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Full Name of Author — Nom complet de l'auteur

Gary Philip BELL

Date of Birth — Date de naissance

November 27, 1953

Country of Birth — Lieu de naissance

Canada

Permanent Address — Résidence fixe

P.O. Box 306

R.R. 3

Manotick, Ontario

K0A 2N0

Title of Thesis — Titre de la thèse

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Name of Supervisor — Nom du directeur de thèse

Dr. M.B. Fenton

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PREY LOCATION AND SENSORY ECOLOGY OF
TWO SPECIES OF GLEANING, INSECTIVOROUS BATS,
ANTROZOUS PALLIDUS (VESPERTILIONIDAE) AND
MACROTUS CALIFORNICUS (PHYLLOSTOMATIDAE).

by

© Gary Philip Bell, B.Sc., M.Sc.

A thesis submitted to the Faculty of
Graduate Studies in partial fulfilment
of the requirements for the degree of
Doctor of Science.

Department of Biology
Carleton University
Ottawa, Canada

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1.

ABSTRACT

A series of laboratory and field studies were conducted to determine how the bats Antrozous pallidus and Macrotus californicus hunt, locate and capture prey.

Antrozous pallidus fed primarily on moths, but also included beetles, chilopods and other arthropods in the diet. Most prey (>50%) were >20 mm in body length. These bats used echolocation to assess habitat and detect obstacles, but located prey by listening to their sounds. Echolocation was not used during prey capture. A. pallidus discriminated between sounds which indicated food (i.e. rustlings on open ground) from sounds which offered no reward (orthopteran mating calls).

Macrotus californicus was studied in the laboratory in large flight cages. The bats were tested for their ability to locate small prey items in moderate light and under total darkness. The bats shut off their echolocation in moderate light, indicating that they relied upon vision to locate prey, but always used echolocation in total darkness. These bats could locate prey using vision at luminances below 1.5×10^{-4} mL (millilamberts), and shut off echolocation pulse production at luminances above 3×10^{-2} mL. They also responded to the sounds of prey, including the calls of crickets.

The visual abilities of M. californicus were tested using the bats' optokinetic response to measure acuity and sensitivity. This species showed visual acuity of at least 3'38" of arc, at luminances of 2×10^{-4} mL, better than any species of bat tested to date, including fruit and nectar feeding forms.

These studies suggest that echolocation is not the only sensory mode used by insectivorous bats in hunting prey, and that, in fact, other sensory modes may be more efficient under some circumstances. The bats in these studies revealed greater sensory flexibility than has been previously demonstrated in bats.

The undersigned hereby recommend to the Faculty of
Graduate Studies and Research acceptance of this
thesis, submitted by Gary Philip Bell, B.Sc., M.Sc.,
in partial fulfillment of the requirements for
the degree of Doctor of Philosophy.

Gray Merri
.....

Chairman, Department of Biology

W. Bent
.....

Supervisor

James A. Johnson
.....

External Examiner

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CHAPTER I

GENERAL INTRODUCTION

"I pray you, let mee gleane and gather after
the reaper amongst the sheaves."

Ruth ii, 7 (1611)

INTRODUCTION

The Microchiroptera are a very diverse group, with some 700 species worldwide, feeding on a great range of food-types; fruit, nectar, pollen, insects, birds, mammals, fish, and blood. Of these nearly 540 species eat mainly animal protein, and within this group a number of different strategies for locating and capturing prey have evolved. It has long been apparent that not all carnivorous (sensu stricta) bats capture prey in aerial pursuit; as many as 30% of these carnivorous species capture prey from the ground, tree bark, or foliage, a strategy termed 'gleaning'. Unfortunately we know relatively little about this foraging strategy. The classification of bats as gleaners is, in fact, almost circular; bats suspected of gleaning have big ears, therefore bats with big ears are usually classified as gleaners (e.g. Handley, 1959; Wilson, 1973; Black, 1974; Fenton, 1972; Hindley, 1976; Norberg, 1976; Bell, 1980). While this may often be the case, the recent observations on the foraging behaviour of Euderma maculatum (Vespertilionidae), a bat with ears that are proportionately among the largest in the order, clearly indicates that this species is not a gleaner, but captures prey in rapid, aerial pursuit (Leonard, 1981; Woodsworth et al., 1981). Gleaning is still undoubtedly an important feeding strategy for many bats, but there are few actual data on gleaning. Circumstantial evidence for gleaning by some species

includes capture of individuals on the ground in small mammal traps (e.g. Grinnell, 1918; Huey, 1936), and the inclusion of non-flying prey in the diet (e.g. Vaughan, 1959; Wilson, 1971; Baurova, 1978). There have been a few recent studies of gleaning behaviour, including Cardioderma cor (Megadermatidae; Vaughan, 1976), Megaderma lyra (Megadermatidae; Fiedler, 1979), Myotis auriculus (Vespertilionidae; Fenton and Bell, 1979), and Trachops cirrhosus (Phyllostomatidae; Barclay et al., 1981).

How do gleaning bats locate prey? The importance of echolocation in gleaning is unknown, but often assumed. Fenton and Bell (1979) recorded echolocation calls produced by Myotis auriculus attacking stationary prey, but they did not rule out the use of other sensory cues. Fiedler (1979) reported Megaderma lyra capturing mice they located without echolocation by listening to the sounds of their prey. Tuttle and Ryan (1981) demonstrated that Trachops cirrhosus locates frogs by listening to their mating calls, albeit while producing echolocation calls (Barclay et. al., 1981), and Belwood (1981) reported that Tonatia sylvicola (Phyllostomatidae) uses the calls of katydids (Orthoptera: Tettigoniidae) to locate them. Other species of gleaning bats may rely on sounds of their prey, on vision, and on olfaction for locating prey (Kolb, 1961).

Echolocation is a very efficient means of locating targets in 3 dimensional space, and determining such parameters as velocity, range, texture and identity (Simmons et al., 1979; Simmons and Stein, 1980). Bats produce echolocation pulses of different, apparently species-specific, patterns depending upon the type of information required under different circumstances (Simmons, 1980; Simmons et al., 1979; Simmons and Stein, 1980; Fenton and Bell, 1981). Studies of the design of echolocation calls and processing of information in echoes has provided us with a theoretical framework for the ecology of echolocation, allowing us to make some predictions of the type of calls best suited to a particular type of feeding strategy, and, conversely, we might predict a bat's foraging strategy based on the types of echolocation calls it produces. In the very simplest of terms, bats which fly rapidly, and hunt in open situations at high altitude might be expected to produce calls of high intensity and long duration to maximize range. Slow-flying bats feeding on evasive prey, and hunting in cluttered habitats (i.e. many obstacles) should use echolocation pulses of lower intensity and shorter duration, which are modulated over a range of frequencies, to obtain maximum information on identity, velocity, and size, but limit range to a few meters at best. In addition, operable range depends on the frequency structure of the calls. Lower frequencies tend to be attenuated less (Griffin, 1971; Lawrence and Simmons, 1982);

thus bats using low frequency echolocation may operate at long ranges while high frequency may limit a bat to working at very short ranges (Simmons and Stein, 1980). The only actual measure of the effective range of echolocation comes from Kick (1982) who determined that, in the laboratory, Eptesicus fuscus, a bat with high intensity (100-110 dB), moderate frequency (50-25 kHz) echolocation calls, is able to detect a 19mm sphere at a distance of 5m. The observed distance at which a bat appears to respond to prey may provide an estimate of the effective range of echolocation. Brosset (1966) estimated that Taphozous peli, using low frequency (20 kHz) high intensity calls, first responds to prey at distances of at least 15m, and Griffin (1971) estimated that the high frequency calls of Hipposideros galaratis (150 kHz) limit that species to ranges of less than 2m. One might expect that bats gleaning prey from surfaces should use calls of very low intensity, very high frequency, extremely short duration, and in addition, complex frequency structure to provide maximum resolution. Fenton and Bell (1979) estimated that the gleaning bat Myotis auriculus, using moderate intensity calls in the 140-50 kHz range, were locating prey at approximately 1m, while the African gleaner Nycteris thebaica appears to operate at even shorter ranges using low intensity calls of 100-60kHz. Whether such calls exist, and whether echolocation can be used in gleaning is another matter. The

background noise of echoes from the substrate, not a factor in aerial foraging, must be a major problem, and even if prey can be located on surfaces in theory, the confusing background clutter in foliage and ground gleaning situations may make location of stationary prey impossible.

Other sensory modes are available to hunting bats. Fiedler (1979), and Tuttle and Ryan (1981) have shown that some bats orient on the sounds produced by the prey itself. The hearing of bats is adapted for processing fine, faint echoes. It is reasonable to expect that other sounds, such as the sounds of prey would be exploited wherever possible. Unfortunately most of our knowledge of bat hearing concerns the ultrasonic range, and sounds of prey are often much lower in frequency. Despite the incorrect assumptions of many workers, all echolocation is not ultrasonic (e.g. Woodsworth et al., 1981), and the hearing range of species with ultrasonic echolocation calls is not necessarily limited to that range of frequencies.

