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Behavioural basis of foraging flexibility in three species of insectivorous bats:
an experimental study using captive Antrozous pallidus, Eptesicus fuscus and Myotis lucifugus

University — Université

Carleton

Degree for which thesis was presented — Grade pour lequel cette thèse fut présentée

M.Sc.

Year this degree conferred — Année d'obtention de ce grade

1982

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BEHAVIORAL BASIS OF FORAGING FLEXIBILITY IN THREE
SPECIES OF INSECTIVOROUS BATS; AN EXPERIMENTAL STUDY
USING CAPTIVE ANTROZOUS PALLIDUS, EPTESICUS FUSCUS AND
MYOTIS LUCIFUGUS

by

© CONNIE LEE GAUDET, B.A.

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

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ABSTRACT

Captive Antrozous pallidus, Eptesicus fuscus and Myotis lucifugus all express a range of behavioral abilities that could enable them to cope with a patchy and unpredictable food resource. All species exhibit some degree of sensory modality in "prey" detection. Low-frequency sounds indicative of prey are used by each species to locate targets. All species use echolocation to locate small moving discs and Antrozous pallidus and to a lesser extent E. fuscus will rely on vision to locate these discs under certain conditions. Only A. pallidus will abandon echolocation and use vision when light permits. All species use memory to locate food sites and will remember some sites for long periods of time as well as incorporating new sites readily. The ability to learn a novel foraging behavior through observation of an experienced bat is expressed in each species. As well, A. pallidus and E. fuscus significantly reduce search time when locating a food patch in a group as opposed to individually. Eptesicus fuscus will reduce activity in response to food limitations dependent on weight of the bat and food availability.

ACKNOWLEDGEMENTS

I thank my supervisor, M.B. Fenton, for his constant support, advice and understanding throughout this study.

I also thank Dr. P.J. Weatherhead for his helpful advice and editing as well as Drs. G.R. Carmody and R. Thomas for their help and suggestions.

To all those "bat" people, R. Barclay, G. Bell, D.Herd, R. Herd, C. Furlonger, V. Cucarro, D. Cairns, I extend my warmest thankyou for their constant help.

I especially thank Marty Leonard, Judy Geggie and Lynn Bray-Brodsky for their moral support and suggestions.

Finally, I thank Mr. L. Lefkovitch for his help with the final draft and Jessica Gaudet and Arnet Sheppard for support at home.

This study was supported by operating and equipment grants from the Natural Sciences and Engineering Research Council to M.B. Fenton and by a grant to C.L. Gaudet from the the Natural Sciences and Engineering Research Council of Canada.

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SECTION 1

GENERAL INTRODUCTION AND METHODOLOGY

" It is suprising how little we actually know about mammalian feeding behavior. In many cases we know what constitutes normal food. In others we also know, in greater or less detail, the patterns involved in finding food and eating it, but very rarely has description been followed by analysis and experiment to elucidate the factors responsible for releasing and orienting the animal's responses." (Ewer 1968:28)

GENERAL INTRODUCTION

Many species live in environments which are not sufficiently predictable to "allow genes to plan out their lives in any great detail" (Gould 1982). As external variables change, limits are posed and opportunities created to which an animal must react. Though morphology, physiology and certain innate aspects of behavior have evolved to cope with specific environmental parameters, behavioral flexibility is the ultimate mechanism in maximizing fitness in a variable and unpredictable environment (Norberg 1977, Pulliam 1976).

The basis of flexibility is not clear. The ability to modify behavior in response to the environment is a phenomenon with genetic, physiological , ecological and evolutionary components (Gould 1982). Though most animals are capable of modifying behavior in response to external variables, they will do so within a framework of species-specific rules. Many animals sample the environment and modify future behavior in order to avoid unpalatable or noxious insects. Thus they are flexible in reacting to certain prey parameters and do not exhibit rigidly fixed prey preferences. There are definite limits and directions to such flexibility within species however. A toad (Alcock 1975), will quickly learn to

avoid a noxious millipede but will not recognize the unpalatability of buckshot and will eat it until it is literally a "bean bag".

Even programmed behavior enables animals to meet substantial environmental variability if they are sensitive to immediate external conditions. In insects, certain highly specialized and rigid responses ensure a degree of coping with scattered and unpredictable resources. Bee communication (Lindauer 1978) enables a colony to sample extensively a complex environment and to alter foraging patterns in response to the feedback available from many group members.

Though coping with variability does not necessitate "novel" behavior, behavior does appear in response to certain environmental opportunities that seems to represent modifications so unusual or atypical that it is difficult to imagine that they were programmed to any extent. Many animals exhibit flexibility only when conditions change in dramatic ways. Oystercatchers, thought to be mollusk specialists, have greatly expanded their feeding range in response to environmental pressures (Dare 1966, Heppleston 1971). Chimpanzees will resort to cannibalism (Kawabe 1966) though typically grazers.

All these behavioral modifications can be considered to be existing but rarely used parts of a foraging

repertoire. Highly novel activities observed in certain animals make it obvious that behavior can be modified in ways for which evolution could not have prepared them. Great Tits have learned to open milk bottles to get the cream (Fisher and Hinde, 1949), and Japanese Macaques have learned to wash potatoes and separate sand from grain by throwing it in the water (Kawai 1965).

There are no clear answers as to the limits and controls on flexibility. It is clear that no one 'behavior' can confer on a predator the degree of flexibility observed in many animals and therefore it is necessary to specify that underlying 'complex' of behavior which is manifested as 'flexibility'. Working within a framework of environmental variability of potential biological importance to a species, it is possible to generate testable hypotheses concerning expected behavior under certain conditions.

Flexibility in diet and foraging is an important adaptive trait in many insectivorous bats (e.g. Bell 1980, Fenton and Morris 1976) which deal with a mobile, variable and often unpredictable resource (e.g. Anthony and Kunz 1977). There has been little critical analysis of behavioral abilities that underlie this observed flexibility. Some of the more critical parameters along which prey may vary (Fig.1) include aspects of spatial distribution, type and density . It is possible to make

certain assumptions as to adaptive behavioral responses that may have evolved to cope with these kinds of variation.

Fundamental to every organism in comprehending the environment is sensory perception. An animal that copes with variable prey must have sensory modes available allowing recognition of a number of prey cues in a variety of situations.

Recognizing and locating prey at close range could not deal with all kinds of variability. Insect prey is patchily distributed in time and space and therefore evolving mechanisms to cope with efficient location and exploitation of highly variable patches is important. Spatial memory could be fundamental to coping with a patchy resource and it is flexible ~~if~~ that it enables adjustment to the available food supply rather than random responses to it.

Other aspects of a bat's behavior may help it cope with variable prey densities through adjustment to the available food supply. Aggression under food stress or certain conditions of distribution may enable a bat to apportion itself a larger or more optimal feeding area. A bat may also resort to methods of conserving energy in times of stress.

Bats are highly social animals (e.g. Barbour and Davis 1969). The feeding activities of other bats may

often be the best indication of resource availability. If detailed information could be used then a bat could expand its foraging repertoire in many directions by "learning" new prey responses or locations. Thus there may be both an individual and social basis for dealing with resource variability.

The purpose of this study was to examine the ability of insectivorous bats to respond to a range of foraging problems involving elements of spatial memory, sensory modality, information sharing and behavioral responses to food stress and to establish a framework of strategies or behavioral capacities which underlie the observed flexibility of bats.

Myotis lucifugus, Antrozous pallidus and Eptesicus fuscus are common species in certain areas of North America and are known to exploit prey opportunistically (e.g. Bell 1982b, Barclay 1981) and show considerable dietary flexibility (Bell 1982b, Anthony and Kunz 1977, Belwood and Fenton 1976, Hamilton 1933). Though all three species are broadly similar in habit and therefore should show a great deal of overlap in foraging strategies, each species has clearly evolved to deal with specific problems of maximizing fitness in their particular foraging environments. Though the degree of overlap in behavior may be more than expected, behavioral differences should exist in areas related to foraging

specialities. A notable difference between the species is the gleaning habit of A. pallidus (picking prey off of surfaces) as opposed to the pursuit of flying prey practised by the other species. Thus we might expect measurable differences to exist in their ability to respond to certain prey types or contexts.

By developing a comprehensive picture of the range of foraging strategies available to these species it may be possible to achieve a better understanding of the nature of behavioral flexibility.

Though addressed in terms of foraging for the sake of continuity in this research, interpretation of behavior observed in a laboratory setting must be approached with caution. All available information has been incorporated into formulation of underlying assumptions upon which experimental design is based. For this reason also, only species for which a body of literature from the field and laboratory is available were used. However constraints, especially those of distance, implicit in the experimental design may elicit behavioral responses not directly analogous to those exhibited in a natural setting.

This research is not intended to provide an ultimate answer to the question of foraging flexibility in bats. It is offered as a preliminary framework of basic behavioral responses upon which further research may be

built. Interpretations may be subject to future modifications but in a group of animals presently understood as little more than sophisticated acoustic machines the present study provides an important stimulus for the study of chiropteran behavior in areas hitherto ignored.

THE STUDY ANIMALS

All three species belong to the family, Vespertilionidae. Eighteen Antrozous pallidus were taken from a roost site in Rodeo, New Mexico. Eighteen Myotis lucifugus and seven Eptesicus fuscus were taken from a roost at Renfrew, Ontario. Ten additional Eptesicus were acquired from various roosts in Ottawa, Ontario and Gatineau Park, Quebec.

The species differ in morphology (Fig. 2) and size. Myotis lucifugus is clearly smaller and for this study , was used at weights of 6-8 g. Eptesicus fuscus and A. pallidus weighed between 24 and 12 grams.

All species echolocate, i.e. orientate and pursue prey at least partly guided by sonar. Echolocation calls are high-frequency and cannot normally be heard by the unaided human ear. The term echolocation implies active use on the part of the bat though reference to "production of echolocation calls " does not. For the sake of brevity, the term echolocation may be used when active use is not implied in this study.

HOUSING AND MAINTENANCE

All bats were housed in holding cages of approximately 0.5 m X 0.5 m X 0.3 m at 20° C. They were

fed Tenebrio larvae (mealworms) exclusively with a liquid vitamin supplement (Tri-Vi-Sol) and calcium lactate. All bats were kept at maintenance weights (Appendix B) for experimental purposes.

GENERAL METHODS

All parts of this study were broadly based on the ability of a bat to perform target discriminations and locate displaced targets: Initially, each bat was conditioned to approach a target (Fig 3), secure a mealworm from a clip and return to a starting position on the other side of the room. Weights of bats were kept at a consistent minimum to ensure constant motivation.

Beyond the initial conditioning exercise, bats were NOT conditioned to respond to the cues used in various aspects of the study in order to elicit a spontaneous not conditioned response to any given stimuli. Preliminary conditioning served to familiarize bats with the flight room so that they could be expected to conduct a relatively aggressive search of the area when the situation required. In addition, it enabled presentation of a reward in a controlled way.

EQUIPMENT

A Tektronix 510n dual trace storage oscilloscope was used to monitor the echolocation production of bats in the experimental chamber. A condenser microphone with a built in preamplifier or a Bruel and Kjaer 4135 (1/4 inch) microphone were used for call detection and were either mounted on tripods in the chamber so as to monitor the bats' approach to the target or imbedded directly in a target. High-frequency recorded sounds were presented to the bats through mylar speakers after appropriate amplification, and low-frequency sounds were played through KEF model 427 speakers. A Racal Store 4 DS tape recorder operated at 152 cm/s was used for all taped sounds. Sounds were analyzed for frequency components using a Princeton Applied Research Fast Fourier Transform (FFT) Real Time Analyzer Model 4513.

STATISTICAL METHODS

In all target discriminations the specified stimulus (or cue) was alternated randomly with a control and a bat was rated on its ability to discriminate the cue from the control for a food reward. A lack of response to either target was not recorded as a response option. Because a sufficiently large number of trials were run

for each stimulus condition and data were based on a simple two-choice format, the significance of a bat's response to a cue was calculated using a Normal Approximation to the Binomial Distribution (Malik and Mullén 1973). A chi-square was used to test for differences in response between trials. When observed frequencies were too small for the sampling distribution of the χ^2 statistic to be adequately approximated, Fisher's Exact test was used (Dixon and Massey 1969). Tables used refer directly to probability levels and therefore no other data are presented. The non-parametric Mann-Whitney U test was used to compare scores between groups when data were not normally distributed. When $n \geq 20$, U was converted to an approximate t (Sokal and Rohlf 1981). Welch's approximation to the t (Thomas pers. comm.) was used to compare means where variances were unequal due to artificial limits set on some scores.

SECTION 2

BEHAVIORAL RESPONSE TO FOOD LIMITATIONS

" A prerequisite for investigating optimal behaviour in any animal is an understanding of the relationship between the behaviour of the animal and its internal state. The internal state is a complex notion involving the instantaneous values of all causal factors relevant to behaviour. Many of these causal factors are physiological variables such as level of food reserves...; others may represent such things as the animal's estimate of food availability..." (McCleery 1978:386)

BEHAVIORAL RESPONSE TO FOOD LIMITATIONS

INTRODUCTION

Rosenzweig (1974) predicts that inactivity may be more profitable to an animal than foraging when food is limited. Food density alone may not be the critical deciding factor in an animal's ultimate decision. Internal factors such as body weight or social condition may be an equally important factor in formulating a foraging strategy (e.g. McCleery 1978).

The purpose of this study was to assess individual bat's reactions to a limited food supply and to determine major factors which contribute to a foraging decision.

METHODS AND RESULTS

Eight adult E. fuscus were taken into an experimental chamber and conditioned to fly to a target and retrieve a mealworm reward (Section 1). The daily intake was limited to 10 mealworms per day; previously, all bats had been fed ad libitum and were not expected to work for their food. Within one week, the eight bats could be characterized into two groups based on differences in behavior. Group "A" consisted of 3 males and 1 female. Performance in this group was erratic and

consequently food reward inconsistent . Weight loss was rapid over the first 14 days (Fig. 4). On the average, bats lost 12.5% of their body weight within two weeks. After 3 weeks, weights leveled off at an average 16.2 g. Group "B" consisted of 3 females and 1 male. Performance steadily improved in the first week , reward was more consistent, and this group lost only 8.2% of body weight on the average . Weights leveled off at 20.5 g (Fig. 4).

