchiroptera (Chase 1972; Hope & Bhatnagar 1979a). Electroretinogram response tests have shown sensitivity peaks around 500 nm and 570 nm in the vespertilionid species *Myotis myotis* (Dietrich & Dodt 1970) and *Eptesicus fuscus* (Hope & Bhatnagar 1979a) and the phyllostomid species *Artibeus*

*jamaicensis*, *Desmodus rotundus* and *Carollia perspicillata* (Hope & Bhatnagar 1979a). There is also preliminary evidence that there is a spectral sensitivity peak in the near UV-range (around 390 nm) in the nectarivorous phyllostomid *Glossophaga soricina* (Lopez et al. 2001). It is thus possible that this species is able to perceive ultraviolet light reflected from fruits and plants.

## Vision in orientation and navigation

### *Long distance navigation*

The fact that the eyes of most bats function better beyond than within the range of echolocation (Suthers & Wallis 1970) suggests that visual cues may preferably be used in preference to echolocation for navigation and orientation over longer distances.

Several species of Microchiroptera make long distance movements and some even perform seasonal migration (Griffin 1970). It seems unlikely that ultrasonic echolocation plays any major role in orientation over long distances, as it works only at short range. For example, insect sized targets can be detected a few metres away at best (Kick 1982), although trees, hillsides or the ground obviously may be detected much further away. However, even during the most favourable conditions, bats do not pay attention to echoes returning from more than 100 m or so away (Altringham 1996) and therefore, migration over long distances is almost certainly guided by other senses, including vision (Griffin 1970). Bats can use distant low frequency sounds for orientation over moderate distances, indicating that passive hearing may also be involved in navigation over longer distances (Griffin 1970; Buchler & Childs 1981). There is also some evidence that bats possess magnetic material (Buchler & Wasilewski 1985), but if they possess a magnetic sense like birds (Wiltschko & Wiltschko 1995) or not, is still unknown.

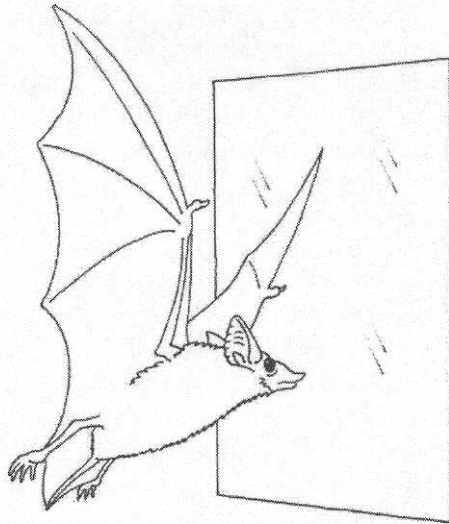
When migrating at night, it is possible that stars can serve as navigational cues for some species of bats. For example, *Eptesicus fuscus* can see point light sources, which simulate bright white and blue stars against the night sky, if these are located at  $> 6^\circ$  angle (Childs & Buchler 1981). This species is also able to orient and navigate in relation to the post-sunset glow in the west (Buchler & Childs 1982).

In homing experiments with bats released within 10 km from their roost, the bats have been demonstrated to do well, using echolocation alone. This suggests that they are acoustically familiar with a relatively large home territory (Williams et al. 1966; Williams & Williams 1967; Davis & Barbour 1970). Nevertheless, blinded bats tend

to fly slower and closer to the ground than non-treated bats (Mueller 1968), indicating that they change their orientation behaviour when they no longer are able to see. Bats also seem to rely heavily on their spatial memory, as they often follow the same paths night after night (Höller 1995).

When commuting between roost- and feeding sites during dusk and dawn periods, bats often follow outlines in the landscape, such as river banks, forest edges, hedgerows and hillsides (Racey & Swift 1985; Limpens & Kapteyn 1991; Verboom & Huitema 1997). The reason may be to minimise predation risk (Swift 1998), or to use outlines as acoustic landmarks, which perhaps facilitate navigation by sonar (Verboom et al. 1999). More likely, however, landscape outlines and silhouettes provide the bats with visual cues, contrasting against the twilight sky, and such cues are probably essential for orientation and navigation along travelling routes (Davis 1966; Layne 1967; Griffin 1970; Manske & Schmidt 1979; Höller and Schmidt 1996).

*Balantiopteryx plicata*  
(Emballonuridae) relies on visual cues when presented with conflicting information from vision and sonar, for example in front of a window (Paper V).



The frequent observation that bats have a tendency to crash into windows of buildings when released indoors (Fenton 1975), during migration (Timm 1988), or commuting (Test 1967), suggests that they predominantly rely on vision rather than on echolocation in situations when both acoustic and visual cues are available. The performance is greatly improved, i.e. there are fewer collisions, when the bats are blinded

(Davis & Barbour 1965) or when they are flown under dark conditions, and hence are “forced” to rely on echolocation alone. The insectivorous *Balantiopteryx plicata* (Emballonuridae) was studied at different times of the day in an empty mesh greenhouse (Paper V). At night they flew smoothly and could easily avoid the ceiling and the walls of the greenhouse, but during the day and at dusk and dawn they often tried to fly through the mesh and thereby crashed into it. The bats used echolocation consistently and without any dramatic change in echolocation call structure that could be related to the prevailing light conditions. The study indicates that emballonurid bats trust their eyes over their ears when exposed to contradictory auditory and visual cues.

### *Close range orientation and navigation*

When moving towards resting places and specific sites within roosts, bats sometimes face extremely unfavourable conditions for orientation, such as darkness, acoustic clutter from the walls of the roost, and simultaneous echolocation calls from many individuals. It is therefore likely that arrays of different sensory cues are used in such situations, and also that a good spatial memory is of great importance (Höller & Schmidt 1996). When introduced in a dark flight cage, *Nyctophilus* spp. (Vespertilionidae) ceased to echolocate after 6-8 hours of flight (Grant 1991), suggesting that they can learn to orient inside the cage, using spatial memory alone. In the same way, *Megaderma lyra* (Megadermatidae) remembers the positions of narrow openings with an accuracy of 2 cm, and if an obstacle is removed from the flight path, the bats may continue to avoid that position for days (Neuweiler & Möhres 1966). However, bats do not trust their spatial memory exclusively, but can compare stored data with new echo-acoustical and visual information (Joermann et al. 1988; Schmidt et al. 1988; Höller 1995). When flying in a room of subdued daylight, the two frugivores *Carollia perspicillata* and *Phyllostomus hastatus* (Phyllostomidae) are able to see and avoid obstacles consisting of 30 cm wide strips of cloth in their flight path (Chase & Suthers 1969). Those that were deafened with earplugs avoided the obstacles significantly better than those that were both deafened and blindfolded, showing that they could obtain visual information of features in the environment during flight. These results are consistent with those of Bradbury and Nottebohm (1969), who found that *Myotis lucifugus* (Vespertilionidae) avoided collisions in a string maze better in dim light than in total darkness. Rother and Schmidt (1982) noted that *Phyllostomus discolor* (Phyllostomidae) uses fewer sonar pulses in adequate illumination than in darkness. When flying the bats in a string maze, the same authors also

showed that fewer pulses were used if the obstacles exceeded 0.25 mm in width. The results suggest that vision can shorten the bats' reaction time for avoiding obstacles in a flight path, as long as there is enough ambient light and the obstacles are of sufficient size (given by the visual acuity threshold and the range).

Joermann et al. (1988) studied landing performance in two captive species of Phyllostomidae (*Desmodus rotundus* and *Phyllostomus discolor*). The bats were presented with visual illusions of landing grids, which thus gave them conflicting acoustic and visual information. Although the grids were not detectable by echolocation, the bats seemed to aim for them, and only ca 30 cm in front of the illusions the bats interrupted the approach and turned away. The authors concluded that bats rely mainly on echo-acoustical cues at close range, but in some situations they defer to visual cues in an early phase of detection, even within the range of echolocation.