Vision in bats is another area that has received insufficient attention. While various workers have shown that bats have vision at least as good as that of other small nocturnal mammals (e.g. Suthers, 1970; Chase, 1972), the old adage 'blind as a bat' is too often believed. While Chase (1972) found that the insectivorous species she examined had the poorest vision, and the nectarivorous and

frugivorous species the best, too few species have actually been studied to draw any firm conclusions. Vision, even at low light levels may be less ambiguous, and may often be superior to echolocation for finding prey.

Other senses available include olfaction, and tactile senses. While evidence indicates that these may indeed be important at close range, Suthers (1970) indicates that the olfactory abilities of insectivorous species are insufficient for location of prey at the distances at which even gleaning bats operate

Finally, there is no reason to expect that a single species of bat will be restricted to using a single sensory system. While sensory redundancy may not seem to be beneficial, in many cases different sensory systems may provide the animal with conflicting information, and a degree of flexibility might be expected. This should be especially true of bats gleaning prey in cluttered situations.

I had four main goals in this study: 1) to examine the foraging behaviour of two species of bats suspected of gleaning to determine whether they were gleaners, and if so, to reveal whether this mode of foraging was obligate or facultative; 2) to determine the mechanics and behaviour of gleaning; 3) to determine the sensory basis of prey location.

by these bats when gleaning prey; and 4) to determine the sensory abilities of these bats; specifically to examine any sensory abilities which allow these bats to locate prey against hard backgrounds. The two species examined were Antrozous pallidus, a 20-25 g Vespertilionid reputed to be a ground gleaner, and Macrotus californicus, a 12-20 g Phyllostomatid suspected of gleaning from the ground and foliage.

CHAPTER II

The feeding behaviour and ecology of a ground gleaning
desert bat, Antrozous pallidus.

"He gleaneth whatsoever is good or ought woorth
through his whole kingdome."

Johnston, Kingdom and Commonwealth (1601)

INTRODUCTION

Antrozous pallidus (Vespertilionidae) is essentially a desert species found from Mexico to southern British Columbia in a variety of arid and semi-arid habitats. Antrozous has long been considered a gleaner (e.g. Grinnell, 1918; Huey, 1936; Vaughan and O'Shea, 1976), but there are no actual data confirming that this species is a gleaning specialist. Brown (1976) and others have reported on the vocal behaviour of this species, but the echolocation calls produced by A. pallidus are of higher intensity and lower frequency than we would predict for a gleaning bat (Simmons and Stein, 1980).

The purpose of this study was to observe and manipulate a wild population of A. pallidus to determine whether these bats are obligate gleaners, to determine whether echolocation is used to locate prey on hard backgrounds, and to explore what other sensory modes might be involved in prey location.

MATERIALS AND METHODS

Field work was carried out near a nursery colony of 150 Antrozous pallidus in the San Simon Valley of Hidalgo Co., New Mexico (31 50'N, 109 2'W), between June and August, 1981. During the day the bats roosted in an adobe bunkhouse, and at night in an old barn 10 m from the bunkhouse. The bats foraged locally (within 3 km) in lower Sonoran desert grassland consisting of patches of vegetation on bare, hard soil (Moir, 1979).

All observations and experiments were done in the field with wild, unmarked bats. Observations were made with the naked eye under available light or with a Javelin model 325 Night Vision Scope. Sounds of prey and bat echolocation calls were recorded on a Racal Store 4D tape recorder operated at 76 cm/s using a broad band microphone (=bat detector; Simmons et al., 1979). Some playback experiments with low frequency insect noises were done using a Panasonic RQ 413MS cassette tape recorder through a KEF SP1032 speaker. Analysis of bat and insect sounds was carried out in the laboratory using a Princeton Applied Research model 4513 fast Fourier transform real time sound spectrum analyzer and a Kay model 7029A sonograph. Insects used in experiments were captured at fluorescent 'black' (i.e. ultraviolet) lights (General Electric F15 T8 BL).

Preliminary Observations

My preliminary observations of the foraging behavior of A. pallidus confirmed earlier reports that it captures prey on the ground (Orr, 1954). To obtain more information about this behavior and to set up a variety of experiments the bats were provided with abundant insect prey near to their roost sites using the black light. Within two weeks the bats had concentrated as much as 80% of their foraging activities within 100m of the roosts, and gleaning behavior was easily (and frequently) observed. For experimental purposes the bats were presented with moths (Sphingidae, Noctuidae, Notodontidae, Arctiidae and Geometridae) that were lightly chilled and from which I had clipped 50% of one set of wings. The moths, set on the ground, vibrated their wings, presumably for thermogenesis (Dorsett, 1962; Heinrich and Bartholomew, 1971), but wing-clipping prevented them from taking flight. Preliminary observations indicated that moths so prepared were not treated any differently by the bats than moths warming up under natural conditions, or unclipped moths on the ground at ultraviolet lights.

Prey Selection

General patterns of prey selection over the summer were assessed by identification of culled prey parts and analysis of fecal material (Belwood and Fenton, 1976) collected from

beneath the night roost. Seven collections of feces and culled parts were made between 17 June and 10 August. The ground beneath the night roost was swept clean before the bats emerged for the evening and all feces and prey remains were collected the following morning.

To determine whether A. pallidus selected prey on the basis of size I conducted experiments, setting out individual sphingid and noctuid moths representing 5 different size classes [A, 45-60 mm body length (BL), 110-130 mm wing span (WS); B, 35-45 mm BL, 80-100 mm WS; C, 25-35 mm BL, 60-80 mm WS; D, 20-25 mm BL, 45-60 mm WS; E, 14-20 mm BL, 30-40 mm WS]. For each individual moth (wing-clipped and chilled) I recorded total time from commencement of wing vibration until capture by a bat (in seconds) up to a maximum of 2 min (on 2 occasions moths were not captured within 2 min). In addition I recorded the number of passes made by bats, within 1 m of the moth, before the capture was made, and the number of attacks that were made on the moth and then broken off (balks) before capture. A balk involved a bat landing on, or beside, and biting or otherwise contacting a moth and then flying away without capturing it. Using these three measures, response to moths on the ground was separated into three components; 1) total search and handling time, 2) amount of uncertainty (expressed by amount of prey item investigation; passes/capture), and 3) a measure of difficulty (or danger) in handling a particular prey item (balks/capture).

Sensory Basis of Prey Selection

To determine how A. pallidus located targets on the ground I conducted several experiments using intermediate-sized sphinx moths (25-45 mm BL, 60-80 mm WS) as prey items. Bats were presented with only the fluttering sounds of the moths, without visual or echolocation cues, in two ways. Initially I used recordings of moth flutterings; later I placed individual moths in lightly dampened brown paper bags. The sounds of the moths fluttering in the bags differed little from the sounds of moths on the ground. In either case I recorded the number of passes within 1 m of the sound source in a 60 s test period, beginning with the onset of fluttering. As controls for these tests I also recorded passes in 60 s periods over; 1) no moth (i.e. a measure of random activity over the test area), 2) a moth killed by freezing (i.e. visual and echolocation cues, but no prey sounds available), and 3) a live, free-fluttering moth (providing all sensory cues which the bats might use).

Other Tests

To test for patterns of habitat use I presented the bats with bagged fluttering moths on open ground, and in areas of high clutter (beneath or within thorny bushes and patches of thistle).

To test whether or not A. pallidus responded to the mating calls of orthopteran insects, I played tape recordings of cricket calls to the bats and recorded passes over the speaker in 60 s test periods. I also observed bat activity over naturally calling crickets (Gryllus spp.) and katydids (Tettigoniidae).

RESULTS

Foraging Behaviour

Foraging Antrozous pallidus flew over areas of desert grassland within 3 km of the roost site. When searching for prey the bats flew at moderate speeds at 0.1 to 10 m above the ground. In flight the bats made frequent dives close to the ground, and frequent dips and turns. On occasion bats appeared to ride in nearly stationary flight on stiff evening breezes and during investigations of potential prey on the ground the bats often performed a short 'hover' for 2-3 wingbeats. Despite this undulating flight, however, these bats are not particularly manoeuvrable over short distances compared to other, lighter, gleaning species such as Macrotus californicus and Nycteris thebaica (Nycteridae).

Approaches to prey were rapid and direct, and it was my impression that the bats located their intended prey at distances of up to 10 m. In a typical capture sequence a bat would fly over the intended prey at a height of 0.2 to 1m, producing echolocation pulses, before making an actual capture attempt. In approaching for an attack the bats apparently never produced echolocation calls (0 of 8 complete capture sequences I recorded on tape (Figure 2-1), and 0 of over 50 capture sequences I monitored with a

broad-band bat detector). Feeding buzzes (Griffin, 1958; Simmons, Fenton and O'Farrell, 1979) were never heard or recorded. The bat flew directly towards a target at a height of about 1 m above the ground, dropping in altitude at 1 to 2 m range to land on its feet and wrists beside or on top of the prey. The bat seized the prey in its mouth, striking at the thorax, and flew away with it immediately. The following variations in this typical feeding style were observed: 1) often several bats (up to 15) investigated the same moth at the same time until one captured it, but no agonistic interactions were ever observed; 2) the bat or bats made from 0 to more than 70 passes over a particular prey item before capturing it; 3) rarely (5 of more than 500 captures observed) a very large prey item was not captured, despite frequent investigation. Occasionally the struggles of large prey required additional handling on the ground (manipulations with wrists, wing membranes and mouth) before capture was completed, lasting up to 10 s, or resulting in complete abandonment of the insect. I never saw a bat feed on the ground, or carry out any manipulations (e.g. culling) beyond capturing and subduing of prey, and on several occasions moths were still heard fluttering as the bat flew off with them. Small prey items were consumed in flight, but large prey were taken back to the night roost where wings, and often legs, heads, and other parts were culled before the prey was consumed. A bat returning to the night roost with a large prey item would not join a cluster of

other bats, but would hang up in isolation to eat, often enclosing the prey item in its wings and interfemoral membrane.