Performance was generally assessed as the time taken to arouse and secure 2 mealworms from the target. At the end of 2 weeks, Group "A" took in excess of 15 minutes to meet these criteria . Arousal was rapid and poor times were due primarily to ineptitude. Group "B" was fullfilling these requirements in an average time of 3.8 mins.

All indications were that Group "B" had successfully mastered the target exercise with minimal weight loss and that they would continue to show peak performance. However, while Group "A" maintained a high activity level Group "B" did not. Between 10 and 16 days, performance peaked while bats continued to show a steady weight loss. Four to 5 days later, a marked deterioration in performance was noted. Bats were sluggish and by day 20, were receiving an average of only 6 mealworms due to refusal to fly to the target. At the same time, despite

reduction in food, weight loss was reduced. On the average, bats lost less than 2% of body weight over the next 2 weeks. Mealworm reward was abruptly reduced to 2 mealworms per day regardless of performance on day 30. Within 3 days, all bats reacted by a dramatic decrease in performance. Arousal alone took in excess of 15 mins and though agitated physically by an experimenter, bats ultimately would not arouse at all to a degree where they could fly to the target. Only when weights approached 17 g did performance begin to improve and when weights averaged less than 17 g, a marked increase in activity was noted.

Two additional experiments were run to ascertain that weight was critical to a bat's response to a limited food supply. Two bats from Group "A" that were at peak performance had diets reduced abruptly to 5 and then 2 mealworms. Both bats retained a high activity level. Experiments were terminated when weights were critical (Appendix B).

Trends in weight and performance are summarized for all groups in Figure 5.

DISCUSSION

Inactivity in response to limited food is not surprising given Rosenzweig's prediction. Bar-tailed godwits may also stop foraging when food is limited (Evans 1976) .

A bat's response to food limitations is clearly dependent on its internal environment as well as the external environment (resource availability). Bats in this study appear to be taking into account more than absolute weight. Group "B" lost weight at a steady rate and food was consistent regardless of efficiency in exploiting the resource. Thus a foraging decision could be based on at least 2 predictable features of the situation, the lack of sufficient available food to compensate for energy expended and the consistently low density of food. On the other hand, bats that lost weight quickly and irregularly may have had no time to form usable precepts on which to base a foraging decision.

The resumption of activity at an approximate weight of 16 g points to the importance of specific weights . At 19-21 grams the bat can apparently afford to wait out adverse conditions of food availability. In the present study, only 2 g carried a bat through several weeks. In the wild, such a profound ability to maintain weight

could carry bats through prolonged periods . This would confer a great deal of flexibility on a bat in an unpredictable environment. When bats reach low weights it appears that they must "gamble" their remaining energy in search of food or surely starve to death. Bats at less than 16 g never tended towards inactivity.

All the bats in this study hibernate and achieve a significant energetic saving by lowering of body temperature towards ambient. But efficiency of energy utilization, even in bats, may not be critically dependent on external temperatures. Though bats were housed at 20° C , energy utilization in maintenance does not vary significantly between 9° C and 20° C (Pagels and Blem 1972), and therefore within a broad range, temperature is not critical in energy conservation. Ability to maintain weight , as in this study, is largely dependent on limiting movement. In E. fuscus, the rate of loss of 1 g of fat ranges from 6.6 days to 50.8 days dependent on relative movement (Pagels and Blem 1972).

Though sample sizes are too small to reach absolute conclusions, it appears that females may be more efficient at adopting strategies to conserve weight. Female bats hibernate more efficiently than males (Ransome 1968, Beer and Richards, 1956) and larger females can maintain homeothermy and can store more fat (Williams and Findley 1978). Differences in behavioral response to

food limitations between males and females is certainly worthy of further study.

In the natural environment, response to prey density can only be generally observed with no indication of the role a bat's internal environment plays. When ambient temperature is low, M. lucifugus retreats to roosts (Kunz et al in prep.) . This behavior could be construed as a direct response to ambient temperatures though results of this study indicate that the decision process of a foraging bat may be based on an integration of information.

As a part of the larger study on flexibility, results of this section are clearly important . Response to a cue might be an irrelevant factor if motivation on the part of the bat could not be controlled. It is evident that weight is a critical factor in maintaining peak motivation under certain conditions and that this information can be applied to the ensuing behavioral studies.

SECTION 3

SENSORY MODALITY

SENSORY MODALITY

INTRODUCTION

Although there are numerous strategies which could optimize foraging (review in Krebs and Davies, 1978), recognition and location of suitable prey are fundamental to foraging success. Each predator must have senses which enable it to gather detailed information of biological significance. Sensory abilities have evolved in response to each species' particular foraging environment ; a fruit bat can recognize ripe fruit through olfaction (Sales and Pye 1974) ; flower colours are important to some bumblebees (Heinrich 1978). Efficiency necessitates some degree of sensory specialization but for many predators variability in the environment demands a measure of flexibility permitting responses to prey varying in quality or the context in which they are found.

The diversity in diet of M. lucifugus , E. fuscus and A. pallidus (Bell 1982a, Anthony and Kunz 1977, Belwood and Fenton 1976 , Phillips 1966) suggests an underlying flexibility in prey detection. Although the Microchiroptera are often treated as "obligatory echolocators" there is now conclusive evidence that many of them use other sensory information as much as or even

instead of echolocation in certain situations.

Low-frequency sounds produced by prey are of importance to many gleaning bats which locate prey on surfaces (e.g. Belwood 1981, Tuttle and Ryan 1981) and some may even locate "noisy" prey without producing echolocation calls (Bell 1982a, Fiedler 1979). Even a bat known for its pursuit of flying prey, Eptesicus fuscus, orientates to distant low-frequency sound fields (Buchler and Childs 1981).

Insectivorous bats have functional vision (Ellins and Masterson 1974, Masterson and Ellins 1973, Chase 1972, Suthers et al. 1969). Though usually discussed in the context of general orientation, one recent study (Bell 1982a) indicates that the gleaning bat Macrotus californicus uses vision to locate prey when light levels permit.

The available research clearly establishes the importance of sensory modality in the feeding ecology of some bats. However, there have been few systematic investigations into the range of senses available to a species in the context of prey location or the behavioral flexibility of bats in integrating or changing sensory modes in response to variations in specific prey situations.

The purpose of this study was to assess and compare the ability of E. fuscus, A. pallidus, and M. lucifugus

to respond to a variety of potential prey cues demanding the use of vision and audition beyond echolocation. Differences in observed abilities of the species should relate to their particular foraging environments since selective pressure would tend to favour the development and maintenance of sensory modes which would increase foraging success. Vision and listening to prey sounds have been cited as adaptations for locating prey on surfaces. Therefore, A. pallidus, a noted gleaner (Bell 1982b), should exhibit a measurably greater ability to use these senses. The degree of overlap between species should be greater than anticipated if dietary flexibility is at least in part facilitated by an underlying sensory flexibility.

MATERIALS AND METHODS

A. The Study Animals and Preliminary Training

Four E. fuscus, 3 A. pallidus and 3 M. lucifugus were used for all phases of the experiments. With the exception of one juvenile E. fuscus born and raised in captivity, all of the bats were adults removed from roost sites and held in captivity for periods of 1 week to 3 months prior to experimentation. Bats were introduced into the experimental chamber only during the

actual testing period. Between tests (approximately 20 min. per day) bats were housed in holding cages under a reversed 12:12 h light/dark cycle. Tests were conducted during the dark phase because these species are active nocturnally in their natural environment. With the exception of 2 M. lucifugus and 1 E. fuscus, all of the bats underwent preliminary training as described in Section 1. Every effort was made to ensure that no bat was inadvertently "conditioned" to respond to any of the stimuli subsequently presented in the context of the present experiments. The other 3 bats "learned" to retrieve a mealworm from the target through observation of a trained conspecific (see section 4) and therefore exposure to laboratory conditions was kept to a minimum.

B. Vision and Echolocation

To assess the role of vision and echolocation in prey detection a series of experiments were designed which offered a range of problems varying in acoustic (echolocation) and visual difficulty. Because of the logistical problems in controlled presentation of a variety of live prey or an attempt to simulate "important" changes in the prey itself, qualitative changes in prey context were primarily used. A preliminary series of experiments was conducted to

determine an artificial "prey" to which each species would respond. Movement was determined to be the critical factor in motivating a response. To this end, a series of small paper discs (see below) which could be rapidly rotated were developed which elicited immediate and consistent responses from individuals of each species.

Methodology was based on the following assumptions:

1. A bat will actively search for a moving cue and can discriminate it from an identical non-moving cue against an acoustically and visually simple background.

2. The movement and therefore attractive quality of the cue is consistent between trials and when a bat's ability to discriminate the moving disc is significantly changed, then it can be attributed to a change in a variable extraneous to the actual movement of the disc.

3. These variables can be systematically controlled to assess their affect on discrimination ability and/or sensory modes.

Manipulations of cue context were designed to vary visual and acoustic complexity based on the following assumptions:

- i) Background characteristics e.g. cluttered, non-cluttered, present problems of increasing complexity in the effective use of echolocation (eg. Simmons et al. 1979, Simmons and Stein 1980) and may elicit the use of

other sensory modes.

ii) When echolocation is not produced in lighted situations then vision alone is being used to detect the cue (all other cues being controlled for).

iii) A total darkness situation in which no visual cues are available (sound from cue is controlled for) demands the use of echolocation in discrimination.

iv) In dim light, use of visual cues is possible in addition to echolocation .

v) All other factors being constant, a significant difference in discrimination ability between conditions iii) and iv) is due to a difference in availability of visual cues.

vi) Bats can visually detect high contrast differences (e.g. Childs 1972), and therefore a black disc on a white background is visually less cryptic than a white disc on a white background and a significant improvement in performance when the white disc is replaced by the black disc indicates effective use of an obvious visual cue.

Based on the preceding assumptions, relative use of vision and echolocation was assessed using the format as illustrated in Figure 6.

To test the ability of each species to integrate contradictory perceptual information one additional series of experiments was conducted. Plexiglass shields

were suspended over the cue (so as not to interfere with the movement) . A bat was then challenged to integrate information returning from the plexiglass barrier (presumably through echolocation due to the visually innocuous nature) and visual information as to the movement of the cue beneath.

For all exercises, response levels were based on a target discrimination format in which a bat was rewarded for detection of a moving disc versus a non-moving disc. Bats were tested singly and were restrained at a starting position (see Fig. 3) between trials. During a presentation, the bat would initially remain at the starting wall in the typical head-down resting position and then fly across the room to the selected target, retrieve a mealworm reward and return to the starting position. There was no reward for approaching the incorrect target. Each bat would make 20 discriminations per day. Sixty trials were run for each individual in each condition unless otherwise specified. Final response levels were calculated on the performance of 3 bats for each species (180 trials) and performance is generally described in terms of percent response.

a). The Experimental Chamber and Targets

The room described in Section 1: Materials and Methods was used for all target discrimination exercises. Except for the floor, the room was entirely lined with 14 cm acoustic foam and 8 cm textured packing foam to diminish confounding echoes which would impair the bats' orientation by echolocation. Two identical 40 cm by 40 cm acoustic foam targets were put on wall "A" (Fig. 8) 1.5 m apart and 1.5 m above the floor. The targets themselves presented no obvious cue but acted as "landing platforms" and contained an imbedded 8 cm X 8 cm X 2 cm piece of styrofoam. A 2 cm metal clip which held the mealworm reward was imbedded in the styrofoam (Fig. 9).

b) The Cue

The artificial "prey" was a circular 5 cm paper disc (white or black) mounted on a 30 cm glass rod which could be rapidly rotated from a "hidden" position behind a false acoustic foam wall (Fig. 9). The rods were rotated by hand approximately 180° from left to right to left so that one sequence was completed within 1 s. Two targets with identical discs were presented at any one time and the "movement" was alternated randomly. Any sound or vibration created by the movement of the glass

rod in the foam was controlled for by placement of another glass rod in each target which was rotated simultaneously with the disc in whichever target was the control at a given time (Fig. 9).

c) The Backgrounds

The basic acoustically and visually simple background consisted of grey acoustic foam placed 4 cm - 5 cm below the disc face and was categorized as condition "A". An acoustically reflective white background of opaque 1 mm rigid plastic (condition "B") was considered of intermediate visual and acoustic difficulty. A cluttered background (condition "C") consisted of 3 cm - 6 cm white paper discs mounted at various heights relative to the actual cue (Fig. 9). This was considered to be visually and acoustically complex.

d) Lighting

Illumination was provided solely by fluorescent lighting located centrally on the ceiling of the chamber and diffused through 8 cm of white foam. Darkness situations were achieved by simply turning off the lights and no external light entered the room. Illumination from equipment used to monitor the bats' echolocation

production was avoided by viewing the output under a black-out curtain while a second experimenter recorded the bats' movements. Between trials, the bat was restrained at the starting point and the lighting restored for experimental manipulations.

C. Low-Frequency Sounds

Sounds (other than echolocation) of importance in foraging would be those which are potentially produced by prey. To test for response to low-frequency sounds indicative of prey a series of experiments were conducted which tested for response to unspecialized prey sounds i.e. sounds of movement or flight; specialized prey sounds i.e. insect calls and buzzing and low-frequency sounds not associated with actual prey sounds.

For the purposes of this study "scratching" was considered generally indicative of prey movement as this sound has proven to be a strong motivator for those bats which respond to prey sounds (e.g. Fiedler et al. 1980, Fenton et al. in prep.). Scratching was produced by rubbing metal forceps over 2 mm nylon mesh in a back-and-forth motion. Sounds were produced either behind the targets (experimenter behind false wall) or at the surface of the target. If scratching was produced at the target surface, the movement was replicated

exactly (minus the noise of contact) on another target as a control.