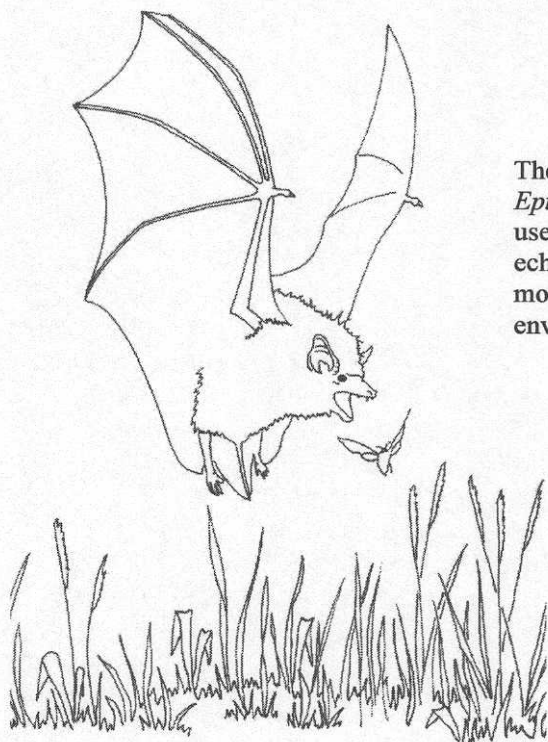
To investigate what sense the *Anoura geoffroyi* (Phyllostomidae) (Chase 1981; 1983) and the *Tadarida brasiliensis* (Molossidae) (Mistry 1990) would defer to when escaping from a roost, the bats were flown in a Y-maze, in which one exit was blocked with Plexiglas and illuminated with a light source. The other exit was open but dark. When tested in daytime, nearly all bats chose the illuminated "exit", thus indicating that they believed the light was an opening. However, when releasing bats at night, the escape behaviour was the opposite, the bats choosing the dark exit. It was suggested that the synchrony of light schedules to the bats' circadian rhythm might determine the use of the appropriate sense (Mistry 1990).

### **Vision in foraging and prey detection**

At close range, echolocation usually gives more detailed information about the prey than vision (Suthers & Wallis 1970; Pettigrew 1980). However, in some situations, it may be favourable to change the modality with which to search for prey, and indeed, many bats use a variety of sensory cues, including smell (Hessel & Schmidt 1994; Kalko et al. 1996; Helversen et al. 2000), passive listening for prey generated sounds (Fiedler 1979; Ryan & Tuttle 1987; Arlettaz et al. 2001), tactile information (Baron et al. 1996c), visual cues (Bell 1985), and vampire bats possess the ability of thermo-perception (Kürten & Schmidt 1982).

## *Insectivores and carnivores*

For bats that search for insects within or near vegetation, separation of prey echoes from the background clutter is usually a severe problem when using sonar alone (Jensen et al. 2001). In such situations bats have to rely on additional sensory cues to locate the prey. Nevertheless, few studies have addressed the obvious possibility that visual cues may be used for detection of prey in acoustically complex environments. However, when northern bats (*Eptesicus nilssonii*) search for stationary targets among high grass (clutter), this seems indeed to be the case (**Paper II, Paper III**). During early summer in Sweden, ghost swift moths *Hepialus humuli* (Lepidoptera: Hepialidae) swarm in stationary display flight over and among grass at dusk. These moths are large (ca 6 cm wingspan) and conspicuously silvery white (Andersson et al. 1998), and in contrast to most other moths, they lack ultrasonic hearing (Rydell 1998), and are intensively exploited by northern bats patrolling in the air over the field (Andersson et al. 1998; Rydell 1998; Jensen et al. 2001). In an experimental set-up, making use of this natural foraging situation, *Hepialus humuli* were presented to the bats, either with their white dorsal side up or with their dark ventral side up. It was found that the white moths were attacked more frequently than the dark ones, indicating that the bats were guided by visual cues (**Paper II**).

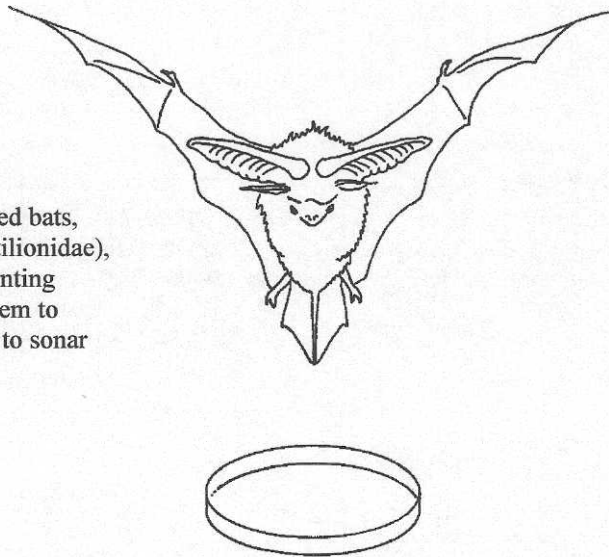


The aerial hawking northern bat, *Eptesicus nilssonii* (Vespertilionidae), uses visual cues as a complement to echolocation when searching for moths in acoustically complex environments (**Paper II, III**).



The brown long-eared bat *Plecotus auritus* (Vespertilionidae) is a gleaner insectivore, which usually uses its large and sensitive ears to passively locate its prey by the noise they make (Anderson & Racey 1991). However *Plecotus auritus* also has relatively big eyes (Cranbrook 1963, Tab 1), suggesting that they have relatively good vision. We investigated if brown long-eared bats exploit visual cues when searching for prey (**Paper I**). By using petri dishes, containing mealworms that either were available to the bats or presented under glass, and presenting these in different levels of illumination, we provided the bats with visual cues, sonar cues or both. The bats did best in situations where both sonar cues and visual cues were available, but the visual information seemed to be more important than sonar.

Gleaning brown long-eared bats, *Plecotus auritus* (Vespertilionidae), feeding from bowls presenting different sensory cues, seem to prefer visual information to sonar cues. (**Paper I**).



The California leaf-nosed bat *Macrotus californicus* (Phyllostomidae), a gleaner that normally searches for prey on the ground, has been shown to locate prey by using auditory- and visual cues as well as by sonar. Indeed this bat shows a particularly flexible hunting behaviour. In moonlight *Macrotus californicus* can see well enough to hunt using vision alone (Bell 1985). This allows the bat to hunt without alerting the prey with ultrasound (Fullard 1987; Rydell 1992a), and also to detect stationary targets, which otherwise would be hard to detect (Arlettaz et al. 2001; Jensen et al. 2001; **Paper II**). In visual acuity tests *Macrotus californicus* responded to stripes subtending  $0.06^\circ$  arc, (Tab 2), which is the best visual acuity found in any microchiropteran bat (Bell & Fenton 1986).

Moreover, the eyes of *Macrotus californicus* are relatively large and have a much higher degree of binocular overlap ( $50^\circ$ ) than in other bats (for example *Antrozous pallidus*  $25^\circ$  and *Eptesicus fuscus*  $19^\circ$ , Bell & Fenton 1986). This suggests that *Macrotus californicus* has good stereoscopic vision and that the near field distance perception is of great importance (McIlwain 1996), as would be expected in a species that forage visually. *Macrotus californicus* exploits diurnal prey, that are stationary at night and therefore unavailable to other bats (e.g. Howell 1920 cited in Bell & Fenton 1986).

The African yellow-winged bat *Lavia frons* (Megadermatidae) employs feeding tactics that involve both gleaning and aerial hawking. This species is a sit-and-wait predator, which scans the vicinity while hanging from a branch, waiting for insects to pass by. *Lavia frons* is active in relative bright ambient illumination, at dusk as well as late mornings, and is often seen catching prey against the sky. It has large eyes and may be able to see insects against the bright sky (Vaughan & Vaughan 1986). *Nyctophilus gouldi* and *Nyctophilus geoffroyi* (Vespertilionidae), also combine aerial hawking with gleaning, and have been shown to use different sensory cues according to circumstances. As in *Lavia frons*, visual cues are preferentially used to detect prey in the air, whereas auditory cues are used to detect prey on the ground (Grant 1991). The visual acuity of *Nyctophilus gouldi* is nowhere near that of *Macrotus californicus* and *Antrozous pallidus*, but rather similar to that of other aerial hawking Vespertilionidae (Tab 2), which explains why they cannot find prey on the ground visually.

Eklöf & Anderson (unpublished) observed northern bats (*Eptesicus nilssonii*, Vespertilionidae) feeding under midnight sun conditions in northern Norway. The bats caught prey against the bright sky and sometimes without detectable sonar signals. However, based on the performance of *Eptesicus fuscus* (Tab 2) it seems unlikely that *Eptesicus nilssonii* has sufficient resolving power to detect small airborne prey visually. A 2 cm insect is first detected at a distance of ca 1 m using vision (considering a visual acuity of  $0.7^\circ$  -  $1^\circ$  arc, Tab 2), but the same object is first detected at ca 5 m using echolocation (Kick 1982), which thus suggests that echolocation would be the preferred sense. On the other hand, when northern bats search for ghost swift moths (described above), vision increases the chance of detection of the prey, only because they exceed 5 cm in wingspan and are detected at rather close range (3.5 m) (Paper III). Smaller targets are detected using echolocation alone.