In over 150 h of observations, I never saw an A. pallidus capture flying prey, although I twice saw short, unsuccessful chases of small (20 mm WS), slow flying insects near the black lights.

Prey Composition and Prey Size Selection

Throughout the summer A. pallidus fed mainly on sphinx moths (44% of 293 prey items identified; Table 2-1). Other important prey included both male and female crickets (Gryllus spp.; 9%) and beetles (Coleoptera; 26%). A single pocket mouse (Perognathus flavus; 7-10 g in weight!) captured by one bat represents the first evidence of this species taking vertebrate prey in the wild.

While all size classes of prey were taken in the prey size class experiments, there is a trend for A. pallidus to capture intermediate-sized prey in the least amount of time (Figure 2-2a). Size class C prey (25-35 mm BL; 60-80 mm WS) were taken in significantly less time than larger prey (size class B: $t=2.56$, $n=21$, $P<0.05$), but the trend is not significant when comparing

capture times of intermediate and small size classes (size class D: $t=0.94$, $n=21$, $P>0.20$). Passes per capture (Figure 2-2b), a measure of the amount of uncertainty the bats have about a particular prey item, is greater for large than for small prey items, which suggests that while larger prey may be easier to locate, as they produce louder fluttering noises, they require more handling time than smaller prey. The trade-off between search and investigation (i.e. handling) times produces an apparent optimum prey size, size class C, which minimizes combined search and handling time functions. Longer investigation of larger prey should be warranted, as large prey could actually be dangerous. Only large moths (size classes A and B) induced balks (Figure 2-2c) and, furthermore, within a size class, balks occurred during tests with long capture times and high passes per capture, suggesting that balks are associated with indecision. Such broken attacks may be due to the formidable (3-5 mm) femoral spurs of the moths used in these experiments (Manduca quinquimaculata, M. sexta). I frequently suffered punctured finger-tips when handling these large sphingids, and a careless bat could very easily lose an eye or sustain other serious injury in a struggle.

Sensory Basis of Prey Location

The responses of foraging A. pallidus to the sounds of moths, and to various controls are summarized in Table 2-2. There was no significant difference between responses of bats to the sounds of moths and to actual fluttering moths, and response to both these situations differed significantly from random activity. The importance of the acoustic cues is emphasized by 9 attacks by bats on paper bags containing fluttering moths; in these situations the bats obviously ignored any conflicting visual and echolocation cues. The bats never responded to dead moths, and bats never captured moths which were not fluttering, and discontinued investigation of a moth shortly after it stopped fluttering. These bats obviously used the sounds of prey on the ground, and did not use vision or echolocation when searching for prey.

The response of these bats to the same prey sounds in cluttered situations was significantly lower than to prey sounds in open situations ($t'=5.81$, $n=20$, $P<0.001$). Antrozous pallidus clearly prefers to capture prey on open ground.

Playbacks of tape-recorded calls of crickets

(Gryllus spp.) elicited no response from foraging bats, in contrast to the obvious responses to the sounds of fluttering moths, and I never observed a bat investigating a calling orthopteran. Field observations of hundreds of crickets and katydids indicted that male orthopterans in this habitat always stridulate from burrows, under rocks, or from heavy, thorny cover.

The average sound spectra for the four largest size classes of moths fluttering on the ground are summarized in Table 2-3. The sounds of the smallest size class of moths (size class E) were of too low intensity to be recorded. Note that all the energy in these sounds falls below 15 kHz, and that the maximum energy of these sounds lies in the range of 4.7 to 8.6 kHz.

The responses of A. pallidus to the sounds of prey are even more striking when compared to the total lack of response to flutterings of grounded insects of any size by any sympatric species of insectivorous bats. A colony of 25 Myotis thysanodes (Vespertilionidae) roosted nearby, and fed nightly over my experimental area. Tadarida brasiliensis, T. macrotis (Molossidae) and Pipistrellus hesperus (Vespertilionidae) frequently fed over my study site as well. These four species all captured prey in aerial pursuit, producing echolocation (complete with feeding buzzes) during each of the prey captures I monitored with a bat

detector (c. 200 captures by M. thysanodes; 100 by T. brasiliensis; 20 by P. hesperus; and 10 by T. macrotis) but I never observed any response by these bats to the sounds which attracted A. pallidus.

DISCUSSION

The A. pallidus in this study captured prey on the ground and consumed it in the air or at a night roost. These bats selectively used some sounds of prey to detect and locate targets, ignoring cues available from echolocation or vision. Echolocation calls were produced while bats searched for prey, and both echolocation and vision may be important in general navigation for estimation of altitude and detection of obstacles, but echolocation was not used in prey capture.

A diversity of prey types was taken, but the bulk of the diet of A. pallidus in this study consisted of intermediate-sized sphinx moths (20-40 mm BL), as well as small- to intermediate-sized beetles and orthopterans (principally crickets) all of which were very abundant in the study area. Grinnell (1918) found that Jerusalem crickets (Stenopalmatus sp.) and sphinx moths (Hyles lineata) were the most common prey of A. pallidus at a site in southern California, and Hatt (1923) reported that in northern California these bats fed primarily on Jerusalem crickets and scorpions (Anuroctonus phaeodactylus). In general, then, Antrozous pallidus preferred larger prey, without any obvious signs of taxonomic selection.

The prey selection experiments in this study reveal that large prey require greater handling time, while smaller prey take longer to locate, resulting in an apparent 'optimum' prey size which minimizes these two opposing functions.

This analysis suggests that A. pallidus are optimal foragers, functioning as energy maximizers (Schoener, 1971; Pyke et al., 1977) taking the largest available prey. Such an apparent strategy is probably due to the lower intensity sounds of small prey, however; such small prey are not easily located, and so are probably included in the diet less often than larger prey, as selection experiments indicate that once a prey item is located, regardless of its size, it is always captured. Such behavior makes A. pallidus a true opportunistic feeder. Opportunistic responses of desert bats to locally abundant prey have been reported by Fenton and Morris (1976), Bell (1980) and Vaughan (1980).

Considering the sensory modes available to A. pallidus for locating prey, echolocation is perhaps the least suitable. In theory, echolocation could be used to detect targets against cluttered backgrounds in gleaning, and we know that A. pallidus can, when challenged in a laboratory situation, make fine target discriminations using echolocation (Gaudet, 1981). Even a relatively generalized echolocating species such as Eptesicus fuscus (Vespertilionidae) can resolve target details of less than

0.8 mm under laboratory conditions (Simmons et al., 1974), and finer resolution might be expected of more specialized species. In the field, however, A. pallidus covers a rather broad foraging range at moderate speeds (4 m/s; Hayward and Davis, 1964) in an acoustically complex environment where echolocation could provide unreliable, ambiguous, and at best, short-range information on prey location and identity. It is therefore not surprising that the echolocation calls of A. pallidus (Figure 2-1) are of moderately low frequency (50-25 kHz fundamental), moderate intensity (c. 90-100 dB SPL) and rather long duration (5 ms), characteristics which are not consistent with predicted optimal call designs for gleaning bats (Simmons, Fenton, and O'Farrell, 1979). We might expect to find high resolution echolocation used for gleaning by smaller, slow-flying, hovering gleaners such as Nycteris thebaica (Nycteridae) and Macrotus californicus (see Chapter III).

The most important sensory cues used by A. pallidus in this study were the low frequency (4-8 kHz) rustlings of prey on the ground. While the frequency spectra of these sounds are probably insufficient to permit size discrimination, the pattern of the sound train, characteristic of the wing beat frequency, is probably used by the bat in decision making (J.A. Simmons, pers.comm.). This species has remarkable hearing sensitivity below 15 kHz (Brown et al., 1978), compared with most other species of

bats examined (Menson, 1970), despite the frequency range of its echolocation calls (above 25 kHz), and suggested that this low frequency sensitivity is associated with low frequency communication calls (8-12 kHz) as well as with less need for accurate localization of targets in three dimensional space. It seems probable, however, that low frequency sensitivity is associated with the detection and localization of the sounds of prey. We know very little of the hearing sensitivity of most bats, including A. pallidus, to sounds below 5 kHz. Trachops cirrhosus (Phyllostomatidae) is sensitive to the relatively low frequency calls of the frogs upon which it feeds (Tuttle and Ryan, 1981), and has increased hearing sensitivity below 5 kHz, in the range of frequencies used by its prey (Ryan et al., 1981). Many other species of bats are probably sensitive to low frequency sound, and use such sounds in foraging. Buchler and Childs (1981) found that Eptesicus fuscus responds to low frequency sounds associated with calling frogs and katydids, and orients towards the maximum sound field in these frequencies to locate areas of high prey abundance.

