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HABITAT USE, FORAGING BEHAVIOUR, AND ECHOLOCATION BY THE
SPOTTED BAT, EUDERMA MACULATUM

by

© Martha Louise Leonard, B.Sc.

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

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ABSTRACT

Habitat use and foraging behaviour of the spotted bat Euderma maculatum were investigated by listening to its audible (below 20. kHz) echolocation calls. Its hunting calls were recorded and analyzed. The role of echolocation in spacing individuals was assessed by presenting foraging bats with a series of taped sounds. Euderma foraged in fields and Ponderosa pine clearings. They were active through all hours of the night and their foraging activity was not depressed by light rain, wind, cloud cover, or moonlight. The bats were active between 4.4 and 18.3 C. Euderma foraged in elliptical orbits in early summer but changed to a more unpredictable pattern in August. This species maintained exclusive feeding areas and its behaviour during intraspecific interactions was suggestive of territoriality. Calls produced during a hunting sequence contain search, approach, and terminal phases.

Responses by Euderma to the taped calls of conspecifics suggest a role in spacing individuals in the feeding area. The communicative function of the echolocation call is discussed.

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INTRODUCTION

The dispersion of animals in time and space is influenced by the distribution of resources in the environment and by the responses of individuals to one another (Brown and Orians 1970). Spatial relationships may be considered as a continuum extending from aggregations or coloniality at one extreme to mutual avoidance or territoriality at the other.

The foraging behaviour of aerial feeding insectivorous bats includes spacing patterns that follow this continuum. At one end of this spectrum are species which feed in large aggregations and show no apparent aggression among individuals. Myotis lucifugus is such a species, feeding in large numbers and exploiting ephemeral patches of insects (Belwood and Fenton 1976; Buchler 1976; Anthony and Kunz 1977).

Some species are flexible in their feeding distributions; e.g., Myotis grisescens (Tuttle et al. 1978) and Pipistrellus pipistrellus (Racey and Swift 1981) feed in large aggregations when insects are abundant but become aggressive towards conspecifics when insect numbers drop.

The other extreme includes mutual avoidance, e.g., Lasiurus borealis (Davis 1960), or an active defense of territory such as in Hesperoptenus tickelli (Phillips

1922), Taphozous longimanus (Brosset 1962), Myotis mystacinus (Nyholm 1965), and Saccopteryx leptura (Bradbury and Emmons 1974).

The only observations on the feeding behaviour of Euderma maculatum (Woodsworth et al. 1981) suggest that individuals of this species maintain exclusive foraging areas. If so, Euder should exhibit a regular distribution in spatial patterning. Although little is known about the spatial distributions of small insectivorous species this would represent a use of space not commonly observed.

Many bats in the Microchiroptera emit high frequency sound pulses, the echoes of which contain information used by the individual for orientation and location of food (Griffin 1958; Simmons et al. 1979). The range, structure, and use of the echolocation call vary with the species and the situation (Simmons et al. 1975). During a hunting sequence many bats characteristically alter the pulse patterns of their echolocation calls (Griffin et al. 1960) and three distinct phases are recognized. A free or search phase occurs when there is no detectable target in the flight path and the bat is searching for food. As a target is neared the bat enters an approach phase and the emitted pulses are shortened and the repetition rate increased. The terminal phase begins when the bat closes on a target. In this stage the pulses are

shortened and the repetition rate is increased further, producing the terminal or feeding buzz.

Many bats also produce low frequency "social" vocalizations during mother-young interactions (Gould 1970; Brown 1976), mating (Bradbury and Emmons 1974; Barclay and Thomas 1979), territory defense (Phillips 1922), and roosting (Goodwin and Greenhall 1961; Barbour and Davis 1969).

Recent studies have shown that some species will listen to the orientation calls of other bats and gather information about resources. For example, Barclay (1981) demonstrated that Myotis lucifugus use the echolocation calls of conspecifics to locate resources such as patches of food and roosts. Mohres (1966) also suggested that a newly volant Rhinolophus ferrumequinum listen to the echolocation calls of their mothers to follow her on first foraging trips. As these calls facilitate aggregation and resource location in Myotis lucifugus (Barclay 1981), so they may also function in the spacing of individuals in species such as Euderma maculatum.