Little brown bats (*Myotis lucifugus*) have been observed to catch prey apparently without using echolocation (D. R. Griffin personal comm.) This species' visual resolving power is even poorer than that of the northern bat, and in addition, its prey items are even smaller,

so it is thus highly unlikely that vision is involved in prey catching. In this species the apparent absence of echolocation calls must have another explanation. In fact, earlier observations of northern bats (Rydell 1992b) and little brown bats (Rydell et al. 2002) have suggested that attempted insect captures are always associated with echolocation calls, even in bright light conditions at high latitudes.

Under conditions that appear to us to be completely dark (0 lux), bats may still be able to see conspicuous insects. For example, it has been reported that bat activity is high where fireflies occur (Lloyd 1989), and it has been shown that some fireflies stop flashing when approached by bats (Farnworth 1973). This suggests that the light emitted by fireflies may guide the bats or at least evoke their curiosity. More interestingly, fireflies are not eaten by bats and were rejected by *Eptesicus fuscus* in feeding experiments (Vernon 1981). In the same study, the bats were presented with flashing fireflies as well as with artificial flashes. The bats responded to the flashes, although it was not clear if they associated the flashes with food or with unpalatability. It seems possible that firefly flashes may function as a visual aposematic signal to bats.

#### *Frugivores and nectarivores*

In general, fruit- and nectar feeding bats have larger eyes (Tab 1), better visual resolving power (Tab 2) and enlarged visual and olfactory bulbs, compared to insectivorous species (Jolicoeur & Baron 1980; Barton et al. 1995; Barton & Harvey 2000). They also perceive and respond to different patterns more readily than insectivorous species (Suthers & Chase 1966; Suthers et al. 1969), suggesting that vision may perhaps play a more important role in these bats than in most insectivores.

Hessel and Schmidt (1994) investigated which sensory cues *Carollia perspicillata* (Phyllostomidae) uses when orienting toward a food source. The bats were presented with a triple choice of passive acoustic-, olfactory-, and visual cues. At least initially, the visual cue was the most frequently preferred stimulus. But after training the bats changed their behaviour and responded more to the olfactory stimulus. The experiment suggests that *Carollia perspicillata* can detect new sources of food using visual cues, and that they subsequently rely more on olfaction as the food source becomes known. Indeed these bats seem to possess a remarkable sense of olfaction (Fleming 1988; Laska 1990). Kalko et al. (1996) showed that fig eating Microchiroptera do not use vision when foraging, presumably because figs eaten by these bats are visually inconspicuous. Instead, they rely mainly on olfactory cues,

combined with broadband echolocation. In fact, most bat-pollinated plants are greenish, pink and white, which presumably reflect the fact that bats are most likely colour-blind (Suthers 1970; Faegri & van der Pijl 1979). On the contrary, many species of bat pollinated *Parkia* (Leguminosae: Mimosoideae) have bright red and yellow colours (Hopkins 1984). It is also suggested that dark flowers can be seen as silhouettes, against the sky and that pale flowers appear conspicuous against dark foliage (Start 1974, cited in Hopkins 1984). If the bats make use of such differences in contrast, one would expect to find that the position of differently coloured flowers vary accordingly in relation to the foliage, i.e., red flowers far from foliage and yellow flowers closer, which in fact, seems to be the case.

The capitula of *Parkia* are also highly reflective under moonlight and starlight conditions, and are therefore presumably visible to pollinating bats (Hopkins 1984). Many pollinators make use of a broad spectrum reflected from flowers, fruits or seeds, including ultraviolet (UV) light (for example insects, Kevan et al. 2001; and birds, Church et al. 2001). Ultraviolet vision seems, however, to be absent in most mammals, although some rodents have been shown to have UV sensitive retinas (Jacobs et al. 1991). Recently, it was suggested that bats might perceive UV-light, as there is evidence for a spectral sensitivity peak around 390 nm (i.e. in the near UV-range) in the nectarivorous *Glossophaga soricina* (Lopez et al. 2001). However, if the bats actually use UV reflecting surfaces as orienting cues is still uncertain, although Willson and Whelan (1989) have shown that UV-reflectance is indeed relatively common throughout the plant kingdom. The *Passiflora* species, *Passiflora galbana* and *Passiflora mucronata*, two plants which flowers are exploited by the nectarivorous glossophaginae bats, reflect light down to ca 400 nm and 370 nm (upper UV range), respectively. This should be compared to the hummingbird pollinated *Passiflora speciosa*, which has its main reflection above 570 nm (Varassin et al. 2001), perhaps reflecting the spectral sensitivity of the pollinators. Furthermore, 80% of nocturnal Lepidoptera have wing patterns that reflect UV, compared to ca 30% in diurnal species (Lyytinen 2001 cited in Honkavaara et al. 2002). On the other hand, this may imply that bats cannot make use of the ultraviolet light, in contrast to birds, which usually forage in daylight.

## Predator surveillance and social behaviour

As discussed earlier, vision seems to be important in escape behaviour (Chase 1981; Chase 1983; Mistry 1990). Presumably it is also important in detection of predators; it is much easier to approach a blindfolded bat than a non-blindfolded individual (Chase 1972). Species of the family Emballonuridae often fly earlier in the evening than most other bats, and sometimes even in the afternoon and they often roost on exposed and well lit sites such as tree trunks (e.g. Bradbury & Vehrencamp 1976). A *Saccopteryx* sp. will quite easily detect an approaching person, and take flight without emitting any echolocation calls (Suthers 1970), and *Rhynconycteris naso* seems to be disturbed more easily by seeing an approaching figure at a distance, than by sudden sounds or vibrations at close range (Dalquest 1957). Vaughan and Vaughan (1986) noted that *Lavia frons* (Megadermatidae), which also roosts exposed, seems to be constantly alert during the day, scanning its surroundings for predators. In fact, the authors almost never saw a bat with its eyes closed, and were never able to approach one undetected.

The evidence for the use of vision in social behaviour is mainly anecdotal. Social grooming occurs in the vampire *Desmodus rotundus* (Phyllostomidae) and may serve to identify individuals (Wilkinson 1986), although it is generally rare (Fleming 1988). Goodwin and Greenhall (1961) noted that avian vampire bats (*Diaemus youngi*) show grooming behaviour when seeing a mirror reflection, indicating that vision might be involved in this behaviour. Sometimes bats are also observed to imitate other individuals grooming themselves (Vaughan & Vaughan 1986).

Some bat species have distinct fur patterns, which may serve as visual recognition signals (Fenton 2001), in addition to scents and sound, although fur patterns may also serve as camouflage (Neuweiler 2000). Threat displays are common in for example *Carollia perspicillata* (Phyllostomidae), and includes wing shaking, harsh sounds, and aggressive looks such as extension of the tongue (Fleming 1988). Sexual displays are also common. The monogamous *Lavia frons* and *Cardioderma cor* (Megadermatidae), perform stereotypical circular flights, described as aerial ballets (McWilliam 1987; Vaughan & Vaughan 1986). Among *Saccopteryx bilineata* (Emballonuridae), the males defend territories where they maintain harems. In front of the females of the harem, they perform sexual displays, which include stereotyped singing, and also shaking of wings and hovering. The wing shaking presumably enhances the effect of olfactory glands by spreading pheromones, but it may also function as a visual signal to draw the females' attention (Chase 1972).

## Multimodality – vision and echolocation

The echolocation detection range of a 19 mm insect is around 5 m for *Eptesicus fuscus* (Kick 1982), and the visual acuity of this species is  $0.7^\circ$ - $1^\circ$  arc, Tab 2). This allows visual detection of the 19 mm object only when it is closer than ca 1 m. This simple calculation strongly suggests that echolocation is the more accurate sense at close range and for small objects. However, larger objects can be detected visually at distances of hundreds of meters, far beyond the range of echolocation. For example, an object of 5 m diameter can potentially be detected visually by *Eptesicus fuscus* at a distance of ca 300 m. Using echolocation; the same object is detected at a distance of only 25-30 m at most (depending on call strength, attenuation etc., Lawrence and Simmons 1982; M. B. Fenton personal comm.). This supports the general view that vision is used primarily for detection of large objects and landmarks and for navigating over longer distances (Davis 1966; Layne 1967; Griffin 1970; Höller and Schmidt 1996). Nevertheless, for bats with better visual resolving power, vision can be used and even replace echolocation, at short distances. The California leaf nosed bat *Macrotus californicus*, referred to above, can visually detect a 19 mm insect at a distance of ca 18 m. This presumably gives this bat a longer range of operation if they use vision instead of echolocation, at least under conditions of moonlight or bright starlight (Bell & Fenton 1986). Other bats, such as some Emballonuridae, which have visual acuities below  $0.4^\circ$  arc (Tab 2), can visually detect insect sized objects (1 cm) at distances less than 1 m, suggesting a range of operation roughly similar for vision as for sonar. One could therefore assume that emballonurid bats could use either vision or echolocation to detect prey, as suggested by Pettigrew (1980). He observed one species of Emballonuridae (*Craseonycteris thonglongyai*) catching prey against a bright sky apparently without using echolocation and suggested that the bats could see the insects as silhouettes against the sky.