Belwood (1981) demonstrated that Tonatia sylvicola (Phyllostomatidae) responded to recordings of orthopteran mating calls in Panama. In my study area A. pallidus failed to respond to cricket or katydid calls. Crickets were common in the study area, and formed a significant component

of the bats' diets, but male and female crickets were equally represented in the diet analysis. In the rainforests of Panama where T. sylvicola forages, orthopterans call rarely and quietly, and because of the agility and foliage-gleaning abilities of this bat, orthopterans may be much more susceptible to bat depredations in that setting (Belwood, 1981). In New Mexico, however, orthopterans are very abundant and call loudly and almost continuously from concealed locations. The lack of manoeuvrability of A. pallidus, and the high risk of investigating prey in heavy cover (Davis, 1968), is a very different situation, and this bat has probably never learned to associate the calls of orthopterans with potential prey.

Fenton (1980) has indicated that echolocation is a mixed blessing. While it can provide accurate information about target range, velocity, and identity, it also alerts prey, competitors, and predators. Werner (1981) demonstrated that some tympanate moths respond to simulated bat echolocation calls by ceasing movement and reducing their profile when walking or resting on a surface. Some bats which feed on moths have echolocation calls falling outside the frequency range of maximum sensitivity of the ears of their prey, which may allow the bat a distinct advantage (Fenton and Fullard, 1979). In this study cessation of production of echolocation pulses could be yet another counter to the

acoustic-based defensive strategies of prey. In this context Roeder et al. (1968) located auditory organs in sphingid moths of the subfamily Choerocampinae, including Hyles lineata, one of the principal prey species of A. pallidus in this study. Fiedler (1979) found that Megaderma lyra (Megadermatidae) captured mice it located without the use of echolocation, and suggested that their silent attacks could be a counter to the ultrasonic sensitivity of some rodents. In contrast, Trachops cirrhosus produces echolocation calls when attacking frogs, which are apparently insensitive to such ultrasonics (Barclay et al., 1981).

This study has indicated nothing of the behaviour of Antrozous pallidus in other habitats, or at other times of the year. The feeding behaviour of insectivorous bats is much more flexible than previously believed (e.g. Howell, 1980), and we should remain cautious when drawing hard and fast conclusions about the foraging strategies of these animals.

CHAPTER III

The sensory basis of prey location by the
California Leaf-nosed Bat, Macrotus californicus.

"And I come after glening here and there."

- Chaucer, The Legend of Good Women, Prol, 75 (c.1385)

INTRODUCTION

In Chapter II I examined the sensory ecology and feeding behaviour of a heavy-bodied, relatively unmanoeuvrable ground-gleaning bat, in a habitat in which thorny clutter made echolocation inefficient, and foliage-gleaning dangerous. Antrozous pallidus did not use echolocation for locating prey, but relied on sounds produced by its potential victims. In theory, however, prey on cluttered surfaces should be locatable using refined echolocation.

Macrotus californicus is smaller than A. pallidus (12-20 g), and shows high manoeuvrability in flight, including the ability to hover. It is a resident of the barren, Colorado desert of Sonora, Baja California, southwestern Arizona and southeastern California (Hall, 1982). Macrotus has long been thought to be a gleaner (e.g. Vaughan, 1959), and produces echolocation calls of very low intensity, and high frequency (P.E. Brown, pers. comm.), characteristic of the type of call predicted for gleaning (Simmons and Stein, 1980). In addition Macrotus is notable for its large ears and its large, forward directed eyes. These suggested that this species might be using prey sounds and vision to locate prey as well.

The purpose of this study was to examine the ability of M. californicus to locate and capture prey using

echolocation, and other senses, and to determine the characteristics of its echolocation calls.

Materials and Methods

All work with Macrotus californicus was carried out in the laboratory; experiments were run at facilities at the Department of Biology, University of California, Riverside, Ca., and the Department of Biology, Carleton University. Bats were captured in the wild at roost sites in the Colorado desert in Riverside Co., Ca. Captive Macrotus took readily to their new conditions, and in most cases experiments could be run within 1 week of introduction to the laboratory. Bats were housed in large hardware cloth flight cages; the cages at Riverside measured 2.5 X 2.5 X 2.5 m, and 2.5 X 2.5 X 1.5 m approximately; the cages at Carleton measured 1 X 1 X 1 m, and 2 X 1 X 1 m approximately. Captive bats were fed on and tested using mealworms (Tenebrio larvae) and crickets (Gryllus spp.). Water was provided ad libitum.

During sensory tests bats were monitored for the use of echolocation by a broad-band ultrasonic microphone coupled with a small ultrasonic amplifier (Simmons et al., 1979) through a set of headphones. Echolocation calls were recorded using the microphone and amplifier, and a Racal (Lockheed) Store 4D tape-recorder operated at 76 cm/s. Bats were observed under total darkness using a Javelin model 325 Night Vision Scope and two small infrared LED light sources.

Sensory Basis of Prey Selection

Preliminary work with M. californicus suggested that this bat might use vision to locate prey, and was, in fact, shutting off production of echolocation pulses when light was sufficient for visual location of prey. To test this more fully a series of experiments was run using both individual bats and a flock of 6 bats in a large flight cage. In tests with individuals the 'prey' items consisted of 1/2 or 1/4 mealworms, placed in small (5 cm diameter)

● Petri dishes in groups of 1 to 5 prey items. A total of 10 mealworms arranged in 7 Petri dishes was always presented, but the dishes were moved about semi-randomly before each test. Often at least one dish contained no prey items. In experiments with the flock the bats were presented with 10 crickets in each test set out at random in a 0.6 X 1 m earthen-floored arena. For each test I recorded; 1) the number of passes made by bats within 0.5 m of the prey items without the production of echolocation calls, 2) the number of passes over the prey items with the production of echolocation calls, 3) the number of attempts (i.e. landings) made by bats to capture a prey item, and 4) the number of successful captures made during the test (usually, but not always, 10). Tests were run under moderate room light and under total darkness using the flock and a number of individuals. In each case the bats were allowed to adapt to the lighting conditions of the test for at least 30 min. before the test run was begun.

To determine whether M. californicus responded to the sounds of prey the bats were presented with tape-recordings of the calls of crickets. These play-backs were made through one of a pair of KEF SP1032 speakers, and the response of the bat to the sounds was noted.

To determine the light intensity threshold at which Macrotus is able to use vision (or, conversely, the intensity at which echolocation is needed) I used a series of experiments similar to the sensory mode experiments outlined above. In the largest flight cage available at Carleton University a flock of 7 Macrotus was presented with an array of small Petri dishes containing whole mealworms. The illumination of the cage was controlled using a 100 watt light bulb filtered through a 460-580 nm band filter. Using a series of neutral density filters (Hoya ® ; X2 = Neutral Density (ND) .3 = 50% transmission, X4 = ND .6 = 25% transmission, X8 = ND .9 = 12.5% transmission), I was able to test the bats under a range of known intensities of light. Before conducting a test the bat(s) were allowed to adapt to the lighting conditions for at least 30 min. In each test the activity of the bats was monitored using the bat detector apparatus mentioned above, and the night vision scope (when needed), for a period of 10 min. The number of passes made by the bats over the array with and without the use of echolocation was recorded. Sample size (n= number of passes by all bats) for each intensity level was at least

130, and several critical values were retested to ensure accuracy. Light levels were measured using a B. Lange Model 1902 light meter, and a radiometer.

RESULTS

The Macrotus californicus used in this study captured prey from the ground in a fashion similar to Antrozous pallidus (Chapter II). A bat would investigate the prey area from 1 to several times before attempting a capture. In capture the bat would approach the prey item directly, landing on or beside it, and seizing it in the mouth, launch into flight again by pushing off the ground with the wings and feet. These bats never fed on the ground. In contrast to A. pallidus, Macrotus is not an agile bat on the ground; in order to move even a few mm over the ground to pursue or search for a prey item this species had to launch into flight and drop again at the desired point. Prey were not eaten in flight, but were carried back to a perch before being consumed. While these observations were all made under laboratory conditions, this species probably uses a similar strategy under natural conditions. I would predict that Macrotus 'sallies' after prey from a convenient roost, as their slow, hovering flight is likely to be energetically costly.

This bat is apparently quite flexible in its sensory abilities. Table 3-1 presents a comparison of data from the prey capture experiments run under light and totally dark conditions, showing quite clearly that not only does M. californicus use vision to locate prey when there is

sufficient light, but that echolocation pulse production is essentially shut off under such conditions. This behavioural trend is somewhat variable; in the individual runs some bats tended to rely more on echolocation, even under light conditions, than others. It is also interesting to note (Table 3-2) that in the flock runs, the bats were actually more successful at locating prey under light conditions (i.e. when vision was used) than under dark conditions (when echolocation was used). This trend was not found in the individual runs however, suggesting that the bats may have been watching one another to find locations of prey.

Responses of this species to playbacks of orthopteran (Gryllus sp.) mating calls indicated that this species is also able to locate prey by the sounds they produce (G-test (Sokal and Rolf, 1969); $n=30$, $G=12.2$, $P<0.01$). While no tests were conducted with simple rustling sounds such as those that attracted A. pallidus in the field (Chapter II), it was observed that Macrotus has excellent hearing, and scanning continuously with their ears, cued on even the faint rustlings of a cricket on the bottom of their cage.