To support the hypothesis that bats are responding to sounds indicative of prey movement, cockroaches and fluttering moths in fine mesh bags concealed inside linen bags and live mealworms in styrofoam containers were presented in conjunction with identical controls using dead specimens.

To test for response to specialized insect prey sounds, recorded cricket calls and live bot-fly buzzing were presented.

To test for a general response to low-frequency sounds not potentially indicative of prey, static was produced through speakers.

All sounds were analyzed for frequency components using an FFT (see Section 1 : Equipment).

Response to sounds was tested using a target discrimination format and adhering to the general criteria for data collection as outlined for the previous section.

Localization ability was assessed using "displaced targets" with selected sounds. Two target positions were selected randomly from available sites (Fig. 7) with the provision that neither site had been previously visited by the bat to be tested. In addition, a procedural control was conducted to ascertain that the bat could not

locate the target in the new position without a cue (40 circuits of the room or 20 minutes, whichever came first). The audible cue was then associated with one target and a response was scored as the number of repeated cues needed to locate the target (up to 10). Duration of a single cue presentation was 10 s.

RESULTS

A. Vision and Echolocation

a) Antrozous pallidus

Antrozous pallidus is an optional echolocator under these conditions. Generally, cues are detected visually in dim light and the same cues are detected using echolocation in darkness (summary: Fig. 10). In an acoustically and visually simple situation (i.e. condition "A") individuals immediately switched from the effective use of vision in target detection to the use of echolocation as light levels demanded (Fig. 11). Background complexity affects this basic pattern of cue detection. Production of echolocation in dimly lit situations occurred when the backgrounds were unfamiliar (i.e. initial encounters) and visually cryptic. In both conditions "B" and "C" , echolocation was initially

produced but experience with the backgrounds and/or an additional visual cue resulted in an ultimate reduction in production of echolocation in dim light (Fig. 12). In the acoustically and visually complex situation (i.e. condition "C") there is a significant decrease in performance as well as a significant increase in the production of echolocation in lighted situations (Fig. 10). Replacing the white disc with the more visually obvious black disc (same background) resulted in an immediate and significant improvement in performance and a return to the typical pattern of optional use of vision and echolocation (Fig. 13). When the cryptic white disc was returned, performance was significantly improved (Fig. 10), the obvious visual cue apparently enabling the bats to "solve" the problem.

Experimental results indicate that echolocation is used in appropriately lit situations to detect cues only when the cue context is cryptic and unfamiliar. Anecdotal observations support the notion that echolocation is used as a "back-up" system to gather maximum close-range information in a novel or difficult situation. When bats first entered the experimental chamber for preliminary training, one bat echolocated constantly (more than 80% of the time) for the first 11 days and 3 bats echolocated constantly for 3 - 5 days. After this period, bats did not echolocate in dim light

under normal circumstances. On more than 20 cumulative occasions addition of unfamiliar equipment or an extra observer caused bats to begin production of echolocation temporarily and any sudden movement or noise extraneous to the bat resulted in an immediate burst of echolocation pulses.

The quality of echolocation production also varied dependent on background complexity. When dealing with background "B", one Antrozous reduced the intensity of the echolocation call by at least 50% (interpretation of peak-to-peak ratio on visual out-put of oscilloscope). In condition "C" three individuals reduced the intensity of the call similarly.

b) Eptesicus fuscus

Eptesicus fuscus individuals did not demonstrate an optional use of echolocation as did A. pallidus. Throughout the study, no individual was ever detected to have stopped production of echolocation pulses (Fig. 10).

In the simplest condition, "A", there is no significant difference in performance or echolocation between light and dark situations (Fig. 15). The role of echolocation in lighted situations is not clear from this condition. As background complexity increases, it is apparent that though echolocation is constantly produced,

it is not necessarily being used effectively (Fig. 16). During initial trials in condition "B" performance is significantly better in light than in darkness, indicating a use of visual cues in discriminating the moving disc (Fig. 17). In both conditions "B" and "C" individuals performed significantly better when the white disc was replaced by the less visually cryptic black disc in dim light (Fig, 18). This indicates an important use of visual cues in difficult background situations.

There is evidence that vision is used to some extent to assess immediate background information. In dim light, a bat generally landed slightly below a moving disc to avoid direct confrontation. In darkness, however, approaches were directly to the disc which, particularly in cluttered situations, often resulted in entanglement in backgrounds or direct collision with the disc and the unyielding glass rod affixed beneath. Without the visual information about the immediate background it ~~was~~ difficult for a bat to make the manoeuvres necessary to achieve a 'comfortable' landing.

As for Antrozous, experience with difficult backgrounds resulted in significant improvement in performance. Ultimately, the cryptic white disc could be located effectively in conditions "B" and "C" (Fig. 10) in both light and dark after intervening experience with a less cryptic black disc.

c) Myotis lucifugus

M. lucifugus individuals coped well with all degrees of clutter in both light and dark (Fig. 10). Behavior was erratic and landings irregular, however. Though there were no significant differences between performances when visual cues were and were not available, when a black disc was used in cluttered situations there was an observable improvement in the directness and rapidity of the approach to the target.

d) Eptesicus fuscus Born in Captivity

Though data collected from one individual cannot be viewed as conclusive, response to movement appears to be innate and not dependent on a critical period of early learning. The juvenile E. fuscus had never been exposed to moving prey and was reared on a diet of mealworms placed in a petri-dish or secured in a metal clip. Despite this, at the age of approximately 8 weeks, this bat responded immediately and consistently to the moving paper discs when presented simultaneously with a non-moving disc ($z = 13.08$; $p < .05$; $n = 180$).

e) Plexiglass Barrier Over Moving Cue

Only A. pallidus dealt effectively with the Plexiglass barrier. A significant increase in echolocation indicates that it was used to deal with the visually innocuous Plexiglass while vision was necessarily used to locate the moving disc beneath (Fig. 14). Expertise in dealing with the Plexiglass was gained only after initial encounters with it. It was evidently experience that enabled the bats to integrate sensory modes effectively to deal with this novel problem.

B. Response to "Prey" Sounds

Results for target discrimination exercises are summarized in Figure 19 . Clearly, the range of sounds to which all bats respond are more indicative of "movement" than specialized calls. This contention seems supported by poor response to specialized insect sounds used. In 180 trials per species low-frequency sounds not associated with actual prey or sounds of "movement" elicited no significant response from any species (A.p. : $z = 1.6$; $p > .05$; E.f.: $z = 1.1$; $p > .05$; M.l.: $z = 0.6$; $p > .05$). Analysis of sounds indicated that no

component of the sounds had a frequency of greater than 6 kHz. Scratching, the strongest motivator, had peak power at $< .1$ kHz and a highest frequency of < 4 kHz (Fig. 20).

In displaced target exercises, targets were easily located by all species when scratching was associated with them (6 new site locations for each of 9 individuals). Control targets were never located (Table 1). E. fuscus and A. pallidus always localized sounds of live cockroaches (3 new site locations for each of 6 individuals) in a mesh-lined cloth bag and only once located a control site. Myotis lucifugus located sites with live cockroaches less successfully than the other species (Table 1).

a) Novel Sounds

No effort was made to condition responses to new sounds. The bats themselves often expanded their own repertoire of important sounds, however. During early target discriminations a bat never responded significantly to the sound of putting a mealworm in the clip created by the pressure exerted on the styrofoam base (40 trials per individual) but waited for a cue to be presented. Within the next 40 trials per individual, 2 E. fuscus and 3 A. pallidus were using this sound as a cue to locate the correct target (they would respond correctly aver 90% of the time when no other cue was

available). When this event was controlled for, one *A. pallidus* learned to differentiate between sounds created when an experimenter was actually putting a mealworm on a clip and only "pretending " to (when actually affixing a mealworm, she would rub her fingertips lightly across the target when withdrawing her hand from the clip to remove mealworm residue).

Though readily expanding the range of sounds to which they might respond, bats were also capable of selectivity in response to sounds. Initially, individuals of each of the three species would respond to the sounds of other bats scrambling in a metal holding container (n=53). This response was never repeated after experiencing the sound for one to two experimental periods. The sound of writing research notes attracted the attention of *A. pallidus* individuals but only initially (n=13). Bats were thus capable of "screening out" sounds which proved to bear no association with food reward.

The tendency to generalize certain sounds (i.e. sounds of movement) to similar though not identical sounds would seem to be an innate "predisposition" in that the bat born and raised in captivity had to be first "taught" the importance of a single sound (scratching) through conditioning (approx. 40 trials) but thereafter, with no further prompting, expanded her repertoire to

include a range of varied sounds and successfully located the sounds of cockroaches scrambling ($z = 12.7$; $p < .05$; $n \text{ trials} = 180$) in a target discrimination exercise.

B) Other Senses

All species responded to sound in isolation and required no supporting cues. Though apparently able to rely solely on sound other than echolocation to locate a target, E. fuscus and M. lucifugus never stopped production of echolocation calls. Since echolocation was not being used to assess prey characteristics, (there being no actual prey present) it may be used to assess background information and/or potential hazards though it is possible that feedback from echolocation calls is largely ignored when an obvious audible cue is available.

Antrozous pallidus did not usually echolocate when orienting to sounds but could potentially assess similar background information using vision.

SUMMARY OF RESULTS

In darkness, A. pallidus detected moving targets using echolocation. Calls were reduced in intensity when the cue was presented against an acoustically reflective or cluttered background. In dim light, A. pallidus stopped production of echolocation calls and used vision. Cluttered backgrounds posed initial difficulty but the addition of a visually obvious cue lead to a dramatic improvement in performance. The improvement continued over subsequent trials, even when the visually obvious cue was replaced by a more cryptic one. Echolocation was at least temporarily integrated with vision in unfamiliar or potentially hazardous situations.

Eptesicus fuscus continually produced echolocation calls both in darkness and in dim light. However, visually obvious targets were more easily located then cryptic ones. When challenged to rely on a visual cue which blatantly contradicted information from echolocation, the bats did not respond to the visual cue. Eptesicus fuscus individuals generally had more trouble with the reflective and cluttered backgrounds than either of the other species.

Myotis lucifugus individuals constantly produced echolocation calls and responded to all exercises with no apparent reliance on visual cues.

The performance of the E. fuscus born in captivity would indicate that response to a moving target is innate in that she responded immediately to rotating discs though she had no previous experience with locating live moving prey.

All species responded to a similar range of low-frequency sounds generally indicative of prey movement. With the exception of scratching, M. lucifugus performance was consistently weaker than that of the two other species. All species localized sounds accurately and responded to sound in the absence of any supporting cues. Eptesicus fuscus and A. pallidus exhibited a tendency to increase the range of sounds to which they would respond without any overt conditioning to do so. All species exercised a degree of selectivity in the sounds to which they would respond and learned quickly which sounds, though initially attractive, were relevant to food availability.

The performance of the juvenile E. fuscus born in captivity indicated a possible innate "predisposition" to use sound to locate prey and to generalize one sound to similar sounds without prompting.

DISCUSSION

These results indicate that the dietary flexibility of M. lucifugus, E. fuscus and A. pallidus in part reflects sensory flexibility in prey detection. All species are flexible in reacting to changes in prey context and learn rapidly from their own experience. Though echolocation is generally effective across a range of prey conditions, Antrozous and to a lesser extent, Eptesicus, use visual cues to locate targets in some situations. By using an obvious visual cue, both quickly improved performance in a cluttered situation and then generalized this ability to more cryptic situations.

The bats respond to a range of low-frequency sounds and the three species showed some plasticity in response to their immediate acoustic environment (other than echolocation), readily learning to recognize sounds that meant food and to ignore sounds that did not.

The distinct divergence in use of sensory modes between the species can be related to particular foraging environments. Antrozous faces different problems in foraging than the other two species and shows greater flexibility in optional use of echolocation and vision.

Low-Frequency Sound

The accurate response of A. pallidus to low-frequency sounds is not surprising given the data implicating response to sounds of prey in gleaning lifestyles (Bell 1982b, Fiedler et al. 1980, Vaughan 1976). As early as 1961 it was predicted that many insectivorous bats would locate terrestrial insects by listening to their sounds (Kolb 1961). Sounds of prey may provide an important cue when echolocation and vision are impaired by conflicting background information or lighting. That E. fuscus and M. lucifugus respond to a similar range of sounds challenges the notion that the sound of prey is important only to gleaning bats. Two species of European Myotis will respond to the flight sounds of insects in mesh bags (Nyholm 1965). The reported selection of beetles by E. fuscus (Black 1974, Phillips 1966, Hamilton 1933), could reflect the noisy flight of some Coleoptera. Myotis lucifugus may also select for beetles at certain times of the year (Anthony and Kunz 1977).

The "kinds" of sounds to which the species in this study respond is not necessarily typical of all bats which respond to prey sounds. Tonatia bidens responds to specialized insect calls (Belwood 1981) and the

carnivorous Trachops cirrhosus responds to both specialized frog calls and general sounds of movement (Tuttle and Ryan 1981). The bats in this study as well as some carnivorous (Fiedler 1979, Vaughan 1976, Fenton et al. in prep.) and gleaning insectivorous bats (Fiedler et al. 1980, Fenton et al. in prep.) respond to a range of general sounds of "movement" (terrestrial or flight). The number of divergent species which respond to this final category of sounds indicates the ecological importance of this foraging cue. Regardless of diet or mode of pursuit, movement may be the critical factor which alerts a predator to the presence and exact location of prey. Though movement may be equally important to detection by echolocation (Simmons et al. 1979) or vision, moving prey create "noise" and provide an obvious cue for a predator with sensitive low-frequency hearing. A general response to sounds of movement is important in maintaining dietary flexibility as these sounds would cue a foraging bat to a range of prey in a variety of situations. I would predict that response to unspecialized prey sounds is well developed in many bats characterized by broad dietary range, both gleaning and non-gleaning.