The Australian ghost bat *Macroderma gigas* (Megadermatidae) also has a similar prey detection range for vision as for echolocation. Since this species also has good auditory sensitivity in the sonic range (Fiedler 1979; Kulzer et al. 1984), it switches between vision, echolocation and passive listening (Pettigrew et al. 1986; Pettigrew et al. 1983). For frequencies below 20 kHz, the acoustic axis (as defined from the directionality of the pinna and noseleaf) of *Macroderma gigas* is aligned with the visual axis (defined by areas of highest ganglion cell density), indicating that auditory cues help the bats to visually detect the source of the sound (Pettigrew 1988). In fact, a major function of sound localisation in animals is to direct the eyes toward the sound-source

(Heffner & Heffner 1992; Heffner et al. 1999). This reflex is even quicker than the reaction to a flashlight (Whittington et al. 1981), and hence suggests that hearing is closely co-ordinated with vision (Heffner 1997).

Sound localisation acuity is related to retinal organisation and the width of fields of best vision (defined as the portion of the retina with at least 75% of maximum ganglion cell density, Heffner et al. 2001). Animals with narrow fields of best vision (foveae) have generally better localisation acuity than animals with broad or elongated fields of best vision (visual streaks). The retinas of microchiropteran bats are loosely arranged in visual streaks and the density of ganglion cells falls irregularly toward the periphery. The field of best vision is concentrated in the temporal part of the retina and seems to be broader in frugivores than in insectivorous species (Heffner et al. 2001). Overall, there is a higher ganglion cell density in the inferior part of the retina than in the superior (Marks 1980; Pettigrew et al. 1988; Koay et al. 1998; Heffner et al. 2001; Eklöf unpublished). This means that the sharpest image on the retina results from light reaching the eye from above, and consequently, the bat eyes focus slightly upwards. Without moving their heads, bats are looking up (Pettigrew 1988). The functional significance of this can be difficult to establish, but it seems likely that vision and echolocation have evolved to provide the bat with as little information overlap as possible. While echolocation call emission and hearing is most effective in the flight direction and downwards (Schnitzler & Grinnell 1977; b), vision serves as a complement by being most effective upwards it thus gives additional information of obstacles and landmarks further away. In Megachiroptera, which do not echolocate, one would thus expect the fields of best vision to be above rather than below the optic disk, which in fact seems to be the case (Pettigrew 1986).

All bats have well developed retinofugal projections (pathways of information from retina to visual cortex) to the lateral geniculate nuclei as well as to the superior colliculus (see above), which are the main targets for retinal projections in mammals (Pentney & Cotter 1976; Suthers & Bradford 1980; Reimer 1989). In the superior colliculus, different sensory modalities are integrated and transformed, and the output may be perceived as a “new product” (Stein & Meredith 1993). The capacity to deal with multisensory information is however developed first after experience of multimodal inputs (Wallace & Stein 2001). The superior colliculus controls for example eye movements, which serves to keep objects of interest in the focal field. Auditory projections to the superior colliculus are generally sparse in mammals. However, in the mustache bat *Pteronotus parnellii* (Mormoopidae), at least three areas in the brain stem contribute with well-developed auditory projections to the

superior colliculus. It has been shown that pinna movements can be controlled in the same way as eye movements in other mammals (Covey et al. 1987), and thus that orienting behaviour can be influenced through auditory as well as through visual feedback. It is also known that auditory stimuli can trigger visuomotor neurones and hence that the eyes can respond to sounds (Stein & Meredith 1993). Combined sensory inputs can enhance perception and detection, but also cause behavioural depression, for example when the cues are contradictory, as in the case with bats and windows (discussed above). Cats have been shown to respond “half way” between contradicting sounds and images (Stein & Meredith 1993), but in most cases when animals have multiple cues to choose from, one can see a clear sensory hierarchy (e.g. Dyer & Gould 1981), so also in bats (Chase 1983). However, the hierarchy can change depending on the behavioural context. Visual cues have been shown to have precedence over auditory cues in for example escape behaviour and when commuting (Chase 1981; Chase 1983; Mistry 1990; **Paper V**). In cases where echolocation and visual cues are complementary rather than contradictory, the bats may still rely on vision over sonar. In a study on brown long-eared bats (*Plecotus auritus*), feeding from bowls presenting different sensory cues (**Paper I**), the bats scored best in situations where both visual and sonar cues were present. The visual information seemed however to be the more important.

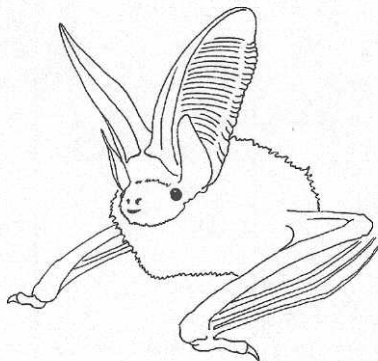
It has been suggested that there sometimes can be interference between the two senses. For example, Simmons (cited in Chase 1981) has noted that some bats have a problem learning acoustic discrimination when visual cues are present, but can easily perform the same task in darkness. When trained to respond to black or white triangles of different size, *Myotis lucifugus* (Vespertilionidae) responded to brightness cues rather than the size of the triangles, although these bats are capable of size discrimination by echolocation (Ellins 1970; Masterson & Ellins 1974). This suggests that interference may have occurred, or at least that the bats had a preference for visual cues in this case.

It is not yet known if bats can perform cross-modal recognition, i.e. learning an object using one sense and then immediately recognising the same object by using another sense, which is the case with for example bottle nose dolphins *Tursiops truncatus*. These animals can integrate information from vision to echolocation just as well as from echolocation to vision. Hence, what the dolphins perceive from one sense is functionally similar of what it perceives from the other (Pack & Herman 1995).



Although the question of how sensory inputs are combined in bats remains unsolved, several authors have shown the importance of multimodality (Pettigrew et al. 1983; Schmidt 1988; Hessel & Schmidt 1994). In a two choice test, two phyllostomid bats (*Desmodus rotundus* and *Phyllostomus discolor*) were trained to respond to a combination of visual, olfactory and acoustic stimuli, and were then presented with one of the three modalities separately (Schmidt et al. 1988). It was found that *Phyllostomus discolor* chose the visual stimuli to a higher degree, whereas *Desmodus rotundus* preferred the passive acoustic stimuli. However, both bats were able to respond to all three modalities, although responses to the olfactory stimuli needed additional training, as also noted by Hessel and Schmidt (1994), when studying *Carollia perspicillata*. However when the *Carollia* had learned to respond to the olfactory cue, this became the preferred stimuli, which was not the case with *Desmodus* or *Phyllostomus*, which both used two other senses. This clearly shows that bats use an array of different senses in the field, and that ecology, feeding strategies and behavioural context all influence the use of different modalities.

Echolocation may be the most important innovation throughout bat evolution, allowing these animals to explore a niche of their own. But there is more to the sensory ecology of microchiropteran bats, where vision is an important piece of the puzzle and certainly needs further attention in the future.



## Acknowledgements

First of all I would like to acknowledge all the co-authors of this thesis for obvious reasons, and I wish to thank Olof Helje for making the splendid bat illustrations. Then I wish to thank my supervisor and mentor -Jens Rydell – and also, many thanks to the rest of the Rydell family for your great hospitality.

There are several people having answered several more or less stupid questions on bats, vision, statistics, experimental design, the meaning of life and other various topics throughout the years. Especially I would like to thank Donald R Griffin and Brock Fenton, but also Eric Warrant, Dan E Nilsson, Tom, Gareth Jones, Susan Swift, Kristina Mieziewska, Winston Lancaster; and of course, many thanks to Cajsa, John G, Christoffer, Gim, Jen, Christin, John R, Marc, Jenny, Kalle, Kristina, Cess, Bomull, Tobias, Annika, Christoffer and Staffan, just to mention a few of you.

Just as many people have helped me to make the every day work possible; at the department, by joining me in the field, on conferences, courses and work shops and to some extent even in the lab (although some may think I do not know what that is); having helped me arrange field work and experiments, being guides, eye suppliers, hosts, or just good company during batting. Especially I wish to thank Monica, Tompa and Cajsa, thanks also to Maria, Héctor, Henke, Luis-Bernardo, Hans, Marie, Gabriela, Stefan, Åsa, Per, Britt-Louise, Anna, Lee, Dr. F-Jo, Blomman, Karl-Johan, Stefan, Sean, Jorge, Jenny, Andreas, Eric, Lars-Erik, Cess, Annemarie, Magnus, Berndt, Dave, Anne-Sofie, Bengt, Mia, Lilioth, the “NASBR and Chamela-students”, the Lövhauks, all other department employees not mentioned, and of course Mexican hospitality and British humour.