The echolocation calls produced by M. californicus during prey location exercises in total darkness are illustrated in Figure 2-1. These calls were of extremely low intensity (ca. 50 dB SPL @ 10 cm) and therefore were

very difficult to record, requiring additional amplification of the microphone signal to obtain adequate tape recordings. The calls are short in duration (<1 ms) and consist of a steep FM sweep from 90 to 50 kHz. These calls were produced in rapid bursts, but without a definite 'feeding buzz' such as is found in aerial foragers (Griffin, 1958; Fenton and Bell, 1979).

Given that M. californicus is very flexible in its sensory abilities in locating prey, the next question was what determined the switch from one mode to another, especially the switch between vision and echolocation? Figure 3-1 shows the results of the light intensity threshold experiments with a flock of 7 Macrotus. While no clear threshold level is evident, the curve indicates a gradual decay in visual ability with decreasing luminance, with a corresponding increase in the production of echolocation. The curve of Figure 3-1 is a hyperbola of the form $y = 450 / (200x + 10) + 27.5$. The asymptote of 27.5% echolocation call production is perhaps a little high, as the flock produced much more sound under light conditions than individuals. The experimental design did not allow me to differentiate between echolocation pulses and 'honks' (Griffin, 1958) made by individuals when they were on a collision course. During the tests, however, I could clearly tell that in the bright light tests most of the 'echolocation' calls scored were rapid buzzes produced when

2 or more bats were approaching the food tray at the same time. With no clear threshold level we can apply some arbitrary threshold levels for a comparison of luminance levels. The 50% echolocation level, the level at which echolocation is being produced 50% of the time, occurs at a luminance of 6.25×10^{-2} mL (millilamberts), and the 75% level, i.e. the level which most of the bats are producing echolocation most of the time (but vision is none the less being used a significant proportion of the time) falls at a luminance of 1.5×10^{-3} mL.

DISCUSSION

The M. californicus used in this study captured prey from the ground, sallying from a perch when a potential prey item was located. These bats were very flexible in their sensory abilities; prey were located using echolocation, vision, or the sounds of prey rustling or stridulating. Vision was used preferentially over echolocation, and when there was sufficient light these bats ceased production of echolocation calls. When feeding in a flock situation these bats were actually more successful at locating prey when vision was used than when the bats were restricted to the use of echolocation.

The echolocation calls produced by M. californicus when hunting prey are of low intensity, high frequency, and short duration, characteristics which are compatible with theoretically 'ideal' echolocation calls for locating prey under high clutter gleaning situations (Simmons and Stein, 1980). That these bats use vision preferentially over echolocation suggests that while echolocation can be used to locate prey under such conditions, it is not as efficient as other sensory modes. The double frequency sweep of the calls of Macrotus (Figure 2-1) is similar to the call pattern of the similar Old World gleaning bats of the genus Nycteris (e.g. N. thebaica; Figure 2-1). Novick (1963, 1977) indicated that the double sweep in the calls of

Macrotus waterhousii is a double fundamental, not a harmonic relation. How the bat produces such calls has not yet been determined, but the similarity of the calls of Macrotus and Nycteris suggests that there may be an important function in such a call pattern for gleaning prey, probably by increasing resolution and reducing ambiguity (J.A. Simmons, pers.comm.; Simmons and Stein, 1980).

The visual threshold experiments indicate that Macrotus operates with fullest reliance on vision (i.e. shuts off echolocation to maximum extent) at light intensities as low as 0.03 mL (or 50 ergs/cm²/s), approximately the level of luminance under full moonlight ($3 - 4 \times 10^{-2}$ mL; Levi, 1980). The 75% visual threshold value in Figure 3-1 indicates that vision is still used supplementally at light intensities as low as 1.5×10^{-3} mL. The use of vision by Macrotus may have evolved to supplement echolocation under the high clutter situations of gleaning terrestrial prey, but operating without echolocation is probably a response to the defensive strategies of insect prey (Fenton and Fullard, 1979; Werner, 1980), in a manner similar to the behaviour of Antrozous pallidus (Chapter II) and the carnivorous bat Megaderma lyra (Fiedler, 1980). The ability of Macrotus to rely entirely on sensory modes other than echolocation suggests a step further in coping with the defensive strategies of tympanate prey.

Its ability to switch between sensory modes, depending upon the situation or the conditions makes Macrotus the most flexible bat for which we have comparable data. There has been a tendency to assume that because most bats have small eyes, and because echolocation is so efficient, and has been so well documented, that vision is a sense of negligible importance to the Microchiroptera, despite the work of Chase (1972) and others who have demonstrated that bats have vision at least as good as other small nocturnal mammals. Among the bats, echolocation is clearly not the be-all and end-all when it comes to locating nocturnal prey, and it is my guess that further research will reveal that other insectivorous bats may use vision in some aspects of prey location.

Although these data clearly show that M. californicus use vision to locate prey, they do not demonstrate just how good the vision of this species is and how it compares with other species of echolocating bats. The next chapter deals with the visual acuity and sensitivity of M. californicus, and a comparison of other species of gleaners and non-gleaners.

CHAPTER IV

The visual performance of a glean^oing insectivorous bat,
Macrotus californicus.

"For many a Joy he could
from the Night's soft presence glean."

Byron, Childe Harold II, lxx (1812)

INTRODUCTION

The eye of the microchiropteran bat is very typical of most small, nocturnal mammals (Suthers, 1970; Chase, 1972; Rochon-Duvigneaud, 1943). In general the eyeball is spherical, the cornea large, and of greater curvature than the eyeball, the pupillary opening large, and the retina thin. There is apparently no tapetum lucidum; while several species show eyeshine, this is probably due to reflection of light off the choroidal capillary network because of the thinness of the retina (Dieterich and Dodt, 1970; Chase, 1972).

The sensory cells are mainly of the rod type, although some cones have been identified in some species (Chase, 1972). The receptors are densely packed (47,000 to 400,000/mm²) and there is a high degree of convergence - as much as 100:1, receptors:ganglia (in some of the foliage roosting, and partially diurnal *Emballonuridae*, the summation is on the order of 10 or 20:1). There is no fovea, or area centralis.

The dioptrics of the microchiropteran eye, examined with a retinoscope, show refractive errors on the order of +3.5 to +13.00 Diopters (D), all hypermetropic (i.e. farsighted; Suthers, 1970; Suthers and Wallis, 1970). Glickstein and Millodot (1970) have indicated, however, that retinoscopy of

small animal eyes may be very inaccurate, and reflections from the inner-limital membrane of the retina, rather than the retinal cell layers, may produce refractive measures which are off by several diopters. Applying correction factors based upon retinal thickness, these authors found that the small bats they examined were emmetropic (i.e. normal vision). With small, round eyes, and with apparently emmetropic vision, microchiroptera should enjoy a remarkable depth of field, and a near point (i.e. closest possible point of focus without accommodation) on the order of only a few centimeters at most (Suthers and Wallis, 1970).

To date, very little work has been done to determine the visual performance of the microchiropteran eye. Some degree of pattern discrimination has been demonstrated by Eisenstraut (1950), Curtis (1952), and Suthers, Chase and Braford (1969). The sensitivity and acuity of the eyes of bats have not been well tested (Dieterich and Dodt, 1970; Hope and Bhatnagar, 1979a; Chase, 1972). Using optokinetic responses of bats to a moving visual field, Suthers (1966) and Chase (1972) revealed that some microchiroptera have acuities as fine as 0.29' of arc under moderate light. They found that species which feed on fruit and nectar (Anoura and Carollia) tended to have the best nocturnal vision and finest resolution, while insectivorous bats tended to have acuities on the order of several degrees of arc (e.g. Myotis lucifugus; 3-6°). The following values of acuities of

different species are provided for comparison; primates and birds 1', most diurnal rodents and lagomorphs 30-85", and opossum 11" (Warkentin, 1937), pigmented rat 23' (Hermann, 1958), and man 30" (Riggs, 1965).

The importance of vision to echolocating bats is obviously variable, depending upon such factors as feeding strategy, roosting behaviour, mating strategy, and time of activity; this is reflected in the approximately 40 fold range in relative eye sizes reported by Chase (1972). She categorized bats as nocturnal insectivorous (with the poorest vision), nocturnal nectarivorous or frugivorous (with the best nocturnal vision) and partially diurnal insectivorous (with good diurnal vision). Chase found very few exceptions to these general categories, and proposed that (among the nocturnal bats) vision and echolocation were reciprocal; those with 'poor' echolocation had good vision, and vice versa.

In Chapter III we saw that Macrotus californicus used vision to supplement, if not replace, echolocation in the location and capture of insect prey. While Macrotus has very low intensity echolocation calls, it can hardly be considered a 'poor' echolocator, as it locates prey almost as well under total darkness as in good light with no echolocation. Macrotus would seem, therefore, to be an exception to the categories set out by Chase (1972). The

purpose of this study was to extend the work with M.
californicus using behavioural tests to determine visual
performance of this bat.