Few predators can afford to be absolute "generalists" (e.g. Morse 1975) as efficiency demands some "streamlining" of foraging in response to immediate

pressures or opportunities . Some birds , though broadly categorized as generalists, will modify their search image for prey in response to their availability at any one time (Krebs et al. 1977). Adult Myotis lucifugus may be more selective in choice of prey than juveniles (Belwood and Fenton 1976) that have had little experience with the actual prey environment. Specializations in diet as a result of competition have been reported in E. fuscus (Black 1974) and Myotis evotis (Husar 1979). Adjustments in diet in response to immediate pressures and opportunities may be facilitated by the flexibility noted in both juvenile and adult bats in this study. The bats readily modified their response to audible cues dependent on their own experience with them . This behavior may be applicable to other sensory modes.

Central to understanding the extent to which a species uses prey sounds is accurate assessment of hearing sensitivity . Though high frequency sensitivities related to echolocation are well understood, few data exist on low frequency sensitivity in bats. A. pallidus has "good" hearing sensitivity below 15 kHz (Brown et al. 1978) though this was only recently associated with detection of prey (Bell 1982b). Data for Eptesicus fuscus indicates that it can hear frequencies of less than 1 kHz (Simmons pers. comm.) and another vespertilionid , Scotophilus leucogaster, similar in

foraging habit to E. fuscus, has a "best frequency" of 3 kHz (Suthers pers.comm.). Indeed, many bats may prove to be sensitive to low-frequency sounds and further work is needed to clarify the role of low-frequency hearing sensitivities in foraging. Results of this study indicate that despite a broad overlap between A. pallidus, E. fuscus, and M. lucifugus, there are differences in behavioral responses to sound. A critical comparison of hearing sensitivities would quantify the limits and differences between species in use of low-frequency sound as a prey cue. The suggestion that the "large-eared gleaners" such as A. pallidus (Fig. 2) could better localize sound (Schnitzler and Henson 1980) still awaits proof.

Vision

Reasons postulated for the preferential use of vision over echolocation are that it is less "noisy" as well as less metabolically costly (Chase 1972) and that it alerts neither prey (sensu Fenton and Fullard 1979) nor competitors (Barclay 1981). Antrozous pallidus may integrate the use of vision into its foraging repertoire for all or any of these reasons. However, effective use of vision is surprisingly well developed in A. pallidus in light of the fact that the Vespertilionidae are not

generally noted for acuity in this area (e.g Suthers and Braford 1978). Its development and maintenance therefore represents an important evolutionary departure from the "typical" vespertilionid and points to a compelling selective pressure. Because the most notable divergence in lifestyle between Antrozous and the other vespertilionids under study is its gleaning habit, it would seem that the need to detect prey on surfaces could be a major impetus for the evolution or maintenance of good visual acuity in some gleaning bats.

Although field evidence indicates that in certain situations A. pallidus hunts preferentially by attention to prey sounds (Bell 1982b), it is now apparent that individuals are able to rely solely on vision to locate small moving targets. Where sound is not available or diagnostic, vision alone may be the important cue in detection of prey. Macrotus californicus picks small non-moving and therefore noiseless prey from surfaces using vision where light permits (Bell 1982a). In situations where acoustic cues are prominent, the ability to resolve detail visually may enable Antrozous to identify prey even though it may be located through sound. Both in the laboratory and in the field (Bell 1982 b) , individuals may pass several times over a noisy prey item before a final approach as if "checking it out."

Attention to specialized prey sounds may limit the range of prey taken but a response to a general range of "movement" sounds introduces some "sloppiness" into the system. Therefore a bat may approach an unpalatable or dangerous prey not immediately recognizable by its sounds. In this case, use of an additional sensory mode i.e. vision (or in some cases echolocation), may reduce some of the sloppiness by enabling a greater degree of discrimination and selectivity. However, as for all species in this study, a sound may compel a response when no supporting cues are present thus indicating a certain lack of attention to details when a bat is "sure" of the implications of the sound.

Vision is not particularly well developed in E. fuscus compared to other more visually orientated bats (Bell 1982a, Chase 1972). However, visual cues can confer significant advantages on an individual detecting prey in cluttered situations and background details may be assessed visually. Nocturnal insectivorous birds track prey visually using the night sky as a background (Fenton 1980). Eptesicus fuscus often forages in lighted areas in response to insect patches (Geggie pers. comm.) and in these conditions and others where at least some light is available, may increase effective prey detection by locating insects visually as well as through echolocation. Though visual cues may be integrated with

sonar and may even be the primary cue in final target detection, echolocation pulses are constantly produced indicating a dependence on the sonar system. Except in certain situations involving general orientation (Chase 1981, Griffin 1958) and in the laboratory in response to prey sound, this and many other echolocating species are reluctant to disregard important information returning from echolocation production in favour of other sensory cues. With few exceptions (Fiedler et al. 1980) Antrozous is unique as a vespertilionid in its independence from obligatory production of echolocation pulses and the resultant flexibility in use of other sensory modes.

Echolocation

Detection of prey independent of light conditions is of obvious importance to nocturnal predators and therefore it is not surprising that functional use of echolocation remains in all three species. Though an ability to modify pulse intensity was observed in A. pallidus generally the "typical" call structure of each species is flexible enough to deal with a variety of situations (Simmons et al. 1979). Antrozous does not use echolocation when other cues are available and it may be due to the "costs" involved (as discussed) or the

fact that the intensity and structure of the call are not ideally suited to resolving detail on surfaces (Simmons and Stein 1980). The observed ability to reduce the intensity of pulse emission in the laboratory enables A. pallidus to deal more effectively with dense or cluttered surface situations. The ability to modify pulse emission adds another dimension to the sensory flexibility of this species though it may be a seldom used capacity.

Integration of Sensory Modes

The ability of A. pallidus to integrate important and even contradictory information from echolocation and vision makes it clear just how flexible can be the use of senses. The senses can be used separately as the situation demands or combined to deal with complex or confusing situations. If an animal is to make most effective use of its senses, it must sort out incoming information and choose either to emphasize one level of feedback or to integrate senses and respond accordingly. Even Eptesicus and Myotis will respond to certain sounds when prey are "hidden" and feedback from echolocation and/or vision do not support the fact that prey are available. In other situations, Eptesicus may ignore echolocation and approach a light source behind glass (e.g. Chase 1981). Clearly, there are certain

established "hierarchies" which may help sort out the relative importance of incoming information, but specific situations may demand a departure from rigid adherence to any mechanical sensory "rules". Thus A. pallidus can cope with a novel situation (Plexiglass over visual target) by integrating senses whereas normally it would respond to a visual cue without use of echolocation. Much more work is needed in understanding the extent of sensory flexibility.

Learning and Senses

Though both A. pallidus and E. fuscus had initial difficulty with cluttered backgrounds, when given a visually obvious cue, immediate improvement in performance resulted and was carried over to subsequent visually cryptic trials. Perceptually a single change in a cue variable was important in "solving the problem" for the bat. When this extra cue is removed the bats adjust effectively using other sensory cues suggesting that though a single sensory cue may initiate a response, the bat does not ignore other less obvious details of the situation. What exactly a bat has "learned" from the first situation that enables it to improve subsequent performance is not clear. It is obvious however that individuals are capable of rapid modification of

performance based on experience. In an environment too unpredictable or complex to enable expertise in every potential prey capture situation, the ability to rapidly learn from and expand past experience to similar and even more difficult situations is of obvious adaptive importance.

SECTION 4

SPATIAL MEMORY AND FORAGING STRATEGIES

SPATIAL MEMORY AND FORAGING STRATEGIES

INTRODUCTION

As animals move about in search of food or shelter, they expend energy. Natural selection should favour individuals that efficiently locate resources. Spatial memory has proven fundamental to efficient orientation in a wide array of animals : mammals (e.g. Ewer 1968, Tinbergen 1965), birds (e.g Royama 1970), fish (e.g. Aronson 1951) and insects (e.g. Tinbergen and Kruyt 1938).

Spatial memory may be applied to efficient location of many kinds of resources but it confers particular adaptive advantages on predators foraging in patchy environments. Prey-location learning is an adaptive strategy in that animals that can locate food-rich sites are likely to thrive better than those that hunt widely over a wide area with highly variable food densities (Alcock 1975). Predators that not only exploit spatially patchy food resources but return to a "central place" (sensu Hamilton and Watt 1970) to consume prey or roost will particularly benefit from an ability to locate food patches .

The well developed "memory sense" of bats was

documented as early as 1908 (Hahn). Recent work has substantiated the use of spatial memory as an important orientation mechanism in a variety of bat species (Meuller and Meuller 1979, Konstantinov 1966, Neuweiler and Mohres 1966) but little work has been done on the role of spatial memory in foraging.

Considering the well developed spatial memory of bats, their dependence on roost sites which would not normally enable them to remain at a food site (e.g. Barbour and Davis 1969), and the patchy nature of their insect prey, it is expected that they should exhibit an ability to locate food sites by memory. Field observation indicates that many insectivorous bats exploit ephemeral food patches (e.g. Bell 1980) . If spatial memory were instrumental in relocating even such short-term sites, then a bat should exhibit an ability to remember food locations almost immediately without any long-term familiarization with the location.

The purpose of this study was to examine the use of spatial memory in location of food sites in three species of insectivorous bats. A situation was created in the laboratory in which A. pallidus, M. lucifugus and E. fuscus could benefit from memory of several food locations both on the long and the short-term. As studies on other animals have revealed the importance of certain characteristic and rigid behavior in efficient

site relocation (e.g. Baerends 1941), a second purpose was to ascertain strategies and senses which enable these bats to effectively locate sites.

Terminology used in this section may not strictly correspond to the meanings as established in the psychological literature (MacIntyre pers. comm.). Long and short-term spatial memory are used simply to refer to the ability to locate a site with which a bat has had either long-term or short-term experience. A more critical definition would demand a knowledge of storage processes . Spatial memory is used in reference to an ability to locate a known site by "memory" i.e. in the absence of any cues such as sound. Again, this use may not hold with a stricter definition which demands orientation in space not based on use of external reference points i.e. landmarks. For the sake of continuity of terms, any ability to locate a familiar site more effectively than an unfamiliar one will be referred to as spatial memory. It must be kept in mind however that use of reference points in target location may render the act one of " cue-response learning " rather than spatial memory (MacIntyre pers. comm.).

MATERIALS AND METHODS

A. The Study Animals

Four individuals of each species were used for all phases of the experiments. Details of preliminary training, housing, the experimental chamber and lighting are as described for the previous section : Materials and Methods. Because bats adopted regular "search " paths which entailed one complete circuit of the room, such a circuit could be regularly classified for any bat as a "trial".

B. Spatial Memory and Target-Location Experiments

A bat was considered to be using "spatial memory" if, after initial familiarization with a target location, it returned consistently to the site in the absence of any cue. Acoustic foam targets (as described in previous section) were placed at sites to be tested but they themselves provided no obvious cue. Experimentation indicated that bats responded to the target location and not to the target image when locating it.

Both short-term and long-term spatial memory were assessed because either may have important ecological implications. Long-term memory , as considered in this

study, would apply to location of habitual sites after intervening use of short-term sites or inactivity. Short-term memory would enable efficient exploitation of ephemeral sites .

Long-term spatial memory was considered to be exhibited by a bat if it could consistently locate a previously conditioned site that had not been used for periods of up to 2 weeks. A bat was considered to exhibit short-term memory if a target site could be relocated after minimal conditioning (i.e. less than 10 cued visits). The number of cued visits needed before a site was accurately relocated by memory was assessed.

a) Spatial Fixation

A series of experiments were conducted to ascertain the bats' fidelity to a target location rather than the target image. All bats were initially conditioned to site "1A" (Fig. 8). After 7-9 days of consistent returns to this site for a mealworm reward (20 trials per day), the acoustic foam target was replaced with a target which differed in several ways. It was 50% smaller in area, rectangular instead of square, white instead of grey and entirely made of styrofoam . Each bat was tested for 20 trials under this condition. After this series of trials, all targets were removed from this location and

the "normal" target was placed on the opposite wall. Each bat was allowed to search for the target for 20 minutes.

To assess the accuracy of the response to the site location, the target was replaced on the original wall at various locations in relation to the original site (Fig. 21). Three positions were tested for each bat and the bat was allowed 20 trials (circuits of the room) to locate the target at each site.

b) Long-Term Spatial Memory

Two long-term sites were used. The first site was at "1A". Bats were conditioned to this site as previously described. The second site was located centrally on the opposite wall. Bats were conditioned to this site via a mealworm reward for two days only (40 trials). Prior to conditioning, a control exercise was conducted to ensure that bats could not locate these sites. During this control period, each bat was allowed 40 trials (circuits of the room.) or 20 minutes to locate the target.

After preliminary conditioning, food was made available at these sites at 1-2 week intervals. An identical control target was placed at another site on the same wall during testing. A bat was expected to

search for the target upon entry into the room based on the absence of any other available cues which would indicate a food location (as in previous section). The motivation level of the bats was sufficiently high so that there was never an incident when a search effort was not made. Between test periods, bats were used in the same chamber for short-term memory exercises or target discriminations (preceding section). Though intervening exercises may be viewed as confounding, it was considered "realistically" challenging for a bat to be active at other sites between spatial memory exercises. In addition, motivation to search for food in the chamber was maintained.

A response was quantified as the number of trials (circuits of the room) flown by the bat before the target was located. Only if the bat landed on the target and retrieved a mealworm was it considered a response.

c) Short-Term Spatial Memory

To test short-term spatial memory, a target site was randomly selected from 11 potential positions (Fig. 8) with the stipulation that a bat had not visited it before. A control site was similarly selected. A preliminary set of 40 trials was run for each bat to ensure that it could not find the target in the new

location. An audible cue to which bats were known to respond was then associated with a target. A bat was expected to locate the target in response to this cue. It was then considered to have had an opportunity to incorporate the location into its "memory". The bat was forced to leave the target and cue production was stopped. If the site was relocated without the cue within 10 circuits of the room, performance was quantified as "1" (i.e. one cued visit needed to memorize location). If the bat could not locate the site within ten circuits of the room, then the cue was again issued and the sequence repeated. Short-term memory was assessed as the number of cued returns required before a bat could locate a site by " memory " (10 consistent returns with no cue). As many as 3 locations were introduced to a bat on any one day.