With one exception (Woodsworth et al. 1981), information on the behaviour and ecology of Euderma maculatum is based on scattered trapping records and anecdotal observations. The discovery of a population in the Okanagan Valley of British Columbia presented an opportunity to study a seemingly unusual use and

maintenance of space by an insectivorous bat in addition to the life history of this rare mammal. With these points in mind I had three main purposes in this study: to investigate habitat use and foraging behaviour of Euderma maculatum, to describe its foraging calls, and to assess experimentally the role of echolocation in the spacing of individuals.

The Study Animal

The spotted bat, Euderma maculatum (J.A. Allen), is distinguished from all other species by the presence of three white spots on the dorsum and proportionately the largest ears of any North American bat (Fig. 1). This species ranges from northern Mexico to southwestern Canada but is considered a rare mammal in the western United States and included on the endangered species list of some states. Euderma has been trapped and observed from low desert to mountain locations (Findley and Jones 1965; Easterla 1971) and is reported to roost solitarily in high cliffs (Easterla 1965; Poche and Ruffner 1975; Woodsworth et al. 1981).

Preliminary observations in the Okanagan Valley of British Columbia (Woodsworth et al. 1981) suggest that Euderma maintains exclusive feeding areas in Ponderosa pine (Pinus ponderosa) woodland.

Although nothing is known of the foraging strategies

of this species, there is a suggestion in the literature that all large-eared bats glean their prey from surfaces (Ingles 1949; Barbour and Davis 1969; Findley 1972). It is thought that the large pinnae of gleaning bats could be used to localize sound produced by prey on the surfaces (Schnitzler and Henson 1980). One may predict then that Euderma takes insects from the ground or foliage rather than on the wing.

This species has only one young per year (Findley and Jones 1965; Easterla 1971; Poche 1981). Lactating females have been reported from June to August throughout the species' range (Easterla and Easterla 1969; Poche 1975) and specimens collected during March and April in Utah carrying mature sperm led Poche (1981) to suggest that Euderma breed in the early spring.

The echolocation calls of these bats are low frequency modulated (FM) calls sweeping from 15 to 8.6 (kHz) (Woodsworth et al. 1981). Because the echolocation call is audible to humans (below 20 kHz) it is possible to monitor directly the behaviour of the bat without the limitations imposed by the use of ultrasonic bat detectors (Fenton and Bell 1981) and mist nets (Kunz 1973a). The call of Euderma is loud to the human ear and can be detected at distances of 250 m (Woodsworth et al. 1981).

MATERIAL AND METHODS

This study was carried out between 5 May and 20 August 1981 in the southern Okanagan Valley of British Columbia, Canada ($42^{\circ}12'N$, $119^{\circ}33'W$; Fig. 2). This area ranges from 300 to 1500 m above sea level (a.s.l.) and has a mean annual rainfall of 38 cm. The vegetation is dominated by sagebrush (Artemisia spp.) and grasses in the lowlands, and Ponderosa pine montane forest (Hosie 1973) in the foothills.

Preliminary Observations

From 5 to 30 May 1981 I conducted preliminary observations on the whereabouts and behaviour of Euderma maculatum in this region. During this time I located potential roosting and feeding sites by listening to the echolocation calls of this species. To determine where and how the bats foraged, I initially spent 1 h at each feeding site recording the number of Euderma present, duration of their stay, number of feeding buzzes, and the foraging pattern. Results from these initial observations provided the basis for the design of the habitat study.

Study Sites

Habitat

I selected six study sites (Fig. 2) representative of the more common habitats in the area. They were located within 8 km of one another to allow for ready movements between sites.

1. Old field. This 0.84 ha field was 500 m a.s.l. The dominant ground vegetation was knapweed (Centaurea spp.) with patches of bunch grass (Apropyron spp.) in lower moist depressions and scattered Ponderosa pine along three sides of the field (Fig. 3).