MATERIALS AND METHODS

All work was done in the laboratory at Carleton University. Macrotus californicus were kept in flight cages as outlined in Chapter II. To compare visual capabilities of Macrotus with other gleaning and non-gleaning bats, Antrozous pallidus and Eptesicus fuscus were also kept in captivity and examined. These bats were housed in standard hardware cloth small mammal cages, and maintained on a diet of mealworms with protein and vitamin supplements (Theralin ®, Linatone ®, and Polyvisol ®).

To determine the visual acuity of Macrotus and other bats, I used an optomotor system similar to that described by Suthers (1966) and Chase (1972), measuring the optokinetic response of the bats to moving stripes. To summarize the methodology, the bat to be tested was placed in a 12 cm diameter, 20 cm high Plexiglas ® cylinder cage, which was then suspended inside a 38 cm diameter revolving drum (Figure 4-1). The drum was lined with a white field on which was marked a pattern of black stripes of known width. If the bat could resolve the pattern of stripes, then rotation of the drum resulted in a shift in the bats visual field contradictory to vestibular information, and the bat would respond, attempting to maintain the same visual field, by turning its head, or shifting its whole body. Liners

marked with progressively narrower stripes were introduced until the bat ceased to respond, indicating that it could no longer resolve the stripes and detect their movement. The only major difference between the apparatus used here, and the system used by Suthers (1966), Chase (1972), and by most other workers using the optomotor method, is that I used a mainly white card background, with all stripes separated by the same angle (10°), regardless of stripe width, while others have used black stripes separated by white stripes of equal width. The latter method, which is relevant, perhaps, in psychobehavioural work, gives an approximation of 2 point resolution; however, I wished to determine the minimum angle visible to the bat against a background - a question much more relevant to the overall biological question at hand. To obtain threshold data, bats were tested with liners on which were arranged patterns of stripes subtending angles of 1° , $30'$, $15'$, and $3'38''$ of arc to the bats in the apparatus.

To further investigate the visual abilities of these bats the optomotor tests were run under controlled lighting conditions. The apparatus was illuminated by a 100 watt light source passed through a 460-580 nm band filter, chosen to span the probable absorption spectrum of the bats' visual pigments (Hope and Bhatnagar, 1979b), and exclude other frequencies of light to allow for a more accurate estimate of light intensity. The measured luminance in the apparatus, from the bat's perspective, was 6.25 mL, and

using a series of optical glass neutral density filters (Hoya R X2 = Neutral Density (ND) .3 = 50% transmission, X4 = ND .6 = 25% transmission, X8 = ND .9 = 12.5% transmission), I controlled light intensity to obtain a minimum sensitivity threshold for each species at different stripe widths. Light levels were measured using a B. Lange Model 1902 light meter.

Superficially, Macrotus appeared to have large eyes arranged in a very frontal position compared with other species. Since M. californicus use vision to locate prey, it is reasonable to expect a high degree of binocular overlap for more accurate depth and range perception (Walls, 1947). To determine just how much binocular overlap this species has, I tested a single individual using ophthalmoscopy. One individual of each of Antrozous pallidus and Eptesicus fuscus were tested as well for comparison. The bats were heavily sedated using Ketamine hydrochloride (150mg/kg), and their pupils were dilated using Cyclogel. The bat was arranged on a white card on which was drawn a reference grid, and I then used the ophthalmoscope to determine monocular fields, based on retinal reflection, at a distance of 10 cm. The furthest extents of the monocular fields of both eyes were drawn on the white card to determine the degree of binocular overlap.

For comparison of eye structure with other species one individual, which was injured early in the study, was sacrificed, and its eyes preserved in an FAA-glycerol solution. Relative eye weight was determined, and the eyes were sent to Julia Chase at Columbia University, who sectioned them and provided a general description, cell layer counts, and photographs of thin sections.

RESULTS

Results of the optomotor tests are summarized in Table 4-1. Macrotus californicus clearly stands apart from Antrozous pallidus, another ground gleaning species, and Eptesicus fuscus, an aerial forager. M. californicus may actually have more acute vision than the figures suggest, however the liner patterned with lines subtending 3'38" of arc was the finest available. There was some variability within each species (Table 4-2), both in acuity and sensitivity, but some Macrotus could resolve the finest lines available under the lowest light levels the apparatus would allow (approximately 2×10^{-4} mL), equivalent to luminance on a clear moonless night (Levi, 1980), and comparing well with the threshold values calculated in Chapter III (Figure 3-1). Some Antrozous and Eptesicus also achieved this level of sensitivity, but not at the same level of acuity. It should be stressed that these are conservative estimates of both acuity and sensitivity, as behavioural estimates of visual abilities are generally poorer than actual perceptual abilities (Reinecke and Cogan, 1958).

Of the three species, Antrozous was the least responsive to the moving visual field, and proved the most difficult to test; in many instances, even under bright light conditions and using broad stripes, many individuals of this species

fell asleep in the apparatus, or simply ignored the proceedings. By contrast the Macrotus were very attentive at all times, and the slightest rotation of the drum usually elicited a pronounced (often humorous) response from the bat. Slow rotation of the drum elicited a slow turning of the head in the direction of rotation until it could be turned no farther, and then the bat would either snap its head back as far as possible in the opposite direction and then continue the tracking of the direction of rotation, or simply continue following the direction of rotation by turning the entire body. Faster rotation of the drum usually resulted in the bat shaking its head back and forth in order to try to follow the rotation of the visual field.

Macrotus californicus has the largest relative eye-size of the three species examined. In addition it has the broadest field of binocular overlap (Table 4-2).

Structurally the eye of Macrotus is not remarkable (J. Chase, pers. comm.). It is what might be termed a typical microchiropteran eye. The sclera are essentially round, and heavily pigmented. The retina is thin, and without a capillary network, nutrition probably coming from the choroid (Julia Chase, pers. comm.). Similarly the retinal cell counts are typical for a microchiropteran bat; approximately 300-400,000/mm², and with a high degree of convergence; approximately 120-140 receptors/ganglion. In short the eye of Macrotus is representative of nocturnal

bats which fly in darkness and roost in dim places, having
retinae adapted to low light levels.

DISCUSSION

The visual abilities of bats have been largely overlooked, yet there is a substantial literature documenting the structure, responses, and function of the eyes in the Chiroptera. The eyes of most microchiropteran bats are small, but normal, functional nocturnal eyes (Kolmer, 1929; Rochon-Duvigneaud, 1943; Suthers, 1970; Chase, 1972).

The function of vision in bats appears to be diverse. The importance of visual cues to long-distance orientation and homing is well documented (e.g. Williams, Williams, and Griffin, 1966; Williams and Williams, 1967; Chase and Suthers, 1969; Bradbury and Nottebohm, 1969) and has been reviewed by Griffin (1970). A number of species, particularly the partially diurnal emballonurids appear to use a variety of visual social signals (Chase, 1972), and vision in most species appears to be important for predator avoidance, and in escape behavior (Suthers, 1970; Chase, 1972, 1981). While Chase (1972) has speculated on the importance of vision to fruit and nectar feeding Phyllostomatidae, there has been no evidence of insectivorous species using vision for location of prey.

The results of this study clearly indicate that Macrotus californicus has superior visual acuity to other

insectivorous species tested in this study, and to other species tested in other studies (Suthers, 1966; Chase, 1972), although the results may not be directly comparable. Table Opt3 indicates results for Macrotus obtained in this study compared with visual acuity estimates for other species obtained from the literature. In addition M. californicus appears to retain good acuity even under extremely low light levels (2×10^{-4} mL; comparable to luminance levels on clear, moonless nights (Levi, 1980). These results are comparable with sensitivity estimates obtained for Pteropus giganteus (Neuweiler, 1962), and Myotis myotis (Dieterich and Dodt, 1970), however Macrotus apparently has better acuity than these species at much lower luminance levels (Neuweiler, 1962, Suthers, 1970).

The most impressive thing about these findings is that Macrotus is apparently the only insectivorous species known to use vision in prey location, and has refined visual abilities consistent with this. Chase (1972) noted a reciprocity between echolocation and visual abilities in the bats which she studied; bats with poor vision tend to use more intense echolocation cries, and demonstrate better overall echolocation performance. The only exceptions she noted to these rules were Micronycteris and Plecotus, both of which produced low intensity calls, had smaller eyes, large ears and poorer vision than she predicted. The foraging behaviour of these species is too poorly documented

to make any conclusions about the relative importance of vision and echolocation in foraging, although both are reputed to be gleaners. My own observations of Plecotus townsendii foraging suggest that this species is a high, fast forager, and, contrary to reports from laboratory studies (e.g. Griffin, 1958) uses moderate to high intensity echolocation; however, it is interesting to note that Micronycteris is remarkably similar and closely related to Macrotus.