Exercises were conducted in dim light and darkness to determine the sensory basis of spatial memory. Usually, a cue was issued and all trials assessed under the same lighting condition for any one site. An additional series of experiments were conducted in which the cue was issued with the lights on. The bat was allowed to repeat the exercise until the site could be located by memory (as specified). The lights were then turned off. Differences in performance were considered to be due to the difference in availability of visual

cues between light and dark conditions.

C. The Basis of Spatial Memory

a) Habitual Routes

Experiments concerning the importance of habitual routes in target location by memory were based on preliminary observations during training (Section 1).

During this training, two behavioral phenomena of interest emerged. After 2-11 days of conditioning to the target location individuals of each species adopted a characteristic and rigid flight path which generally encompassed a complete circuit of the room at 1.5 m - 2.0 m above floor level. Flight paths were not identical between individuals though they invariably included a single landing site at wall "A" and another at "B" or the proximal corners. There were no regular deviations to the side walls (over 150 observations of 12 individuals).

When a target was relocated by a bat, the bat often repeated exactly the route by which it had first reached the target. One E. fuscus repeatedly followed a convoluted route (Fig. 22) to the target. By removing the screening on which he crawled, I encouraged it to change tactics.

During long and short-term memory exercises the

importance of habitual routes was assessed through detailed observation of flight paths used to locate targets. Routes were recorded by two observers at opposite sides of the room. In darkness, routes were approximated. Wing-beats and landings were clearly audible.

Secondly, to assess the effect of a bat's inability to replicate a habitual route when locating a target, an acoustic foam barricade was placed 0.5 m in front of a habitual landing site. For each of 12 bats, 3 barricades were placed during long-term memory exercises and 3 during short-term memory exercises (3 different sites for each bat).

b) Landmarks and Sensory Basis of Orientation

Use of specific landmarks is important to spatial memory in some animals (e.g. Tinbergen and Kruyt 1938) and therefore may be an important orientation mechanism in bats.

Use of landmarks by bats was assessed largely through behavioral observation. The sensory basis of spatial orientation was examined in terms of the bats' use of visual and/or acoustic (echolocation) cues. Determination of the use of vision and echolocation was based on differences in light and dark performance as

previously discussed.

RESULTS

B. Target Location Experiments

a) Spatial Fixation

None of the bats I tested used a well developed "search image" to locate the target but returned to a point in space apparently guided by some system of cues external to the target. After initial conditioning to site "1A", a change in target size, shape, texture or even its complete removal never (480 trials with 12 individuals) affected the bats' response to the site.

When the target was moved any distance greater than 0.5 m from the original location (Fig. 21), the new site was successfully located only 5 times out of a cumulative 72 new locations. Anywhere within an approximate 0.5 m radius extending from the original target location, it was located significantly more often ($\chi^2=79.27; p < .05; d.f.=1$). Bats located 58 of these new sites out of a cumulative 72 presentations with 12 individuals. The ability to locate slightly displaced targets suggests the involvement of the target image as a salient cue in location only if it does not conflict too strongly with

the spatial sense.

b) Long-Term Spatial Memory

Over a four month period, each bat was able to remember accurately the location of both the primary and secondary long-term sites (Table 2). This ability did not diminish despite intervening periods of up to 2 weeks during which bats were subjected to a number of different sensory cues and target locations.

c) Short-Term Spatial Memory

All species remembered new locations without extensive conditioning to the sites. Control sites were never located (Table 3).

C. The Basis of Spatial Memory

a) Habitual Routes

When bats were involved in spatial memory exercises, the trends noted during early training remained. Ten recorded flight paths per individual indicated that the same habitual route was used each time (e.g. Fig. 23A) to locate long-term sites.

Location of short-term sites necessitated some deviation from the habitual route (Fig. 23B). In observation of 78 flight paths for 12 bats, the route by which a target site was first located was repeated "exactly" in returning to the target by memory (Fig. 23B). This route incorporated the entire habitual route as well as the deviation each time.

When barricades were placed so that a bat could not repeat exactly its original route to the target site, there was a significant reduction in ability to locate the target on the short-term (chi-square= 57.60; $p < .05$; d.f.=1; n sites = 36). In 36 manipulations, a target was located successfully only 4 times. More typically, disorientation followed placement of a barricade (Fig. 23C).

In location of long-term sites , there was no significant reduction in performance when barricades were in place (chi-square= 3.55; $p > .05$; d.f.=1; n sites= 36). Bats were reasonably flexible in adjusting to minor changes in the approach to the long-term site.

Only when completely disoriented would a bat adopt a route to a new target site that did not include the habitual route (e.g. Fig 23D). Initially A. pallidus was disoriented in darkness (see following) and would use a new flight path only under these conditions (n=6). This was presumably due to the "disappearance" of certain

landmarks that aided in orientation. Assuming adoption of a new route requires integration of a new set of "landmarks" then bats can quickly assess and incorporate new orientation cues on the short-term.

b) Landmarks and the Sensory Basis of Spatial Memory

There was no suggestion in this study that orientation was guided by response to magnetic fields or other diffuse cues. Locations seemed to be memorized in terms of visual and presumably acoustic (assessed by sonar) "landmarks". In the initial conditioning exercise, a 40W red light bulb was mounted 0.7 m from the target to provide occasional illumination. When the target was first removed from this location, 11 of 12 bats repeatedly checked the light by walking to it from the now vacant target location and then "pacing" the distance back to the target site. This checking occurred whether the light was off or on indicating that light level had not been the only attractant feature though it may have been the initial one. A bat repeated this checking exercise with periodic intervening flights up to 100 times and removal of the light stopped this behavior. The position of the observer relative to the target was used as a cue to short-term target location 4 times by a M. lucifugus individual and 3 times by different A.

pallidus. In each case, movement of the observer relative to the target disoriented the bat so that it could no longer locate a target previously located with ease. One Myotis which had located a target on the floor successfully returned not to the target but to a position beside my feet (I had moved 1 m from the target). She repeated this twice (each time I moved slightly).

Other landmarks were implicit in the configuration of the room itself. Certain "hard" features of the room were incorporated into most flight-patterns. The corners of the room, a door frame and a metal light box were the only obvious (to me)* above ground features not covered with foam and it was these which were usually closely associated with landing sites (though they were not of a quality which made it possible to land on them directly). The importance of the incorporation of these sites in orientation is apparent when access to a key area is blocked (details in preceding section) or when they are not visually obvious (A. pallidus only), resulting in disorientation and inability to locate a target.

When a cue to a short-term site was issued in darkness and lighting was not changed for location, there was no significant reduction in ability to locate the target (A.p.: $\chi^2=1.62$; $p > .05$; d.f.=1; n light sites=14; n dark sites = 9 ; E.f.: $\chi^2=0.01$; $p > .05$; d.f.=1; n light sites= 18; n dark sites=

9; M.l.: chi-square= 1.74; $p > .05$; d.f.=1; n light sites = 15; n dark sites = 9) when compared to previous performance in dim light (see Short-Term Spatial Memory). When the cue was issued in dim light and the lights were turned off when a bat could locate the site by memory, M. lucifugus and E. fuscus showed no significant reduction in performance (M.l.:chi-square=0.06; $p > .05$; d.f.=1; n sites = 12 ; E.f.: chi-square=0.00; $p > .05$; d.f.=1; n sites= 12). The behavior of A. pallidus indicated a reliance on visual cues. Initially, there was a deterioration in performance in darkness after location of a site in dim light (chi-square=12.44; $p < .05$; d.f.=1; n sites = 16). This behavior did not continue after initial tests (numbers as stated) but bats quickly adjusted to unpredictable light levels. In location of a subsequent 16 sites, there was no significant deterioration in performance in darkness (chi-square=1.07; $p > .05$; d.f.=1).

These observations suggest that both E. fuscus and M. lucifugus depend on echolocation when possible to orientate (i.e. in a confined space) and detect "landmarks" but that A. pallidus uses visual cues preferentially when light permits. The fact that Antrozous must adjust to differences in light levels clearly supports the argument that certain "landmarks" or

features of the room are critical in orientation. If a bat was guided by a more kinesthetic sense, an innate sense of direction or response to a sound field, then a bat should orientate equally effectively in both dark and light regardless of previous experience with light

DISCUSSION

Use of spatial memory in a confined laboratory setting may not be directly analagous to its use in a more expansive natural setting. However, the ability to incorporate into "memory", accurate information concerning food availability and to effectively retrieve and use this information at a later date to increase foraging success is a behavioral phenomenon not restricted by distance. Furthermore, in a more natural setting, a bat is intimately familiar with the area and adapted to use the kinds of orientation cues available. If one can reasonably expect an animal to perform better in the environment in which it has evolved, then it is probable that the behavior noted in this study is not limited by natural conditions.

Short and Long-Term Spatial Memory

A well developed use of spatial memory in efficient

location of food sites is characteristic of the range of bats studied despite obvious differences in diet and foraging behavior under natural conditions. This capacity may well characterize a number of species that have in common the fact that they exploit spatially patchy resources. Some fruit bats (Morrison 1978) return repeatedly to habitual feeding sites despite closer available resources. Though exploitation of a known resource may therefore increase commuting time, it can be assumed that this cost is met by the saving in search time.

A fundamental saving in energy could be achieved by an ability to locate a single productive site. Memory of several distinct resource locations could carry an animal through an extended period of time. Bees (Heinrich 1978) switch to known secondary sites when primary sites are depleted. The bats in this study remembered more than one site and some sites for long periods of time suggesting that they too could make extended use of memory of food locations. The immediacy with which a bat in the laboratory incorporates a site into its "memory" suggests that spatial memory is important not only in dealing with relatively long-term sites but could be instrumental in location of extremely ephemeral sites.

There is obvious advantage to remembering a number of productive food sites but adjusting behavior to the

relative quality of these sites would "optimize" the use of spatial memory. Birds (Smith and Dawkins 1971, Royama 1970) may select rich food patches over poorer ones. Preliminary observations (Appendix A) suggest that a bat is also capable of remembering differences in quality between sites and will make a choice based on this information.

In summary, bats will readily exploit known sites for food and accurately remember the location of these sites. They can remember a number of sites simultaneously and will immediately incorporate new sites as well as remember some sites for long periods of time. They may also be capable of taking into consideration the quality of different sites. In an environment where prey may fluctuate on a seasonal and even daily basis, there is an obvious advantage to maintaining this kind of flexibility in use of spatial memory.

Habitual Routes and Landmarks

The fact that all three species tended to use habitual routes and landmarks to locate food sites points to the importance of this mode of orientation. A site itself may be innocuous or similar to several other sites in the area and therefore more easily relocated in terms of its relation to more significant features of the

environment. In the laboratory bats are limited in the kind and number of landmarks they may use but in the wild presumably landmarks may include features of the terrain as well as such things as stars (Childs and Buchler 1981, Chase and Suthers 1969), sound (Buchler and Childs 1981) or other visual or acoustic cues.

Findings in the laboratory as to the use of habitual routes are substantiated by observations in the field. Use of habitual routes has been noted in bats (Buchler 1980, Hough 1957, Harrison pers. comm.) and the "trick" to successfully trapping quantities of bats is to place the trap or mist net across a habitual route. Dependence on routes and landmarks even in relatively close-range orientation would now be seen to be critical in mammals as well as insects (e.g. Tinbergen and Kruyt 1938) and well may be a pervasive feature in orientation over a range of animals.

Short-term sites are remembered as deviations from habitual flight paths by the bats in this study either by the additon of new temporary landmarks or potentially, a more kinesthetic sense regarding distances in relation to established landmarks (i.e. three wingbeats past the lamp and turn left). Even in the rather simple environment of the laboratory, there is apparantly some advantage to remembering not an entire new route but only that portion of the route that deviates from normal. Though this

behavior appears rigid, it would in fact confer a great deal of flexibility . If there are absolute limits to the amount of spatial information that can be retained , then remembering only deviations from habitual flight paths rather than entire new routes and concomitant landmarks should allow for a greater number of sites to be remembered. In addition, there would be less chance of a bat not being able to locate an important resource because the route is complex and unfamiliar .

Sensory Basis of Spatial Memory

It is clear that under these experimental conditions, A. pallidus will use vision preferentially over echolocation when light allows. Under identical conditions the other two species depend largely on echolocation . These results are consistent with those of Mueller and Mueller (1979) in that , even with obvious visual cues available, E. fuscus relied on cues detected by echolocation in relocating a target . Their conclusion was that the role of vision in orientation of vespertilionid bats "remains an open question". Results from this study indicate that at least one vespertilionid, A. pallidus, may rely on vision for spatial orientation when conditions permit. Despite the reliance of E. fuscus and M. lucifugus on non-visual cues in a confined

space, these bats are capable of visual discrimination (Masterson and Ellins 1974, Suthers et al. 1969) . In homing experiments the inferior ability of blinded bats implicates the use of vision in long distance orientation (summary in Griffin 1970). However, echolocation is clearly important to close-range orientation . Though Antrozous will use vision it has not lost the use of functional echolocation and easily resorts to it when the situation demands. Whether Antrozous is unique in the evolutionary departure from the "typical" vespertilionid as regards orientation can only be assessed by further work on this widespread family.