For unknown reasons, I have been deeply involved, not only in research and teaching, but also in the work of the faculty board, the Swedish Association of Scientists and the Students’ Union. I wish to thank the various members of all the different working groups and committees, not at least Cajsa, Marie, Stefan Henrik, and Andreas.

There are other things but science, like having almost normal conversations, sharing stupid ideas, trying to do music, lying on beaches, e-mailing, having coffee and drinking beer, and presumably some other stuff as well. For those things, I wish to thank Per and Andreas for helping me to create “PSL” which for a while brought order to my life, much in the same way as “Johnny” did, only different. I wish to thank the e-mailers, the floorballers, the chatters, the Herb Boys crew and fan club, the coffee drinkers and the travellers. There is no doubt that the Friday after work sessions have been almost as important as the actual research for being able to finish this thesis. I wish to acknowledge the most frequent ones: Christoffer, Anna, Viktoria, Ågot and lately Jenny P. But of course, Sara, Erik, Fredrik, Jenny T, Linda, Tove, Goran and a whole bunch of other you-know-who-you-are. There are two persons having shared my biology- as well as my non biology-time, to a larger extent than perhaps any others: first of all, thank you Cajsa for not bringing your calculator; and for numerous moments thereafter, and second, Tompa, for making everyday April fools day.

Thank you all on the second floor: Per, Bengt, Stig, Gunnar, Anders, Inger, Lena, Åke, Jan, Sebbe, Björn, Jenny, Malin, Urban, Anna H, Anna Z, Monica, Susanne, Ulla, Mare, Christoffer, Arne, Marcus, other hangarounds, not mentioned, past and present. Thank you mom, dad, and Kristian, and thanks to all friends in the real world. My work has been funded by Kungliga och Hvitfeldtska Stiftelsen, Lunds Djurskyddsfond, Knut och Alice Wallenbergs Stiftelse, Folke Eklöf, Adlerbertska Forskningsstiftelsen, Wilhelm och Martina Lundgrens Vetenskapsfond, Kungliga vetenskaps- och Vitterhetssamhället i Göteborg, Stiftelserna Paul och Marie Berghaus Donationsfond, J A Ahlstrands Testamentsfond, Lars Hiertas Minne, and Rådman & Fru Ernst Collianders Stiftelse FVÄ, and of course CSN.

Finally I wish to acknowledge (please fill out your name); believe me you are not really forgotten.

## References

- Ahlén, I. 1997. Migratory behaviour of bats at south Swedish coasts. *Z. Säugetierk.* 62, 375-380
- Altringham, J. D. 1996. *Bats: biology and behaviour*. Oxford University Press, Oxford UK
- Anderson, M. E. & Racey, P. A. 1991. Feeding behaviour of captive long eared-bats, *Plecotus auritus*. *Anim. Behav.* 42, 489-493
- Andersson, S., Rydell, J. & 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. & Racey, P. A. 2001. Effect of acoustic clutter on prey detection by bats. *Nature* 414, 742-745
- Baron, G., Stephan, H. & Frahm, H. D. 1996a. *Comparative neurobiology in Chiroptera vol. I Macromorphology, brain structures, tables and atlases*. Birkhäuser Verlag, Basel, Switzerland
- Baron, G., Stephan, H. & Frahm, H. D. 1996b. *Comparative neurobiology in Chiroptera vol. II Brain characteristics in taxonomic units*. Birkhäuser Verlag, Basel, Switzerland
- Baron, G., Stephan, H. & Frahm, H. D. 1996c. *Comparative neurobiology in Chiroptera vol. III Brain characteristics in functional systems, ecoethological adaptation, adaptive radiation and evolution*. Birkhäuser Verlag, Basel, Switzerland
- Barton, R. A., Purvis, A. & Harvey, P. H. 1995. Evolutionary radiation of visual and olfactory brain systems in primates, bats and insectivores. *Phil. Trans. R. Soc. Lond. B* 348, 381-392
- Barton, R. A. & Harvey, P. H. 2000. Mosaic evolution of brain structure in mammals. *Nature* 405, 1055-1058
- 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
- Bell, G. P. & Fenton, M. B. 1986. Visual acuity, sensitivity and binocularity in a gleaning insectivorous bat, *Macrotus californicus* (Chiroptera: Phyllostomidae). *Anim. Behav.* 34, 409-414
- Bogdanowicz, W. 1994. *Myotis daubentonii*. *Mammalian Species* 475, 1-9
- Bornschein, H. 1961. Vergleichende Elektrophysiologie der Retina. In: *Das Visuelle System. Neurophysiologie und Psychophysik* (Jung, R. & Kornhuber, H. eds.). Berlin, Springer-Verlag pp 74-79
- Bradbury, J. & Nottebohm, F. 1969. The use of vision by the little brown bat, *Myotis lucifugus*, under controlled conditions. *Anim. Behav.* 17, 480-485
- Bradbury, J. W. & Vehrencamp, S. L. 1976. *Social Organization and Foraging in Emballonurid Bats I. Field studies*. *Behav. Ecol. Sociobiol.* 1, 337-381
- Buchler, E. R. & Childs, S. B. 1981. Orientation to distant sounds by foraging big brown bats (*Eptesicus fuscus*). *Anim. Behav.* 29, 428-432
- Buchler, E. R. & Childs, S. B. 1982. Use of the post-sunset glow as an orientation cue by big brown bats (*Eptesicus fuscus*). *J. Mammal.* 63, 243-247

- Buchler, E. R. & Wasilewski, P. J. 1985. Magnetic remanence in bats. In: Magnetite Biomineralization and Magnetoreception in Organisms: A New Biomagnetism. (Kirschvink, J. L., Jones, D. S. and MacFadden, B. J. eds.). New York: Plenum press, pp 483-487
- Chase, J. 1972. The role of vision in echolocating bats. Ph.D thesis, Indiana University
- 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
- Chase, J. & Suthers, R. A. 1969. Visual obstacle avoidance by echolocating bats. *Anim. Behav.* 17, 201-207
- Childs, S. B. & Buchler, E. R. 1981. Perception of simulated stars by *Eptesicus fuscus* (Vespertilionidae): A potential navigational mechanism. *Anim. Behav.* 29, 1028-1035
- Chung, K. S., Lee, J. H. & Park, S. R. 1990. Visual pattern discrimination in the Oriental discoloured bat, *Vespertilio superans*. *Korean J. Zool.* 33, 127-132
- Church, S. C., Merrison, A. S. L. & Chamberlain, T. M. M. 2001. Avian ultraviolet vision and frequency dependent seed preferences. *J. Exp. Biol.* 204, 2491-2498
- Cotter, J. R. 1985. Retinofugal Projections of the Big Brown Bat, *Eptesicus fuscus* and the neotropical Fruit Bat, *Artibeus jamaicensis*. *Am. J. Anat.* 172, 105-124
- Cotter, J. R. & Pentney, R. P. 1979. Retinofugal projections of nonecholocating (*Pteropus giganteus*) and echolocating (*Myotis lucifugus*) bats. *J. Comp. Neurol.* 184, 381-399
- Covey, E., Hall, W. C. & Kobler, J. B. 1987. Subcortical connections of the Superior colliculus in the Mustache bat, *Pteronotus parnellii*. *J. Comp. Neurology* 263, 179-197
- Cowey, A. & Ellis, C. M. 1967. Visual acuity of rhesus and squirrel monkeys. *J. Comp. Physiol. Psychol.* 64, 80-84
- Cranbrook, The Earl of. 1963. Notes on the feeding habits of the long-eared bat. *Trans. Suff. Nat. Hist. Soc.* 11, 1-3
- Crowle, P. K. 1980. Retinofugal projections to subcortical visual centers in the microchiropteran bat, *Myotis sodalis*. *Proc. Mont. Acad. Sci.* 30, 1-11
- Curtis, W. E. 1952. Quantative studies on echolocation in bats (*Myotis lucifugus*); studies on vision in bats (*Myotis l.* and *Eptesicus fuscus*); and quantative studies on vision in owls (*Tyto alba* practicola). PhD-thesis, Cornell University, Ithaca, NY
- Dalquest, W. W. 1957. Observations on the sharp-nosed bat, *Rhynchonycteris naso* (Maximilian). *Texas. J. Sci.* 9, 219-226
- Davis, R. 1966. Homing performance and homing ability in bats. *Ecol. Monogr.* 36, 201-237
- Davis, W. H. & Barbour, R. W. 1965. The use of vision in flight by the bat *Myotis sodalis*. *Am. Midl. Nat.* 74, 497-499
- Davis, W. H. & Barbour, R. W. 1970. Homing in blinded bats (*Myotis sodalis*). *J. Mammal.* 51, 182-184
- Dietrich, C. E. & Dodt, E. 1970. Structural and some physiological findings on the retina of the bat *Myotis myotis*. *Symp. Electroretinography* (ed. A. Wirth). Pacini, Pisa, 120-132