Such sensory flexibility may provide Macrotus californicus with a distinct competitive advantage in the extreme habitat conditions in which it is found, and where prey may be scarce. In addition, such open, desert habitats as this are probably more brightly illuminated than other habitats, making vision more useful. This brings up the important question of whether such visual ability is primitive or derived. Our knowledge of the evolution of bats is so incomplete as to make firm conclusions in this area risky. It is interesting to note, however, that Simmons and Stein (1980) consider the Phyllostomatidae to be primitive based on their echolocation abilities, and Smith (1976) and Baker (1979) consider Macrotus to be derived from the primitive stock from which the Phyllostomatidae radiated. This may suggest, therefore, that the visual abilities of Macrotus represent a plesiomorphic

microchiropteran character, and that later forms have lost much of this ability secondarily in response to the refinement, in effect the take-over by, echolocation. Such postfact arguments are of little value, and are untestable. The visual apparatus is very flexible evolutionarily (Walls, 1947), and responds too quickly to strong selective pressure to consider the good vision of the 'primitive' Macrotus a plesiomorphic character. Conversely, it is overly simplistic, to conclude that because 'advanced' bats (i.e. Vespertilionids) have poor vision, that the good vision of Macrotus provides additional support for considering this taxon primitive.

CHAPTER V

SUMMARY DISCUSSION AND CONCLUSIONS

"The pillage of the poor people? which are to sore gleaned:
by the needle and never contented professors?"

Mulcaster, Positions XXXIX (1581)

SUMMARY DISCUSSION

From this study we can conclude that Antrozous pallidus is a ground-gleaning specialist. Macrotus californicus appears to use a similar foraging strategy. What generalizations can be made from this about the strategy of gleaning prey from surfaces? In the first place we see that both species have large pinnae (> 40% forearm length). While ear size alone is not a valid indicator of this strategy (e.g. Woodsworth et al., 1981), it is significant that all gleaners so far examined have large pinnae (e.g. Cardioderma, Megaderma, Nycteris, Myotis auriculus, Trachops and Tonatia). What is the function of such large pinnae? While it is possible that big ears are important for collecting low intensity echoes from echolocation calls, this seems unlikely in species which use high frequencies in their orientation calls. Norberg (1976) has suggested that the large ears of Plecotus auritus provide that bat some significant degree of lift in flight, and Chase (1972) has suggested that large pinnae may even aid some species by shading their eyes from sunlight during diurnal flight. My data suggest that large ears enable gleaning bats to detect very low intensity, and low frequency sounds of prey, and detect the source of such sounds more accurately. Lawrence and Simmons (1982b) have shown that the external ear is important in localizing sound in the vertical plane, and this should be especially important for localizing low

frequency sounds. A. pallidus relies entirely upon such sounds for locating prey, Macrotus responds to prey sounds and Trachops (Tuttle and Ryan, 1981) and Megaderma also use sounds of prey to locate food (Fiedler, 1979), supporting this hypothesis. Attempts to find a single 'reason' for big ears in bats is, I suggest, a fruitless task. These data, combined with the recent work on the feeding behaviour of such non-gleaning, big-eared bats as Euderma maculatum (Woodsworth et al., 1981; Leonard, 1981), make it clear that large pinnae are multifunctional.

There is no one clear strategy of echolocation used in gleaning. Macrotus californicus uses the type of echolocation calls we would predict for a gleaning bat, being of high frequency, complex structure, short duration and low amplitude, and does indeed use such calls to locate prey under dark conditions. The calls of A. pallidus, on the other hand, are more similar to those of aerial foragers such as Eptesicus, and echolocation is not used in prey location. Both species shut off their echolocation when conditions permit. While this may be an energy saving strategy, the most important reason for hunting in silence is probably to avoid alerting predators and warning potential prey. The former may be important for ground-feeding bats which are very vulnerable during prey capture, and the latter point may be particularly acute as tympanate insect prey have as much as a 40% advantage over

non-tympanate forms, and Werner (1980) has shown that at least some moths respond to ultrasound when on a surface in ways which would make them less conspicuous to gleaning bats. Megaderma lyra also uses a silent approach, relying on the sounds of its prey, when hunting mice (Fiedler, 1979), which are sensitive to ultrasound, while Trachops cirrhosus continues to produce echolocation pulses while attacking frogs (Barclay et al., 1981), which are insensitive to the frequencies used by these bats. It is not possible at this stage to make generalizations of why some species have echolocation calls suited for gleaning while others have not, beyond determining in each case what alternate sensory modes are used and how prey are located. It must be kept in mind, however, that whatever the theoretical or potential resolution of echolocation, the extreme clutter encountered in ground or foliage-gleaning situations may make echolocation difficult or impossible, and other sensory modes necessary.

Similarly, vision has its pros and cons. It is now well documented that all bats have functional eyes and reasonable vision. Vision has a number of important roles in the ecology of bats. Circadian rhythms are set and maintained by vision (Leen and Novick, 1969; Mueller, 1968), it is important in predator surveillance, at least to those species which roost in well lighted situations (Chase, 1972), and is probably of paramount importance to all

species in escape behaviour (Chase, 1972, 1981). Vision has also been shown to be very important in both local and long-distance orientation, in locating landmarks and obstacles at distances beyond the range of echolocation (e.g. Williams, Williams and Griffin, 1967; Suthers and Chase, 1969; Bradbury and Nottebohm, 1969; Griffin, 1970), and Chase (1972) has also suggested that vision may be important in some social behavioural contexts. Konstantinov (1966) found that Myotis cease production of echolocation pulses in familiar territory, and Griffin (1958) has indicated that many species ignore conflicting echolocation cues when in familiar territory, and when light is available. Ellins (1970) found that Myotis lucifugus relies more on vision in discrimination experiments than echolocation at moderate light levels. It is now apparent that some species, including some insectivorous forms, have very good visual acuity and sensitivity and use vision in finding food. While vision is necessarily limited by the availability of light, it is relatively free from ambiguity, and is 'safe'. It is not clear whether or not vision can take the place of echolocation for obstacle avoidance in rapid flight. In this study A. pallidus produced echolocation while hunting, apparently to orient and avoid obstacles (shrubberies). Whether or not this species used vision at the same time was not determined. Macrotus clearly relies on vision to a great extent for finding insect prey, and has superior visual acuity and sensitivity to other insectivorous species examined.

It is suggested, therefore, that there is more flexibility in the sensory abilities of bats than previously appreciated. It may be very advantageous for some species of bats to possess alternate, or back-up, sensory systems to overcome the problems associated with echolocation. The general success of echolocation studies has all but eclipsed other sensory modes, however; the most striking example of this is the certainty with which so many researchers tacitly assume that bats have poor vision. While sensory 'redundancy' may seem useless, or even conflicting (Suthers, 1970; Chase, 1972), it may provide some species with a distinct advantage in a variety of situations.

CONCLUSIONS

1. Antrozous pallidus captures prey by gleaning it from the ground, locating it by the sounds produced by the prey.
2. While hunting, A. pallidus uses echolocation for general orientation, but ceases production of echolocation during prey capture.
3. A. pallidus feeds opportunistically on whatever moderately large prey it encounters, but avoids large prey, or takes especial care in capturing it.
4. A. pallidus hunts on open ground, and ignores potential prey in cluttered situations.
5. A. pallidus does not respond to the mating calls of its orthopteran prey, although it includes orthopterans in its diet.
6. The sounds of prey rustling on the ground show a peak power in the range of 5-8 kHz, which corresponds with the low frequency sensitivity reported for this species.

7. Macrotus californicus, tested in the laboratory, gleans prey from the ground in a manner similar to A. pallidus. This species probably hunts in the same manner in the wild.
8. M. californicus locates prey in total darkness using echolocation, and also uses the sounds of potential prey, including the mating calls of orthopterans.
9. M. californicus can find prey using vision at luminances much below that of moonlight (1.5×10^{-4} mL), and ceases echolocation pulse production whenever light levels are sufficient to do so (c. 0.03 mL).
10. M. californicus has better visual acuity than any other insectivorous bat tested so far, and comparable, if not superior, to the vision of any other bat, including nectarivorous and frugivorous species. The visual sensitivity of M. californicus is comparable to other species of nocturnal mammals.
11. M. californicus has the greatest sensory flexibility of any species of bat tested to date, able to shift between at least 3 sensory modes as conditions require.

12. These results indicate that while echolocation can be used in gleaning prey from surfaces, as suggested by theory, other sensory modes are of superior efficiency, and are used in place of echolocation by gleaning bats when conditions permit.

TABLES

TABLE 2-1

Daily summary of prey taken by Antrozous pallidus,
June - August, 1981, determined by culled parts
and fecal analysis.

Minimum number of prey items in sample

Date	Lepidoptera		Coleoptera		Orthoptera(4)	Other(5)
	large(1) >20mm BL	small <20mm BL	large(2) >10mm BL	small(3) <10mm BL		
17 June	3	1	4	8	4	4
18 June	2	1		4	5	15
10 July	38	5	3	6	3	7
15 July	33			5	4	2
22 July	15	2	1	6	5	
6 August	27	1	9	15	11	7
10 August	10	2	7	7	8	3

Totals	128	12	24	51	40	38
%Totals	44	4	8	17	14	13

1. Manduca quinquemaculata, M. sexta, M. occulta, Hyles lineata
 (Sphinxidae) predominately.

2. Primarily Scarabidae and Cerambycidae.

3. Primarily Scarabidae (Dynastinae).

4. 26 (9%) Gryllus and 14 (5%) others.