SECTION 5

SOCIAL ASPECTS OF FLEXIBILITY:

LEARNING AND INFORMATION SHARING

"The problems confronting a population...such as bats...seem to be maintenance rather than limiting of size. In such populations, social behaviour seems to keep the population at a high level with mutual benefit to all members". (Twente 1955:1)

INTRODUCTION

There is no one answer as to what benefits a particular individual derives from being a member of a group. Reduced risk of predation has been cited as an important evolutionary force towards a gregarious lifestyle (Rubenstein 1978, Treisman 1975, Pulliam 1973). Communal roosting to resist temperature extremes or aid in metabolism (Fenton and Barclay 1980, Howell 1980, Trune and Slobodkichoff 1976, Vaughan and O'Shea 1976) may be especially critical in bats. One of most compelling reasons for gregariousness is the efficient location and exploitation of food resources (Evans 1982, Ward and Zahavi 1973, Murton 1971). It has been generally accepted that when food is patchy in time and space and therefore unpredictable over a period of time, group foraging may be the most efficient strategy to adopt (summary Krebs and Davies 1978). There is little question that prey of insectivorous bats is patchy (Bell. 1980, Bradbury and Vehrencamp 1976a, Harrison 1978, Anthony and Kunz 1977) and that under certain conditions, information sharing regarding food locations should maximize foraging efficiency (Morrison 1980, Bradbury and Vehrencamp 1976ab, Heithaus et al. 1975) . Though some feeding associations may be more or less permanent (e.g. Howell 1979, Bradbury and Emmons 1974), many bats

forage opportunistically in ephemeral groups which form in relation to food patches (e.g. Bell 1980, Vaughan 1980, Fenton and Morris 1976). The basis of this phenomenon has not been critically assessed in bats. There is evidence that *Myotis lucifugus* cues in on feeding sounds of conspecifics (Barclay 1981). This behavior is analagous to "local enhancement" and is well documented in birds (Krebs et al 1972, Ward 1965, Turner 1964, Crook 1980).

Cueing to general food location is of adaptive significance when food is patchily distributed . Attention to more specific information available from interaction with another individual would enable exploitation of a new prey type, microhabitat or capture technique. Perhaps the best known examples of cultural transmission of a novel behavior are the opening of milk bottles by Great Tits and potato washing in Japanese macaques (summary in Gould 1982). There has been little systematic experimental investigation into this phenomenon in undomesticated mammals other than primates.

One might suspect that information transfer on both the general (location of resource) and specific level (observational learning) might occur in bats which gather and disperse frequently in search of unpredictable food resources. *Myotis lucifugus*, *A. pallidus* and *E. fuscus* all meet these general criteria and therefore might exhibit

an ability to increase individual foraging success by exploiting information provided by the activities of successful foragers.

The purpose of this study was to test two hypotheses regarding the general phenomena of information transfer * in a laboratory situation with individuals taken from natural populations of bats. The first hypothesis tested concerned the more general condition of information transfer . If information sharing is a characteristic of opportunistic exploitation of prey patches then there should be a significant advantage to a bat foraging in a group as opposed to alone when searching for a patchily distributed resource. Secondly , if information provided directly or indirectly by a foraging bat can be used by another bat to learn not only food location but a new foraging behavior, then a naive bat should be able to learn a novel foraging technique from a knowledgeable individual.

* "information transfer" and "information sharing" concern the use of information implicit in the foraging activity of another bat. It does not imply cooperation or intent on the part of the sender.

MATERIALS AND METHODS

A. Learning a New Foraging Behavior

To test the hypothesis that a naive bat can learn a new foraging behavior from an experienced bat, a situation was created in the laboratory in which it was possible for a bat to observe a trained bat retrieving food in a novel way. The behavior was considered novel because the context of prey retrieval was such that it could not have been previously experienced by a bat from a natural population. In addition, controls were conducted to ascertain that the behavior was not acquired without interaction with a trained bat or without extensive conditioning.

a) The Study Animals and Experimental Conditions

Thirty bats were used in the course of the study; 9 A. pallidus, 10 M. lucifugus and 11 E. fuscus. Three bats of each species were randomly selected from the captive population to serve as "teachers". Each bat was individually conditioned to fly to a target, remove a mealworm from a clip (Section 1; Materials and Methods) and to return to a starting point about 2 m away. When

a bat could repeat the exercise consistently without any prompting from an experimenter, it was then qualified as a teacher.

The "pupils" were naive bats that were captured at least 2 weeks before the testing date and kept isolated in holding cages until this date. None were familiarized with the experimental chamber before onset of experimentation. Naive bats were divided randomly into control and experimental groups. For each species, 3 bats were introduced into the room with a trained conspecific and 3 were introduced into the room with no trained bat present. Of the latter 3, two entered the room together to control for the possibility that the presence of a conspecific, whether naive or trained, facilitated acquisition of the foraging behavior. In addition, one E. fuscus was placed with a M. lucifuqus teacher and one with an A. pallidus "teacher" and one M. lucifuqus was placed with an E. fuscus "teacher". These final exercises were intended to assess the ability of the bats to learn from a non-conspecific.

All trials were conducted in dim light. The experimental chamber and housing were as described in Section 3 : Materials and Methods.

b) Procedure

On the first day of experimentation a trained bat was released into the flight chamber . When it was performing consistently, the naive bat was released into the room with it. From this point neither bat was directly interfered with though two experimenters were present in the room at all times and mealworms were replaced on the clip. Controls were treated identically and mealworms were periodically replaced on the clip to provide the same cues as were available to the other bats. The control bats were not fed unless a critical weight (Appendix B) was reached. If fed, they were fed by hand in the experimental chamber. When a "teacher" had completed 20 trials of flying, picking up the mealworm and returning to the starting position, all bats were removed from the room.

When a naive bat first successfully secured a mealworm in the appropriate way , the teacher was removed from the room . The naive bat was observed for an ability to repeat the exercise consistently . The naive bat was considered to have acquired the behavior only when it could repeat the task independently over 10 trials in one testing session (approx. 25 mins.). If these criteria were not met, the "teacher" was returned to the chamber.

This sequence was repeated until all criteria were met. The performance of each bat was then assessed as the number of days or trials (20 trials = 1 day) on the part of the "teacher" which were needed for the naive bat to learn the new behavior.

c) Sensory Basis of Learning

An important component of observational learning is the stimuli that release and direct the response of a naive bat. Certain cues by which a naive bat might monitor the behavior of a successfully foraging bat were isolated. Chewing sounds of bats and field recordings consisting of echolocation calls produced during feeding were presented in both displaced target and target discrimination exercises (as for Section 2). The chewing sounds were isolated by placing feeding bats in cloth bags suspended at the surface of a target. The control was a cloth bag containing a live but non-feeding bat. Chewing sounds were also recorded and played through speakers imbedded in targets. Taped feeding sequences (echolocation) were played with frequencies below 10 kHz filtered out to avoid confounding insect calls present in the background. Controls consisted of identical sections of tape with all frequencies below 100

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kHz filtered out. The quality of sound emission was monitored on an oscilloscope to ensure successful filtering.

B. Group Versus Individual Foraging

a) The Study Animals and Experimental Conditions

Five E. fuscus and 16 A. pallidus were used throughout these experiments. Subjects had been in captivity for periods of 1 - 6 months. Experiments were conducted in one of two chambers. In the first (Fig. 24) petri-dishes were affixed to the floor in positions as illustrated and each was filled with strips of paper saturated with the same vitamin supplement used on the mealworms. The search phase was made challenging in the confined space of the chamber by the placement of opaque plastic partitions throughout. The second chamber was a 3 m x 3 m x 2 m mesh cage. Twelve petri-dishes (as above) were placed on the floor . A small area was separated from the feeding area by a sliding plywood partition. Bats roosted in the large flight cage . Housing conditions for bats used in the smaller chamber were as described in Section 3 : Materials and Methods.

The 2 chambers were used to assess the effect, if any, of the confined space of the smaller chamber on performance when compared to a free-flight situation.

b) Procedure

Four groups of bats were randomly selected from the captive population. Groups were permanent for the duration of the study. The E. fuscus group consisted of 5 members and the 3 A. pallidus groups of 7, 5, and 4 members.

On a given testing date, a petri-dish site was randomly selected from available sites and 8 mealworms per bat placed in it. For individual trials, a bat was placed singly into the starting chamber and time from first exit from this chamber to location of the mealworms was timed to the nearest second. For group trials, all members of a group were placed in the starting chamber and times to food location were recorded for each bat. In the larger chamber, procedure was identical except that only bats to be tested on a given day were allowed out of the roosting section and into the feeding section.

Bats were run once a day, either individually or in a group. Each bat was run for a total of 14 test periods in the small chamber and 10 test periods in the larger chamber.

c) Behavioral Observations

Though the ability to use conspecific information may be central to group foraging, group interactions may in part determine ultimate efficiency of information "sharing" for each individual. In a confined space, behavior may be modified but pronounced differences within and between species under identical experimental conditions would provide important insight as to behavioral potentials. Detailed observations of behavior during group foraging bouts were recorded to assess the effect of group interactions.

RESULTS

A. Learning a New Foraging Behavior

Individuals of each species learned the novel task in its entirety from a knowledgeable individual. None of the control bats even approached fulfilment of the stated criteria and conditioning required an average of about 2 weeks (Fig. 25). Results for conditioned performance were taken from preliminary training of bats (Section 1 : Materials and Methods).

Initial response to the exercise was similar for E.

fuscus and M. lucifugus. On the first day of exposure to trained bats, naïve bats spent 77% of their time in flight. Control bats spent only 12% of their time in flight though they were left in the room for similar lengths of time. The flight consisted of regular circuits around the room and was referred to as a "search phase". During this phase, there was no observable association with the teacher. Within the first 30 trials, this independent search was abandoned and activity was centered on the trained individual. Naïve bats landed directly on a feeding bat and spent more than 60% of their time within 1 m of the teacher. As trained bats left the target to consume the mealworm, this did not immediately lead to an association with the food site. Antrozous pallidus varied from this basic pattern and on the first day of exposure, spent 86% of their time within 1 m of the trained bat, following it so closely they almost mimicked the teacher's movements. All trainees made an ultimate association with the target and the exact nature of procuring the mealworm reward by the fourth day of trials and in one instance, all phases of learning were completed on the first day by a M. lucifugus individual. Initial removal of the trained bat from the room usually led to a deterioration in performance on the part of the naïve bat ($n = 7$). No bat needed more than 2 more partial sessions with the

teacher before performing independently.

Results of bats placed with other species indicates that a bat may learn from a bat which is not a conspecific within certain limitations. An E. fuscus individual learned the entire task successfully from a M. lucifugus "teacher" within four days though extreme aggression on the part of the Eptesicus towards the Myotis was exhibited once the Eptesicus had learned the target location. The Myotis individual had to be removed and was not returned despite the fact that the E. fuscus could not yet perform consistently. This aggression made it impractical to train a M. lucifugus with an E. fuscus teacher. When an E. fuscus was trained with an A. pallidus, the behavior was successfully learned though aggression was again noted.

The Sensory Basis of Learning

Individuals of each species responded not only to the chewing sounds of conspecifics but to other species and even to humans mimicking the sounds (Fig. 25). In addition to making target discriminations based on chewing cues, each bat could also locate a displaced target (Table 4) indicating their ability to localize the noise accurately.

Only M. lucifugus responded significantly to recorded echolocation calls (Fig. 25). It made no difference if the call was played backwards or which species was involved in the taped sequence. The other two species responded randomly to calls. Myotis lucifugus located displaced targets accurately 100% of the time and never located a control (n sites = 9). Neither of the other species located a target though twice, an E. fuscus responded to the general area (9 sites per species).

B. Group Versus Individual Performance

Mean times for all members of each group run in the small chamber indicate that mean group time to food location is significantly better than mean individual time (Fig. 26). Results in the larger chamber are comparable though search times are longer in both group and individual conditions (Fig. 27).

Behavioral Observations

Though grossly similar in performance, observations indicate some important differences in intraspecific interactions. Eptesicus were extremely aggressive and agonistic interactions were always initiated (n = 23) by

the two heaviest bats (mean weight=20.1 g) and directed towards the 2 smallest bats (mean weight = 16.4 g). Aggression was never observed outside the test period or during the search phase leading to final food location. The aggressive bats were not the most efficient foragers i.e. they located food first only twice in 7 group trials and individual search times did not differ significantly (Mann-Whitney $U = 3.5$; $p > .05$; $n = 14$) from those of the smaller bats. Therefore, they often dominated a feeding patch located by another bat. Subordinate bats lost an average of 1.9 g during the study and the aggressive bats lost no measurable amount of weight.

There was no comparable aggression between A. pallidus individuals. Upon entry into the experiment, weights varied from 14 - 24 g but there was not overt intimidation of small bats by larger ones. Performance calculated for each member of a group clearly indicates that certain individuals are more efficient at locating food (Fig. 28). Though this suggests that some bats may be exploiting the superior search efficiency of other bats, bats showing superior food finding ability lost less than 0.1 g ($n = 3$) while inferior bats lost an average of 1.4 g ($n = 5$). This difference is explained by the fact that the first bat to a site got at least one more mealworm than the last bat to the site during each group trial.

In both the smaller and larger cages, A. pallidus were less likely to remain at a feeding site when alone than when in a group. Groups were never seen to disperse from a site ($n=21$) and solitary bats averaged 1.2 departures per feeding bout.

DISCUSSION

Results of this study indicate that one way bats may cope with an unpredictable and highly variable food resource is to exploit information available from the foraging activities of other bats. Previous experimental evidence shows that M. lucifugus responds to the echolocation calls of foraging bats (Barclay 1981). The present study supports Barclay's contention about the importance of cueing on feeding groups of bats . It also shows that the benefits of information sharing may be common to a number of species. Furthermore, bats can exploit not only cues from echolocation but will respond to the chewing noises of other bats and information implicit in the foraging activity of a bat can cue a naive individual not only to the location of a food patch but can be used to "learn" a detailed new foraging technique.

Since bats are long-lived, e.g. up to 30 years in M. lucifugus (Fenton and Barclay 1981), and populations

are large, there would be a tremendous store of information and range of expertise available at any one time. Juvenile bats probably learn a great deal from adult bats (e.g. Möhres 1966) and it now appears that they continue as adults to exploit important information from other bats (Barclay 1981, this study). It may be generally true that in species where variability in diet is advantageous, flexibility in foraging is greatly enhanced by an ability to recognize and use biologically important information available from conspecifics.