- Dyer, F. C. & Gould, J. L. 1981. Honey bee orientation: a backup system for cloudy days. *Science* 214, 1041-1042
- Eisentraut, M. 1950. Dressurversuche zur festellung eines optischen orientierungsvermögens der fledermäuse. *Verein. Vaterl. Naturk. Im Vurttemberg, Stuttgart.* 106, 34-45
- Eklöf, J. & Jones, G. 2003 (**Paper I**). Use of vision in prey detection by brown long-eared bats, *Plecotus auritus*. *Anim. Behav.* (In Press)
- Eklöf, J., Tranefors, T. and Vazquez, L. B. 2002 (**Paper V**). Precedence of visual cues in the emballonurid bat *Balantiopteryx plicata*. *Mamm. Biol.* 67, 42-46
- Eklöf, J., Svensson, A. M. & Rydell, J. 2002 (**Paper II**). Northern bats (*Eptesicus nilssonii*) use vision but not flutter-detection when searching for prey in clutter. *Oikos* 99, 347-351
- Ellins, S. R. 1970. The role of vision in the sensory orientation of the echolocating bat, *Myotis lucifugus*. Thesis, Newark, Del.
- Ellins, S. R. & Masterson, F. A. 1974. Brightness discrimination thresholds in the bat, *Eptesicus fuscus*. *Brain, Behav. Evol.* 9, 248-263
- Erkert, H. G. 1982. Ecological Aspects of Bat Activity Rythms. In: *Ecology of Bats* (Kunz, T. H. ed.). Plenum Press, New York, pp 201-242
- Faegri, K. & Pijl, L. van der 1979. The principles of pollination ecology. Pergamon, Oxford
- Farnworth, E. G. 1973. Flashing behaviour, ecology and systematics of the Jamaican lampyrid fireflies. Ph.D. Dissertation, Univ. Of Florida, Gainesville
- Fenton, M. B. 1975. Observations on the biology of some Rhodesian bats, including a key to the Chiroptera of Rhodesia. *Life Sci. Contr. R. Ont. Mus.* 104, 1-27
- Fenton, M. B. 2001. *Bats*. Checkmark Books, NY.
- Fenton, M. B., Audet, D., Obrist, M. K. & Rydell, J. 1995. Signal strength, timing, and self-deafening: the evolution of echolocation in bats. *Paleobiology* 21, 229-242
- Fiedler, J. 1979. Prey catching with and without echolocation in the Indian false vampire bat (*Megaderma lyra*). *Behav. Ecol. Sociobiol.* 6, 155-160
- Fleming, T. H. 1988. The short-tailed fruit bat, a study in plant-animal interactions. The University of Chicago Press, Chicago and London, pp 365
- Fullard, J. H. 1987. Sensory ecology and neuroethology of moths and bats: interactions in a global perspective. In: *Recent advances in the study of bats* (Fenton, M. B, Racey, P. A. & Rayner, J. M. V. eds.). Cambridge University Press, Cambridge, pp 244-272
- Goodwin, G. G. & Greenhal, A. M. 1961. A review of the bats of Trinidad and Tobago. *Bull. Amer. Mus. Nat. Hist.* 122, 3
- Grant, J. D. A. 1991. Prey location by two Australian long-eared bats, *Nyctophilus gouldi* and *N. geoffroyi*. - *Australian J. Zool.* 39, 45-56
- Greenway, F. & Hutson, A. M. 1990. A field guide to British bats. Bruce Coleman Books, Oyster books Ltd, Somerset
- Griffin, D. R. 1970. Migration and homing of bats. In: *Biology of Bats, Vol. II.* (Wimsatt, W. A ed.), Academic Press, NY pp 233-264

- Heffner, R. S. 1997. Comparative study of sound localization and its anatomical correlates in mammals. *Acta Otolaryngol Suppl.* 532, 46-53
- Heffner, R. S. & Heffner, H. E. 1992. Visual Factors in Sound Localization in Mammals. *J. Comp. Neurobiology* 317, 219-232
- Heffner, R. S., Koay, G. & Heffner, H. E. 1999. Sound localization in an old-world fruit bat, (*Rousettus aegyptiacus*): Acuity, use of binaural cues, and relationship to vision. *J. Comp. Psych.* 113, 297-306
- Heffner, R. S., Koay, G. & Heffner, H. E. 2001. Sound localization in a new-world frugivorous bat, *Artibeus jamaicensis*: Acuity, use of binaural cues, and relationship to vision. *J. Acoust. Soc. Am.* 109, 412-421
- Helversen, O. von., Winkler, L. & Bestmann, H. J. 2000. Sulphur-containing "perfumes" attract flower-visiting bats. *J. Comp. Physiol. A.* 186, 143-153
- Hessel, K. & Schmidt, U. 1994. Multimodal orientation in *Carollia perspicillata* (Phyllostomidae). *Folia Zoologica* 43, 339-346
- Honkavaara, J., Koivula, M., Korpimäki, E., Siitari, H. & Viitala, J. 2002. Ultraviolet vision and foraging in terrestrial vertebrates. *Oikos* 98, 505-511
- Hope, G. M. & Bhatnagar, K. P. 1979a. Electrical responses of bat retinas to spectral stimulation: comparisons of four microchiropteran species. *Experientia* 35, 1189-1191
- Hope, G. M. & Bhatnagar, K. P. 1979a. Effect on light adaptation on electrical responses on the retina of four species of bats. *Experientia* 35, 1191-1192
- Hopkins, H. C. 1984. Floral biology and pollination ecology of the neotropical species of *Parkia*. *J. Ecology* 72, 1-23
- Hughes, A. 1977. The topography of vision in mammals of contrasting life style: Comparative optics and retinal organisation. In: *Handbook of sensory physiology vol VII/5. The visual system in vertebrates* (Crescitelli, F. Ed.). Springer-Verlag, Berlin, pp. 613-756.
- Höller, P. 1995. Orientation by the Bat *Phyllostomus discolor* (Phyllostomidae) on the Return Flight to its Resting Place. *Ethology* 100, 72-83
- Höller, P. & Schmidt, U. 1996. The orientation behaviour of the lesser spear-nosed bat, *Phyllostomus discolor* (Chiroptera) in a model roost. *J. Comp. Physiol. A.* 179, 245-254
- Jacobs, G. H., Neitz, J. & deegan, II. 1991. Retinal receptors in rodents maximally sensitive to ultraviolet light. *Nature* 353, 544-554
- 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
- Jolicoeur, P. & Baron, G. 1980. Brain Center Correlations among Chiroptera. *Brain Behav. Evol.* 17, 419-431
- Kalko, E. K. V. 1995. Echolocation signal design, foraging habitats and guild structure in six Neotropical sheath-tailed bats (Emballonuridae). In: *Ecology, evolution and behaviour of bats* (Racey, P. A. & Swift, S. M. eds.). *Symp. Zool. Soc. Lond.* 67, 259-273