5. 10 (3%) Neuroptera, 11 (4%) Chilopoda, 1 isopteran, 4 Hymenoptera,

1 Diptera, 2 Arachnidae (Scorpiones), 1 Odonata, and 1

Perognathus flavus (Mammalia:Rodentia).

TABLE 2-2 .

Summary of responses of Antrozous pallidus to the sounds of fluttering moths and to various controls. P: significance level of difference (a: Behrens-Fisher t'-test*; b: t-test); N: number of test periods compared. Recordings were of 30mm body length moths fluttering on the ground. The comparisons of recordings vs random activity and free-fluttering moths were of 2 min. test periods. All other tests are of 1 min. test periods.

Comparison	N	P
Recording of moth vs Random activity	10	< 0.005 a.
Recording of moth vs free-fluttering moth	10	n.s. a.
Moth in bag vs random activity	21	< 0.001 a.
Moth in bag vs free-fluttering moth	21	n.s. b.
Dead moth vs random activity	21	n.s. b.
Dead moth vs live moth	21	< 0.001 a.
Free-fluttering moth vs random activity	21	< 0.001 a.

* Behrens-Fisher test used when comparing samples of unequal variances.

TABLE 2-3

Frequency characteristics of the fluttering sounds of different sized moths (FFT averages of 64 samples). Size classes: A, 45-60 mm body length (BL), 110-130 mm wing span (WS); B, 35-45 mm BL, 80-100 mm WS; C, 25-35 mm BL, 60-80 mm WS; D, 20-25 mm BL, 45-60 mm WS. The frequency range of the system, determined by the tape-recorder speed, was 100 to 150,000 Hz.

Frequency in kHz

Moth Size Classes	Frequency in kHz		
	Lowest Frequency	Frequency of Peak Power	Highest Frequency
A	1.4	5.1	14.2
B	3.4	5.1	12.7
C	2.4	8.6	14.0
D	2.3	4.7	14.2

TABLE 3-1

The use of echolocation by Macrotus californicus during approaches to prey under light vs dark conditions. In each test echolocation was used more in the dark (virtually always) than in the light (echolocation essentially shut off). Total individuals is the results from combined data from 8 individuals. Only three of these individuals gave sufficient data for statistical analysis, and the comparisons for these bats are given as well (X, B/R, /B). Probability levels from G-test ($G [0.05] = 3.841$). N = number of passes in sample; G = calculated G value (Sokal and Rolf, 1969); p = probability level.

Bats*	n	G	P
Bat X	314	65.4	<<0.001
Bat B/R	97	10.2	< 0.01
Bat /B	138	44.9	<<0.001
Total Individuals (8)	589	127.3	<<0.001
Flock (6)	1110	245.4	<<0.001
Total All Tests	1699	312.0	<<0.001

* The symbols X, B/R, and /B are banding combination abbreviations identifying individual bats used in these tests.

TABLE 3-2

Success of Macrotus californicus in locating prey under light and total darkness conditions. Flocks of bats were more successful at locating prey (i.e. significantly fewer passes per capture) under light conditions, suggesting that vision is more efficient than echolocation for locating small prey items on surfaces. Probability values from G-test ($G [0.05] = 3.841$). N = number of captures; G = calculated G value (Sokal and Rolf, 1969); p = probability level.

Experiment	n	G	P
Total Indiv.	446	0.72	> 0.03
Flock	300	21.4	<< 0.001
Total	746	6.7	< 0.01

TABLE 4-1

Summary of results from the optomotor tests with Macrotus californicus, Antrozous pallidus, and Eptesicus fuscus, and comparison with Chase's (1972) results for other species of Microchiroptera. Tabled values are best measures obtained of visual acuity and sensitivity for each species.

Species	Minimum Angle Separable	Acuity Units*	Intensity Threshold
<u>M. californicus</u>	3'29"	.29	2 X 10 -4
<u>A. pallidus</u>	15'	.07	4 X 10 -4
<u>E. fuscus</u>	60'**	.02	2 X 10 -4
<u>Carollia perspicillata</u>	16'	.063	
<u>Myotis lucifugus</u>	6°	.003	
<u>Anoura geoffroyi</u>	42'	.024	
<u>Molossus ater</u>	10°	.002	
<u>Saccopteryx leptura</u>	42'	.024	
<u>Desmodus rotundus</u>	42'	.024	

* acuity= 1/ minimum separable angle in minutes.

** 1 Eptesicus responded to stripes subtending 15', but the results could not be repeated with any other individuals.

TABLE 4-2

Optomotor Data*

Species	Visual Angle	Intensity (mL)*	N Trials	Response	Direction
<u>M. californicus</u>	1°	6.25	10	10	+
			10	10	+
		1.6 X10 -3	10	10	+
		1.9 X10 -4	10	10	+
	15'	6.25	10	10	+
			10	10	+
		1.6 X10 -3	10	10	+
			10	10	+
	3'38"	6.25	10	9	+
			10	10	+
		0.625	10	8	+
			10	9	+
		6.25 X10 -2	10	8	+
		1.2 X10 -2	10	10	+
		6.25 X10 -3	10	5	+
			10	9	+
		1.5 X10 -3	10	2	+
			10	10	+
			10	10	+
			10	7	+
		8 X10 -4	10	5	+
		3 X10 -4	10	10	+
			10	10	+
		2 X10 -4	10	8	+
			10	5	+

* millilamberts; luminance measured from suspended cage with light meter
 ** + indicates bat moved in direction of rotation, - means bat moved in opposite direction.

Table 4-2 (continued)

Species	Visual Angle	Luminance (mL)	N Trials	Response	Direction
<u>A. pallidus</u>	1°	6.25	10	10	+
			10	8	+
	15'	0.063	10	10	+
		6.25	10	10	+
		1.5 X10 -3	10	10	+
		3.8 X10 -4	10	8	+
<u>E. fuscus</u>	1°	6.25	10	10	-
			10	0	
	15'		10	0	
			10	10	-
		1.56	10	2	-
		1.5 X10 -3	10	9	-
		2 X10 -4	10	0	
		6.25	10	8	-
		0.01	10	8	-

* Each line indicates a test of 10 trials with a bat. Not all bats were run at all angles, or at all intensities.

PR
SIGNAL WHEN READY

TABLE 4-3

Visual fields of Macrotus californicus, Antrozous pallidus, and Eptesicus fuscus. All measures are estimates made using an ophthalmoscope, on a single individual of each species. Optical axis is the angle, in degrees, between the central optical axis of the eye and the animal's medial longitudinal axis. The monocular field is the angle of vision, in degrees, covered by each eye. Binocular field is the angle of overlap of the two monocular fields.

22
OF / DE

Species	Optical Axis	Monocular Field	Binocular Field
<u>Macrotus californicus</u>	30	120	50
<u>Antrozous pallidus</u>	50	130	25
<u>Eptesicus fuscus</u>	45	110	19

FIGURES

FIGURE 2-1

Sonographs of echolocation calls of some bats
which are known or suspected gleaners:

- a) Antrozous pallidus (Rodeo, NM, July 1981).
- b) Nycteris thebaica (Sengwa, Zimbabwe, Nov. 1979).
- c) Macrotus californicus (Blythe, Ca. March 1980).
- d) Myotis auriculus (Portal, AZ, Aug. 1978).
- e) & f) Plecotus townsendii (Portal, AZ, July 1980).

FIGURE 3-1

Visual threshold curve for Macrotus californicus. The graphs shows the percent of total passes made using echolocation by a flock of 7 bats, while hunting for prey over an array of food dishes at controlled light levels. The total number of passes recorded at each light level was at least 130. Measured values are shown by the + symbol. The curve, representing the best fit which could be obtained, is an hyperbola of the form $xy = K$. Such a curve indicates that the drop off in use of echolocation at high luminances, and the increase in the use of echolocation at low luminances, are asymptotic, and thus there is no 'threshold' value of luminance at which sensory modes are switched. Estimating from the curve, however, the 50% and 75% echolocation values fall at luminance levels of 3×10^{-2} and 1.5×10^{-4} mL (millilamberts) respectively. All the measured values are conservative; at the lowest luminance level (total darkness) echolocation was probably produced by all bats on all passes, however the bats were not always facing the microphone, and their directional signals were not always detected. At high luminances the number of passes with echolocation was overestimated as bats on collision courses frequently made ultrasonic warning signals ('honks') which were detected and recorded as echolocation in the test.

FIGURE 2-2

Prey size selection by Antrozous pallidus: A) Mean total time from onset of fluttering to capture of prey of different size classes (and standard error). B) Mean passes per capture of prey of different size classes (and standard error). C) Total balks at prey of size classes. Sample size (number of trials) for each size class equals 20. Size classes: A) 45-60mm BL (body length), 110-130mm WS (wing span); B) 35-45mm BL, 80-100mm WS; C) 25-35mm BL, 60-80mm WS; D) 20-25mm BL, 45-60mm WS; E) 14-20mm BL, 30-40mm WS.

FIGURE 4-1

Sketch of the optomotor apparatus. The bat tested would hang from the wire top, or rest on the floor of the testing chamber, which was suspended inside the drum. The striped liner in the drum was interchangeable to present the bats with stripes which subtended different angles in their visual fields. The drum could be rotated in either direction by hand. The light source above could be filtered to control light intensity in the drum.

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