Learning a New Foraging Behavior

Through observation of a conspecific, individuals of all three species can acquire an adaptive new pattern of behavior. Despite the novel nature of the flight chamber as a microhabitat, a naive bat will "ignore" the unnatural environment and the lack of prey cues in deference to the compelling information arising from a successfully foraging bat. Even in the absence of immediate reward (food) bats remain attentive to the feeding activities of other bats. Continued response in the absence of reinforcement so contradicts the basic theory of learning through conditioning that response to feeding bats must not be unique to the lab. It is probable that the behavior has been rewarded consistently

during earlier experiences or is, at least in part, an instinctive response to certain cues characteristic of another bat's foraging success. Stimulating a search effort may be the only impetus necessary for a bat to exploit a feeding opportunity. An increase in search effort in response to success of conspecifics has been noted in Great Tits (Krebs et al 1972) and willingness to enter new microhabitats and try new foods when conspecifics are present has been discussed for other birds (Turner 1964).

The critical attention paid by an individual to the details of another's foraging behavior when a "search" has revealed no apparent or familiar prey, is perhaps more relevant to the acquisition of a "novel" feeding behavior. Evidence for observational learning in acquiring new and adaptive behavior rests largely in the bird literature though potato washing in macaques and lever pressing in adult domestic cats (Johns et al 1968) serve as examples that mature mammals are capable of learning new patterns of behavior through observation of conspecifics. There is little direct evidence that truly "novel" behavior has been transmitted through natural populations of bats. Antrozous pallidus has been reported capturing moths from inside cacti and this behavior seems to be typical of one discrete population (Howell 1980). The results of this study suggest that such behavior

could be easily learned from other bats. Searching for behavior that appears novel to us is a misleading enterprise however. It is impossible for us to know what is "novel" to a bat. In the natural environment, many foraging techniques or prey types would be novel to the inexperienced individual. Learning would take place throughout the life of a bat providing them with information either "too complex or too unpredictable to be innately encoded" (Gould 1982).

Such learning is not necessarily indicative of creative intelligence. Even the opening of milk bottles by great tits would have been facilitated by their innate stripping tendency (Morse 1980). The bats in this study clearly responded to certain cues which may be characteristic of a number of foraging situations (i. e. chewing and echolocation). It is impossible to say which part of the behavior is based on application of innate abilities to a new situation or instinctive response to cues. It can only be stressed that it is a complex interplay of learning and instinct that produce an adaptive response.

Sensory Basis of Learning

As discussed, there are certain stimuli inherent in foraging activity which could cue a naive individual to a feeding opportunity. Response to isolated sounds of chewing indicates the importance of this cue. This response is particularly remarkable in E. fuscus and M. lucifugus, bats not previously noted for their attentiveness to sounds of low-frequency (see section 3). Sounds of chewing are very proximal cues, in the laboratory eliciting responses from up to 2 metres. Many cues a bat uses to locate prey are equally close-range. The effective range of echolocation in detecting small prey is only 1-2 metres (Fenton and Bell 1979, Griffin 1971) and may be even further diminished in rain or fog (Pye 1971). Echolocation is highly directional (e.g. Barclay 1981) whereas a bat's initial orientation towards a low-frequency sound such as chewing would not be critical in detection of this "prey" cue. Where prey is innocuous or unfamiliar and itself unlikely to evoke a response, the chewing of another bat may be a naive bat's only cue to the presence of food.

Response to high-frequency components of actual feeding sequences fits with available evidence for M. lucifugus (Barclay 1981). The questionable response of

A. pallidus and E. fuscus to taped echolocation calls reflects their lack of relevance in confined areas. In a natural setting, echolocation calls of conspecifics can be an important long-range cue with an effective range of about 50 metres (Barclay 1981). Data from the field concerning the response of E. fuscus to taped echolocation calls is inconclusive (Fenton 1980). This species responds to distant sounds to locate feeding areas (Buchler and Childs 1982) and A. pallidus definitely are attentive to communication calls of conspecifics (Vaughan and O'Shea 1976). Given this responsiveness to certain long-range cues and calls of conspecifics, it is likely that the echolocation calls of other bats might be used as a long-range cue to locate feeding areas. It may be that supporting cues are necessary before a bat will exploit this cue at close-range.

Other cues implicit in the foraging behavior of a bat are difficult to isolate and test for though this does not rule out their possible importance. It is thought that birds flying purposefully or en masse may attract the attention of unsuccessful foragers (Simmons 1972). Nightly periods of flight may begin with one bat leading the way in E. fuscus (Phillips 1966) and A. pallidus may issue communication calls upon emergence (O'Shea and Vaughan 1977). These activities coupled with

the fact that bats often return to communal roosts leave ample opportunity for following successful bats. Bats may also return to a roost to consume prey (e.g Bell 1982b, Phillips 1966) and the attention paid to a feeding bat (this study) indicates that their feeding success would not go unheeded. Information transfer need not be specialized (Bertram 1978) and bats may be flexible in choosing from a number of foraging cues.

Group Versus Individual Performance

It is generally accepted that when food is spatially or temporally patchy, group foraging may be the most energetically optimal strategy to adopt. Results of this study support this hypothesis in that all species gained a significant advantage in reduction of search time when searching in groups for a patchy resource. Implicit in the findings is that the bats are exploiting information provided by successful members of the group as regards food location. In a natural setting, cues may vary but the analogy is the same. Search time can be significantly reduced when several members of a population "share" (though there is no suggestion of cooperation) the search effort and there are cues available which would alert unsuccessful individuals to the food location.

Observations of intraspecific interactions during feeding point to fundamental differences in the dynamics of the foraging groups. Information from natural populations would suggest that group structure is not permanently maintained in either of these species. Group size and cohesiveness may ultimately depend on food distribution in these and other species of bats (Vaughan and O'Shea 1976, Kunz 1974, Nelson 1974) as well as in some birds (Zahavi 1971, Brown 1964). Some birds (Davies 1976) and bats indulge in the extremes of group foraging and apparent territoriality dependent on food availability (Racey and Swift 1981, Tuttle et al 1975).

Observations of *E. fuscus* suggest that it tends towards this final category, reacting flexibly in terms of aggression. When food within the patch is limited as in the present study, a dominant bat gains an obvious advantage if it can apportion itself a larger share of food through agonistic behavior towards other bats. In the field, such aggression has been noted during foraging, not only towards other bats (Fenton 1980) but a bat tentatively identified as *E. fuscus* even chased birds from a preferred area within a prey patch (Shields and Bildstein 1979). Increase in aggression is not a unique trait. In general (summary in Wilson 1975) aggressive-submissive exchanges increase sharply when food is clumped instead of scattered, and domination of

one piece of food or area of ground becomes profitable. Neither can one assume that aggression observed in the laboratory is a meaningless artifact. The same animals were not aggressive when food was not limited. Aggression has a high degree of heritability (Wilson 1975, and Fuller 1965, McClearn 1970) and therefore can be looked at as a set of responses "programmed" to be released in times of stress.

Despite similarities in group structure between Antrozous and Eptesicus (i.e. both form in response to food patches), the lack of overtly exhibited aggression in Antrozous may be indicative of the more complex social system (Vaughan and O'Shea 1976, Trune and Slobodchikoff 1976). Though, as for Eptesicus, aggression may apportion a larger share of the food to a dominant bat, these bats are tolerant of even habitual "scroungers" (sensu Barnard and Sibly 1981). The behavior cannot be viewed as altruistic (sensu Wade and Breden 1980, Wade 1978). In a rich patch, there is no real cost to the bat that locates the food. Even where food is limited, there may be other compelling pressures for maintenance of a group. Observations of A. pallidus (this study) show that individuals are calmer in a group and more likely to stay at a feeding site. A bat that catches prey on the ground automatically adds to its list of aerial predators, terrestrial ones. For many animals

decreased risk of predation coupled with a decrease in the amount of time any one individual must spend in vigilance (Rubenstein 1978, Pulliam 1973) can confer significant advantages on members of a group at a feeding site.

In summary, all species are stimulated to search for food when in the presence of feeding conspecifics and in some cases, other species. Information can be applied to acquisition of a novel behavior in the laboratory and in the natural environment, this learning capacity would greatly extend the potential foraging repertoire of an individual. A variety of cues may be used to monitor another bat's activity and in the laboratory, *M. lucifugus* seems to respond especially to echolocation calls while the other species show an insignificant response to this cue. Further experimentation in the field and in the laboratory may help understand these observed differences.

Bats may cope with patchily distributed food by responding to bats already at the patch and thus realize a significant saving in search time. Differences in behavior suggest fundamental differences in group dynamics between the species. Additional environmental pressures such as predation or roosting requirements may be central to observed differences between *Eptesicus* and *Antrozous*. Whatever the reasons for the differences, it

is clear that even ephemeral groups forming for identical reasons of resource exploitation are not wholly subject to the immediate demands of the resource environment but their behavior may be modified in relation to other pressures exerted on the species.

GENERAL DISCUSSION

Bats have a number of clearly definable strategies permitting them to cope with a variable environment. Thus we can look at behavioral flexibility as a complex association of discrete behavioral potentials which will be exhibited depending on the immediate environmental cues or stresses. Flexibility lies largely in ability to modify behavior in immediate response to extrinsic cues ; when memory best serves to locate food then it is the strategy adopted but when other cues are available they will be readily interpreted and used. Each bat can adjust its behavior to variations in available prey cues using spatial memory, information from other bats, sensory modalities, and to some degree by modifying aggression levels and activity levels. All of these may be seen as easily retrieved parts of the foraging repertoire which are manifested in response to feedback from the environment. The complexity of flexible responses is further compounded by the fact that ultimate reactions to extrinsic cues may not depend solely on the quality of these cues. Other pressures not directly related to the immediate conditions of food availability (i.e. social, predation, internal state) may be implicated in final reactions.

There is also a large component of "learning" involved which enables the bats to adjust to unfamiliar

and even novel circumstances. Whether the final behavior is little more than a reorganization of available or rarely used but existing abilities is not clear. Bats in this study not only learned novel tasks from other bats but quickly adjusted behavior in relation to their own experience, "learning" to cope with apparently difficult perceptual tasks, to adjust sensory modes to a highly unpredictable environment in the case of A. pallidus, and in expanding the repertoire of prey cues to which they will respond .

The capacity to adjust behavior to the immediate demands of the external environment seems enormous. Though we can establish a framework of behavior which enables an animal to cope with environmental variability, it may never be possible to understand the degree of flexibility of which an animal is capable of unless we imagine and recreate all the stresses and opportunities it could possibly encounter in its lifetime. Neither is there any answer as to what aspects of awareness or intelligence are involved in ability to modify behavior to the extent that these, and many animals can. Continued and comprehensive study are needed before we can hope to understand how an animal views its environment.

CONCLUSIONS

1. The ability of Antrozous pallidus, Eptesicus fuscus and Myotis lucifugus to deal with a patchy and unpredictable prey may depend on a number of discrete, adaptive behavioral abilities.
2. In the laboratory, a bat will react to a limited food supply by a decrease in food-searching activity. This response will be partly determined by the bat's weight and at low weights, under the same food limitation, a high level of activity is maintained.
3. When detecting an artificial prey, sensory flexibility is exhibited to some degree by all species in this study. Sounds indicative of prey as well as echolocation are used by all species. Antrozous pallidus and to a lesser extent, E. fuscus, also use vision.
4. All species respond more to general sounds of prey "movement" than to specialized prey sounds.
5. Antrozous pallidus exhibits an optional use of vision and echolocation and this sensory ability is probably associated with its gleaning lifestyle.

6. All species exhibit an ability to find food sites by memory in a confined space. More than one site can be remembered at any one time, some sites can be remembered for a long time and new sites are readily incorporated.

7. Use of habitual routes and landmarks is basic to effective use of spatial memory in this study. Eptesicus fuscus and M. lucifuqus apparently rely on echolocation for orientation in a confined space. Antrozous pallidus may use vision or echolocation dependent on light levels.

8. All species can learn a new foraging behavior through interaction with an experienced conspecific.

9. Antrozous pallidus, and E. fuscus realize a significant saving in search time when searching for a food patch in a group as opposed to individually.

10. Eptesicus fuscus is more aggressive in a confined group situation than is A. pallidus and this may point to underlying differences in basic social structure, predation or roosting requirements in the natural environment.

Table 1. Location of Low-Frequency Sounds in Displaced Target Exercise

SPECIES	SOUND	NUMBER OF TRIALS TO LOCATE TARGET			CONTROLS		NUMBER OF SITES
		CUE (target + sound)	Range	Mean	(same site)	(diff. site)	
A.p.	Scratching	1.4	1-3	40+	10+	18	
	Cockroaches	2.9	1-5	40+	10+	9	
E.f.	Scratching	1.5	1-3	40+	10+	18	
	Cockroaches	3.2	1-7	40+	10+	9	
M.1	Scratching	1.8	1-4	40+	10+	18	
	Cockroaches	5.7	2-10	40+	10+	9	
						102	

+ : target not located in given number of trials

Table 2. Long-Term Memory in Location of Targets

SPECIES	SITE	NUMBER OF TRIALS TO LOCATE TARGET		NUMBER OF TESTS			
				WITH MEMORY		CONTROLS	
				(initial conditioning)		SAME SITE (before conditioning)	
				Mean	Range	Mean	Mean
A.p.	primary long-term	1.7	1-5	40+	10+	21	
	secondary long-term	4.1	1-12	40+	10+	14	
E.f.	primary long-term	1.6	1-4	40+	10+	17	
	secondary long-term	1.8	1-5	40+	10+	20	
M.l.	primary long-term	2.0	1-7	40+	10+	14	
	secondary long-term	1.9	1-4	40+	10+	18	

† : target not located in given number of trials

Table 3. Short-term Memory in Location of Targets

SPECIES	NUMBER OF TRIALS TO LOCATE TARGET		NUMBER OF SITES	
	WITH MEMORY *		CONTROLS	
	(initial cued response)		DIFFERENT SITE	
	Mean	Range	SAME SITE	Mean
A.p.	1.1	1-2	40+	10+ 14
E.f.	5.6	1-15	40+	10+ 18
M.l.	1.5	1-3	40+	10+ 15

* number of cued responses needed before consistent location by memory

+ : target not located in given number of trials

Table 4. Response to Chewing Sounds in Displaced Target Exercise

SPECIES	TRIALS TO LOCATE TARGET		NUMBER OF SITES	
	WITH CHEWING SOUND			
	CONTROLS			
	SAME SITE		DIFFERENT SITE	
	<u>Mean</u>	<u>Range</u>	<u>Mean</u>	
A.p.	1.1	1-2	40+	10+ 18
E.f.	1.6	1-3	40+	10+ 24
M.l.	4.8 *	1-7	40+	10+ 18

* : significantly different from other species (Fisher's Exact; $p < .05$; d.f.=1)

+ : target not located in given number of trials

Figure 1.