- Kalko, E. K. V & Schnitzler, H. U. 1993. The echolocation and hunting behavior of Daubenton's bat, *Myotis daubentoni*. *Behav. Ecol. Sociobiol.* 24, 225-238
- Kalko, E. K. V., Herre, E. A. & Handley Jr, C. O. 1996. Relation of fig fruit characteristics to fruit-eating bats in the New and Old world tropics. *J. Biogeography* 23, 565-576
- Karlsson, B.-L., Eklöf, J. & Rydell, J. 2001 (**Paper VI**). No lunar phobia in swarming insectivorous bats (family Vespertilionidae). *J. Zool. Lond.* 256, 473-477
- Kevan, P. G., Chittka, L. & Dyer, A. G. 2001. Limits to the salience of ultraviolet: lessons from colour vision in bees and birds. *J. Exp. Biol.* 204, 2571-2580
- Kick, S. 1982. Target-detection by the echolocating bat, *Eptesicus fuscus*. *J. Comp. Physiol. A* 145, 432-435
- Koay, G., Kearns, D., Heffner, H. E. & Heffner, R. S. 1998. Passive sound-localization ability of the big brown bat (*Eptesicus fuscus*). *Hearing Research* 119, 37-48
- Kulzer, E., Nelson, J. E., McKean, J. L. & Möhres, F. P. 1984. Prey catching behaviour and echolocation in the Australian ghost bat, *Macroderma gigas* (Microchiroptera: Megadermatidae). *Aust. Mammal.* 7: 37-50
- Kürten, L. & Schmidt, U. 1982. Thermo-perception in the common vampire bat (*Desmodus rotundus*). *J. Comp. Physiol. A* 146, 223-228
- Lang, A. B., Kalko, E. K. V., Dechmann, D. K. N. & Bockholdt, C. 2002. Associations of lunar-correlated activity rhythms of Neotropical Katydid with activity patterns of the gleaning insectivorous Round-eared bat, *Tonatia silvicola*. Abstract 32<sup>nd</sup> NASBR, p 58
- Laska, M. 1990. Olfactory sensitivity to food odor components in the short-tailed fruit bat, *Carollia perspicillata* (Phyllostomatidae, Chiroptera). *J. Comp. Physiol. A* 166, 395-399
- Lawrence, B. D. & Simmons, J. A. 1982. Measurements of atmospheric attenuation at ultrasonic frequencies and the significance for echolocation by bats. *J. Acoust. Soc. Amer.* 71, 585-590
- Layne, J. N. 1967. Evidence for the use of vision in diurnal orientation of the bat *Myotis austroriparius*. *Anim. Behav.* 15, 409-415
- Lekagul, B. & McNeely, J. A. 1977. *Mammals of Thailand*. Assoc. Conserv. Wildlife, Bangkok
- Limpens, H. J. G. A. & Kapteyn, K. 1991. Bats, their behaviour and linear landscape elements. *Myotis* 29, 39-48
- Lloyd, J. E. 1989. Bat (Chiroptera) connections with firefly (Coleoptera: Lampyridae) luminescence, I: Potential significance, historical evidence, and opportunity. *The Coleopterists Bulletin*, 83-91
- Lopez, J. Winter, Y. & Helvesen, O. von 2001. Behavioural measurements of spectral sensitivity in a flower visiting bat (*Glossophaga soricina*). Abstracts 12<sup>th</sup> International Bat research Conference, Bangi, Selangor, Malaysia, pp 58
- Manske, U. & Schmidt, U. 1976. Visual acuity of the vampire bat, *Desmodus rotundus*, and its dependence upon light intensity. *Z. Tierpsychol.* 42, 215-221
- Manske, U. & Schmidt, U. 1979. Untersuchungen zur optischen Musterunterscheidung bei der Vampirfledermaus, *Desmodus rotundus*. *Z. Tierpsychol.* 49, 120
- Marks, J. M. 1980. Retinal ganglion cell topography in bats. MA thesis. Bloomington, IN: Indiana Univ.

- Masterson, F. A. & Ellins, S. R. 1974. The role of vision in the orientation of the echolocating bat, *Myotis lucifugus*. Behaviour LI, 1-2, 88-98
- McIlwain, J. T. 1996. An introduction to the biology of vision. Cambridge University Press, Cambridge
- McWilliam, A. N. 1987. Territorial and pair behaviour of the African false vampire bat, *Cardioderma cor* (Chiroptera: Megadermatidae), in coastal Kenya. J. Zool. Lond. 213, 243-252
- Mistry, S. 1990. Characteristics of the visually guided escape response of the Mexican free-tailed bat, *Tadarida brasiliensis mexicana*. Anim. Behav. 39, 314-320
- Morrison, D. W. 1978. Lunar phobia in a neotropical fruit bat, *Artibeus jamaicensis* (Chiroptera, Phyllostomidae). Anim. Behav. 26, 852-855
- Mueller, H. C. 1968. The role of vision in vespertilionid bats. Am. Midl. Nat. 79, 524-525
- Nagel, T. 1974. What is it like to be a bat? Phil. Rev. 83, 535-450
- Neuweiler, G. 1967. Interaction of other sensory systems with the sonar system. In: Les Systemes Sonars Animaux Biologie et Bionique (ed. Busnel, R. G.). Nato Adv. Study Inst. Frascati, pp 509-533
- Neuweiler, G. 2000. The biology of bats. Oxford university Press, NY
- Neuweiler, G. & Möhres, F. P. 1966. The role of spatial memory in the orientation. In: Les Systemes Sonars Animaux Biologie et Bionique (ed. Busnel, R. G.). Nato Adv. Study Inst. Frascati, pp 129-140
- Pack, A. A. & Herman, L. M. 1995. Sensory integration in the bottlenosed dolphin: Immediate recognition of complex shapes across the senses of echolocation and vision. J. Acoust. Soc. Am. 98, 722-733
- Pentney, R. P. & Cotter, J. R. 1976. Retinofugal projections in an echolocating bat. Brain Research 115, 479-484
- 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. New York, Plenum Press, pp 645-650
- Pettigrew, J. D. 1986. Flying primates? Mega-bats have the advanced pathway from eye to midbrain. Science 231, 1304-1306
- Pettigrew, J. D. 1988. Microbat vision and echolocation in an evolutionary context. NATO ASI Series A Life Sciences 156, 645-650
- Pettigrew, J. D., Coles, R. B., Guppy, A., Brown, M. & Nelson, J. 1983. Sensory abilities of the Australian ghost bat, *Macroderma gigas*. Neurosci. Letts. Suppl. 11, 568
- Pettigrew, J. D., Baker, G. B., Baker-Gabb, D., Baverstock, G., Coles, R., Conole, L., Churchill, S., Fitzherbert, K., Guppy, A., Hall, L., Helman, P., Nelson, J., Priddel, D., Pulsford, I., Richards, G., Schulz, M. & Tidemann, C. R. 1986. The Australian ghost bat, *Macroderma gigas*, at Pine Creek, Northern territory. Macroderma 2, 10-19
- Pettigrew, J. D., Dreher, B., Hopkins, C. S., McCall, M. J. & 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



- Racey, P. A. & Swift, S. M. 1985. Feeding ecology of *Pipistrellus pipistrellus* during pregnancy and lactation. I. Foraging behaviour. *J. Anim. Ecol.* 54, 205-215
- Reimer, K. 1989. Retinofugal projections in the rufous horseshoe bat, *Rhinolophus rouxi*. *Anat. Embryol.* 180, 89-98
- Rother, G. & Schmidt, U. 1982. Der einfluss visueller information auf die Echoortung bei *Phyllostomus discolor* (Chiroptera). *Z. Säugertierkunde* 47, 324-334
- Ryan, J. & Tuttle, M. D. 1987. The role of prey-generated sounds, vision, and echolocation in prey localization by the African bat *Cardioderma cor* (Megadermatidae). *J. Comp. Physiol. A* 161, 59-66
- Rydell, J. 1992a. Exploitation of insects around street lamps by bats in Sweden. *Funct. Ecol.* 6, 744-750
- Rydell, J. 1992b. Occurrence of bats in northernmost Sweden (65°N) and their feeding ecology in summer. *J. Zool. Lond.* 227, 517-529
- 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. & Eklöf, J. 2002. Capture success of little brown bats feeding on mosquitoes. *J. Zool. Lond.* 256, 379-381
- Ryer, A. 1997. Light measurement handbook. International Light, Newburyport, MA.
- Schmidt, U. 1988. Orientation and sensory functions in *Desmodus rotundus*. In: Natural history of vampire bats (Greenhall, A. M. & Schmidt, U. eds.) CRC Press, Inc. Boca Raton Florida, pp 143-166
- Schmidt, U. & Manske, U. 1978. Visual pattern discrimination in the vampire bat, *Desmodus rotundus*. *Congressus Theriologicus Internationalis* 2, 59
- Schmidt, U., Joermann, G. & Rother, G. 1988. Acoustical vs. visual orientation in neotropical bats. In: Animal Sonar (Nachtigall, P. E. & Moore, P. W. B. eds.), Plenum Publishing Corporation, pp 589-593
- Schnitzler, H. U. & Grinnell, A. D. 1977a. Directional sensitivity of echolocation in the horse shoe bat, *Rhinolophus ferrumequinum*. I. Directionality of sound emission. *J. Comp. Physiol.* 116, 51-61
- Schnitzler, H. U. & Grinnell, A. D. 1977b. Directional sensitivity of echolocation in the horse shoe bat, *Rhinolophus ferrumequinum*. II. Behavioral directionality of hearing. *J. Comp. Physiol.* 116, 63-76
- Simmons, N. B. & Geisler, J. H. 1998. Phylogenetic relationships of *Icaronycteris*, *Archaeonycteris*, *Hassianycteris*, and *Palaeochiropteryx* to extant bat lineages, with comments on the evolution and foraging strategies in Microchiroptera. *Bull. Amer. Mus. Nat. Hist.* 235
- Springer, M. S., Teeling, E. & Stanhope, M. J. 2001. External nasal cartilages in bats: Evidence for Microchiropteran monophyly? *J. Mamm. Evol.* 8, 231-236
- Stein, B. E. & Meredith, A. 1993. The merging of the senses. The MIT Press, Cambridge, MA
- Suthers, R. A. 1966. Optomotor responses by echolocating bats. *Science* 152, 1102-1104
- Suthers, R. A. 1970. Vision, olfaction and taste. In: *Biology of Bats Vol. II* (Wimsatt, W. A. ed.). Academic Press, New York, pp 265-281
- Suthers, R. A. & Bradford, M. R. 1980. Visual systems and the evolutionary relationships of the Chiroptera. *Proc. 5th Int. Bat. Res. Conf.* 331-346