Flowchart indicating parameters along which prey may vary
and potential behavior to cope with these kinds of
variability .

Figure 2.

The study animals.

A) Antrozous pallidus

B) Eptesicus fuscus

A

B

Figure 3.

The experimental chamber.

- A. fluorescent lighting
- B. false ceiling (nylon mesh and acoustic foam)
- C. starting point in flight path
- D. target
- E. acoustic foam false wall
- F. flight path

scale: 1:20

Figure 4.

Eptesicus fuscus: weight loss during target exercise.
Each line refers to an individual bat and circles
indicate members of group "B" (see text) and triangles,
group "A".

weight
in grams

Figure 5.

Eptesicus fuscus: weight loss and performance during target exercise. The solid circles refer to mean weight and the open circles to mean performance (time to arousal plus retrieval of 2 mealworms from target). The symbol "a" indicates maintenance weight. The arrows refer to the mean number of mealworms fed to each bat per day.

- A. Results from 4 individuals from group "A" (see text)
- B. Results from 2 individuals from "A" under extreme food limitation
- C. Results from 4 individuals from group "B" (see text)

Figure 6.

Flowchart of methodology for sensory modality (vision and echolocation). Responses are based on discrimination of a moving cue (a white disc unless otherwise specified). The sequence is repeated for each of three background conditions .

- A. non-reflective acoustic foam background
- B. solid reflective background
- C. cluttered background

Figure 8.

Target positions in experimental chamber.

Figure 9.

Apparatus for sensory modality exercises.

- A. false ceiling
- B. concrete wall
- C. false acoustic foam wall
- D. target
- E. control rod
- F. rod with disc
- G. styrofoam base and clip for mealworm
- H. cluttered background

Figure 10

Summary of results for target discriminations testing for use of vision and echolocation. Numbers represent percent response to a cue (moving disc) in various conditions . All responses are based on 180 trials. Symbols (+ or -)

represent percent echolocation production in each stimulus condition. The lower half of each square refers to response in darkness and the upper half to response in dim light. 1C is significantly different from 1F (chi-square= 18.90; $p < .05$; d.f. = 1) and 3C is significantly different from 3F (chi-square= 21.72; $p < .05$; d.f.= 1). Other important differences are included in subsequent figures.

s : response to cue significant ($z; p < .05$) when compared to response to a control.

+ : echolocation produced in more than 80% of trials

- : echolocation produced in less than 20% of trials

+ - : echolocation produced in 20% - 80 % of trials

	El	MI	Ap
	1	2	3
A NON-REFLECTIVE BACKGROUND	z=12.7 97°	z=11.0 91°	z=12.2 96°
	11.3 92°	10.5 89°	10.7 90°
B REFLECTIVE BACKGROUND	z=6.1 73°	z=9.4 85°	z=8.6 82°
	6.7 52°	7.8 79°	7.3 77°
C CLUTTERED BACKGROUND	z=2.4 59°	z=7.3 78°	z=4.0 65°
	0.0 50°	6.7 75°	2.1 58°
D BACKGROUND "B" + BLACK DISC	z=11.8 94°	nt	nt
	nt	nt	nt
E BACKGROUND "C" + BLACK DISC	z=10.1 88°	z=9.7 86°	z=11.0 91°
	nt	nt	nt
F EXERCISE "C" REPEATED AFTER "E"	z=8.1 80°	z=8.3 81°	z=10.4 86°
	6.4 74°	8.6 82°	7.8 79°
G PLEXIGLASS OVER TARGET	z=1.9 57°	48	z=10.5 89°
	nt	nt	nt
	4	5	6
	+	+	-
	+	+	+
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Figure 11.

Antrozous pallidus: response to cue (moving disc) and production of echolocation calls under different lighting conditions. The shaded bars refer to response in dim light and open bars to response in darkness. All responses are based on 180 trials. Echolocation in dim light is significantly different from echolocation in darkness (chi-square = 311.50; $p < .05$; d.f.= 1). Response to the cue is not significantly different in light and dark (chi-square = 2.859; $p < .05$; d.f.=1). The z values indicate the ability to discriminate the cue from a control in target discriminations.

A: non-reflective background

A

Figure 12

Antrozous pallidus: echolocation production during cue (moving disc) detection in dim light as related to familiarity with an exercise. Echolocation produced during initial trials is significantly different than echolocation produced during final trials in "B" (chi-square= 28.49; $p < .05$; d.f.= 1) and "C" (chi-square = 101.94; $p < .05$; d.f.=1).

B. reflective background

C. cluttered background

Figure 13

Antrozous pallidus: response to cue and echolocation production when the cue is visually cryptic vs non-cryptic. Open bars : cue is white disc on background "C". Shaded bars : cue is black disc on background "C". All responses are based on 180 trials in dim light. The response to the visually cryptic (white) cue is significantly different from that to the non-cryptic (black) cue (chi-square = 44.26; $p < .05$; d.f.=1) and echolocation production is significantly different between the two conditions (chi-square= 143.927; $p < .05$; d.f.=1). The z values indicate the ability to discriminate the cue from a control.

C. white cluttered background

C

Figure 14

Antrozous pallidus: echolocation production and response to cue (moving disc) when overlain by transparent Plexiglass. All responses are based on 180 trials. The response to the cue when overlain by Plexiglass (in dim light) is not significantly different from "normal" cue response i.e. without plexiglass (chi-square = 1.64; $p > .05$; d.f.= 1). Echolocation is significantly different between these conditions (chi-square=297.00; $p < .05$; d.f.= 1). The z values indicate the ability to discriminate the cue from a control.

A. non-reflective background

A

Figure 15

Eptesicus fuscus: response to cue (moving disc) and production of echolocation under different lighting conditions. All responses are based on 180 trials. Response to the cue in dim light is not significantly different from the response in darkness (chi-square=0.35; $p > .05$; d.f.=1) and echolocation is always produced. The z values indicate ability to discriminate the cue from a control.

A. non-reflective background

A

Figure 16

Eptesicus fuscus : response to cue (moving disc) showing relative effectiveness of echolocation in the three background conditions. All responses are based on 180 trials run in darkness. The response to the cue when against a reflective or cluttered background is significantly different from the response to the cue against a non-reflective background (B: chi-square=82.31; $p < .05$; d.f.=1 and C: chi-square=88.06; $p < .05$; d.f.=1). The z values indicate ability to discriminate the cue from a control.

- A. non-reflective background
- B. reflective background
- C. cluttered background

Figure 17

Eptesicus fuscus : response to cue (moving disc)
against reflective background in dim light and darkness .
The use of vision is indicated by the significant
difference in response between the two lighting
conditions (chi-square=18.70; $p < .05$; d.f.=1). The z
values indicate ability to discriminate the cue from a
control .

B. reflective background

B

Figure 18

Eptesicus fuscus : response to visually cryptic and visually non-cryptic cue (moving disc). Shaded bars : white disc on white background (B or C). Open bars: black disc on white background (B or C) . All responses are based on 180 trials. Use of vision is indicated by significant differences in response to white (cryptic) versus black (non-cryptic) cue (B: $\chi^2=34.08$; $p < .05$; d.f.=1 and C: $\chi^2=41.98$; $p < .05$; d.f.=1). The z values indicate ability to discriminate the cue from a control.

B. reflective background

C. cluttered background

Figure 19

All species : response to low-frequency sounds potentially indicative of prey (based on target discriminations). There is no significant difference in response to scratching ($\chi^2=1.61$; $p > .05$; d.f.=1)

or to specialized prey sounds ($\chi^2=0.61$; $p > .05$; d.f.=1) between M.l. and E.f. (relation to A.p. is inferred). There is a significant difference in response to live prey between these species ($\chi^2= 14.270$; $p < .05$; d.f. =1). The z values indicate ability to discriminate the cue (sound) from a control.

Figure 20

Analysis of "scratching" sound showing frequency components.

FFT ANALYSIS OF "SCRATCHING " SOUND

Figure 21

Potential target positions in relation to conditioned position and the ability of bats to find new locations without a cue.

- A. conditioned position
  - B. positions located without a cue
  - C. positions not located without a cue
- (see text for details of results)

6

scale: 1:20

Figure 22

Habitual route used by one E. fuscus to reach target.

- A. target in conditioned position
- B. screening over acoustic foam
- C. portion of route flown from across room
- D. portion of route crawled on screening

Figure 23

Habitual route and short-term spatial memory.

- A. Habitual route of one A. pallidus
- B. Route to new target position when cue given at "c". (route is repeated exactly in absence of cue).
- C. Effect on route of barricade at "d"
- D. Short-term route not incorporating habitual flight path.
  - a. short-term target position
  - b. conditioned target position
  - c. point in flight path when cue issued from target
  - d. barricade of acoustic foam

C

A

D

B

Figure 24

Experimental chamber for group versus individual performance in location of food patches.

- A. petri-dish
- B. starting chamber
- C. barriers of opaque plastic

scale 1 8

DISTRIBUTION OF "FOOD PATCHES"

Figure 25

Learning a novel foraging behavior .

A. Mean time and standard deviation to acquisition of new behavior through observation of a conspecific. Mean time for all bats is significantly less than controls (Welch's approximate $t = 2.56$; $p < .05$; $d.f. = 23$). The symbol "a" refers to time to learn the behavior when bats were conditioned by an experimenter; "b" to time taken by bats that did not observe trained bats (artificial limit); "c" to time at which bats were first fed to maintain weight and "n" to the number of individuals tested .

B. Response to chewing (all types) in target discrimination . All responses are based on 180 trials. The response of M.l. to chewing is significantly different from E.f. (chi-square=19.48; $p < .05$; $d.f.=1$) and there is no significant difference between A.p and E.f (chi-square=1.16; $p > .05$; $d.f.=1$).

C. Response to taped echolocation calls (all types) in target discrimination . All responses are based on 180 trials. There is a significant difference in response between M.l. and E.f. (chi-square=74.10; $p < .05$; $d.f.=1$) and there is no significant difference in response between A.p and E.f. (chi-square= 0.19; $p > .05$; $d.f.=1$)

The z values indicate ability to discriminate the cue.

CHEWING

ECHOLOCATION

Figure 26

Mean group times versus mean individual times to locate a food patch for all members of three groups in the small experimental chamber. Dark bars represent group performance.

The individual performance is significantly different from group performance for each group (Mann-Whitney U test; $p < .05$) as indicated. An approximation to the t is used because of the large n .

Figure 27

Mean group times versus mean individual times to locate a food patch for each member of one group in the large experimental chamber. Dark bars represent group performance. Individual performance is significantly different from group performance for a bat (Mann-Whitney U test; $p < .05$) where indicated.

INDIVIDUALS OF GROUP IV

Figure 28

Mean group times versus mean individual times to locate food patch for each member of one group in the small experimental chamber. Dark bars represent group performance. Individual performance is significantly different from group performance for a bat (Mann-Whitney U test; $p < .05$) where indicated.

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Appendix A

Preliminary observations suggest that a bat can remember not only the location of a previous food site but that a decision based on qualitative differences between two sites can be made.

A single 12 g E. fuscus female was placed in a circular cage of an approximate 0.5 m diameter. Mealworms were presented in petri-dishes placed 0.75 m apart at one end of the cage. In one, 20 mealworms were presented every other day (presentation "A"). In the other, 10 mealworms were presented every day (presentation "B"). The bat was allowed to search freely for the food but once a dish had been located, the other was immediately removed.

Initially the search was random i.e. no site was given preference. After the fifth day, the bat approached presentation "A" and made 4 consecutive (daily) visits to this site. On the next day, the bat located "B" and after this point, exhibited consistent preference for this site, visiting it exclusively for 7 days. Efforts to redirect the bat's path to site "A" resulted in violent protestations and a hasty retreat to the preferred site at the first opportunity.

The positions of "A" and "B" were switched so that the bat found itself approaching the inconsistent presentation, "A". After 3 days, the bat switched locations and visited only site "B" for 7 days at which point the experiment was terminated.

Why the bat chose the consistent reward is not

readily apparent from this preliminary study. At a low weight of 12 grams a period of no reward despite an expenditure of energy may be so costly as to act as strong negative reinforcement. More simply, a more consistent reinforcement schedule may aid in better memory of a location. However, when locations were switched, the bat also switched site preference after only a brief sampling period. Whatever the reason, this bat could remember not only site locations but also assimilate information as to the quality of each site and make a choice based on this information.

Appendix B

Critical and maintenance weights were established for each species through preliminary experimentation . A maintenance weight was considered to be one at which the bat was constantly motivated but in a healthy and vigorous state. Generally, this was 66% of the bats normal resting weight upon arrival from a roost-site though variations due to time (season) of capture made adjustment for each individual necessary.

Critical weights were those which bordered on a fatally low weight. For each species, this weight was approximately 55% of the resting weight (see above) . "Safe" limits were established for each species which never resulted in death if a consistent diet was maintained. Below this critical weight, bats usually died within a few days and it was assumed that all usable body fat was gone. Critical weights were used only rarely in experimentation and for most exercises, maintenance weights were effective in maintaining suitable motivation .

END

1	0	0	9	8	4

FIN