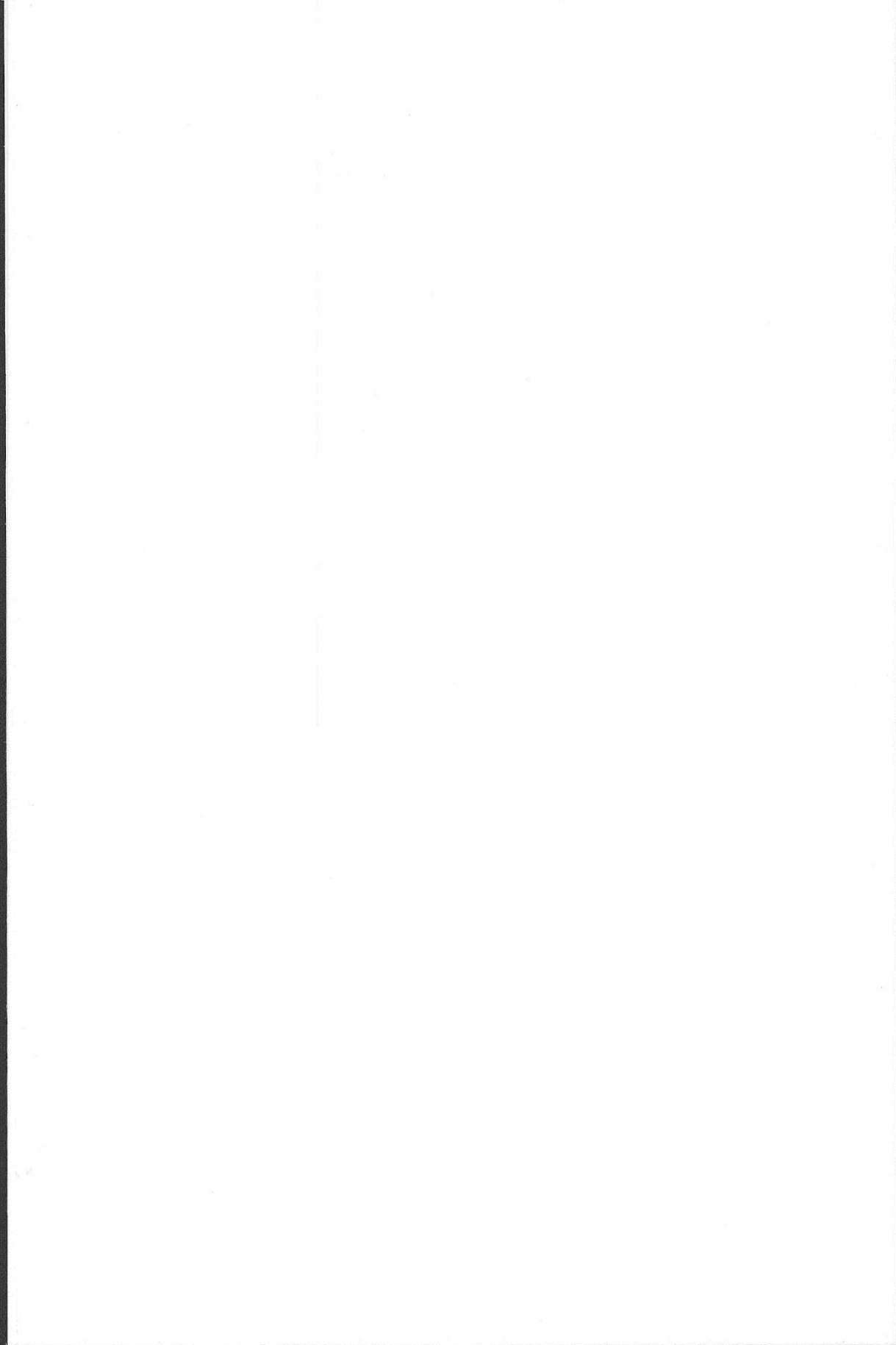
- Suthers, R. A. & Chase, J. 1966. Visual pattern discrimination by an echolocating bat. *Amer. Zool.* 6, 573
- Suthers, R. A. & Wallis, N. E. 1970. Optics of the eyes of echolocating bats. *J. Vision Res.* 10, 1165-1173
- Suthers, R. A., Chase, J. & Bradford, B. 1969. Visual form discrimination by echolocating bats. *Biol. Bull.* 137, 535-546
- Swift, S. M. 1998. Long-eared bats. T & AD Poyser Natural History. London
- Test, F. H. 1967. Indicated use of sight in navigation by molossid bats. *J. Mamm.* 48, 482-483
- Thomson, C. E. 1982. *Myotis sodalis*. *Mammalian species* 163, 1-5
- Timm, R. M. 1989. Migration and molt patterns of red bats, *Lasiurus borealis* (Chiroptera: Vespertilionidae). *Illinois. Bull. Chic. Acad. Sci.* 14, 1-7
- Usman, K., Habersetzer, R., Subbaraj, R., Gopalkrishnaswamy, G. & Paramandam, K. 1980. Behaviour of bats during a lunar eclipse. *Behav. Ecol. Sociobiol.* 7, 79-80
- Varassin, I. G., Trigo, J. R. & Sazima, M. 2001. The role of nectar production, flower pigments and odour in the pollination of four species of *Passiflora* (Passifloraceae) in south-eastern Brazil. *Bot. J. Linn. Soc.* 136, 139-152
- Vaughan, T. A. & Vaughan, R. P. 1986. Seasonality and the behaviour of the African yellow-winged bat. *J. Mamm.* 67, 91-102
- Verboom, B. & Huitema, H. 1997. The importance of linear landscape elements for the pipistrelle *Pipistrellus pipistrellus* and the serotine bat *Eptesicus serotinus*. *Landscape Ecology* 12 (2), 117-125
- Verboom, B., Boonman, A. M. & Limpens, H. J. G. A. 1999. Acoustic perception of landscape elements by the pond bat (*Myotis dasycneme*) *J. Zool. Lond.* 248, 59-66
- Vernon, C. L. 1981. The use of vision in prey selection by the Big brown bat, *Eptesicus fuscus*. Master thesis, the University of Wisconsin-Milwaukee
- Wallace, M. T. & Stein, B. E. 2001. Sensory and multisensory responses in the newborn monkey superior colliculus. *J. Neurosci.* 21, 8886-8898
- Whittington, D. A., Hepp-Raymond, M. C. & Flood, W. 1981. Eye and head movements to auditory targets. *Exp. Brain Res.* 41, 358-363
- Wilkinson, G. S. 1986. Social grooming in the vampire bat, *Desmodus rotundus*. *Anim. Behav.* 34, 1880-1889
- Williams, T. C. & Williams, J. M. 1967. Radiotracking of homing bats. *Science* 155, 1435-1436
- Williams, T. C., Williams, J. M. & Griffin, D. R. 1966. Homing ability of the neotropical bat *Phyllostomus hastatus*. *Anim. Behav.* 14, 468-473
- Willson, M. F. & Whelan, C. J. 1989. Ultraviolet reflectance of fruits of vertebrate-dispersed plants. *Oikos* 55, 341-348
- Wiltschko, W. & Wiltschko, R. 1995. *Magnetic orientation in animals*. Springer-Verlag, Berlin



På grund av upphovsrättsliga skäl kan vissa ingående delarbeten ej publiceras här.  
För en fullständig lista av ingående delarbeten, se avhandlingens början.

Due to copyright law limitations, certain papers may not be published here.  
For a complete list of papers, see the beginning of the dissertation.







“The investigation carried out by Eklöf et al. is a nice piece of science...”

- *Oikos*



“I have trouble in following the logic of the arguments of the authors and to understand what the relevance of this study is”

- *Mammalian Biology*



“This is a very well thought out and thoroughly executed behavioural project that benefits greatly from its innovative design; something that is a pleasing characteristic of the projects of this research group”

- *Oikos*



“A pleasure to read, and resolving a question I have long pondered.”

- *Animal Behaviour*



Göteborg University 2003  
Faculty of Science