2. Ponderosa pine/Douglas fir (Pseudotsuga menziesii) forest. This stand was 400 m a.s.l. and approximately 250 X 100 m in size. The trees were mature and 20 - 30 m high. There was little ground vegetation and the habitat was typical of a montane forest region (Fig. 3).

3. Ponderosa pine burnout. This site was 500 m a.s.l. and located on a rolling hillside covered with Ponderosa pine until a large fire in 1971. At the time of this study the area was barren, with charred tree stumps and a sparse covering of grasses and knapweed (Fig. 4).

4. Hayfield. This site was 300 m a.s.l. and located on the irrigated valley floor. The field was 12.0 ha and cultivated with alfalfa (Medicago sativa). There were numerous Ponderosa pines along the edge and a row bisected the field. Because there were three crops over

the season the height of the ground vegetation varied from several centimeters to 1 m (Fig. 4).

5. Orchard. The orchard site was 300 m a.s.l. and was bounded on two sides by a well used paved road. The orchard was approximately 0.40 ha in size and composed of 10 m tall cherry (Prunus avium) trees (Fig. 5).

6. Okanagan River. This 500 m long section of the river was 300 m a.s.l., and was bounded on the western side by a steep 100 m cliff and on the eastern side by a hayfield. The river was approximately 30 m wide at this point and fast flowing (Fig. 5).

Roost

I monitored two roost sites during the summer. Gallagher Bluff, a steep west facing cliff, was 100 m high and its base was located on the valley floor. McIntyre Bluff was an east facing bluff of approximately the same height located on the valley floor 1.2 km north of Gallagher Bluff. Both roosts had numerous ledges and crevices (Fig. 6).

Survey

A general survey was made in typical Euderma habitat, west 20 km to Keremeos and north 27 km to Penticton (Fig. 2).

Activity

Environmental Conditions

Temperature, cloud cover, windspeed, and precipitation were recorded during nightly observations. I used a minimum/maximum thermometer located at 500 m a.s.l. at the base camp, whereas cloud cover, wind speed, and precipitation were estimated and scaled on a 5, 5, and 4 point scale respectively. These categories ranged from zero cloud, wind, and rain to conditions of total cloud cover (5), and heavy wind (5), and heavy rain (4). I also recorded the phase of the moon and relative moon brightness throughout the cycle.

Behavioural Observations

Because a foraging bat produces characteristic changes in pulse patterns (Griffin et al. 1960) I have assumed that the production of feeding buzzes was indicative of feeding. Feeding buzzes were only heard when a bat was present for periods in excess of 1 min. Thus, I have assumed that if a bat was present for less than 1 min it was passing through the site rather than feeding. Finally, if the echolocation calls of the observed bat stopped then resumed within 65 seconds (based on preliminary observations) I have assumed this was the same bat and this phenomenon was termed "cessation of calling".

Because Euderma maculatum produces a loud, audible

echolocation call I could record the movements and behaviour of individuals over a 250 m range. Thus, I observed Euderma activity at the first five sites from the centre of a circle with a radius of 250 m. The water site included a section of river 250 m long up and down river from my location. Because my ability to hear the calls could be reduced in heavy wind and rain, levels of activity during these times may be underestimated.

To document nightly and seasonal patterns in foraging I monitored each study site from 21:00 to 05:00 three times a month in June, July, and August. During the 250 m sampling period I remained in the centre of a circle and recorded the number of bats present, interactions between conspecifics, duration at the site, number of feeding buzzes and a description of the foraging pattern including height and location in the site. I also recorded whether Euderma attempted aerial or surface captures of prey.

Based on preliminary observations in which 90% of Euderma sightings were within 30 min of my arrival at the site (Fig. 7), each sampling period was 30 min long. Two sites were monitored simultaneously (assistant) for 30 min and sampling was arranged such that every site was monitored for at least two half hour periods on a given night. Eight 30 min periods were completed for each site within three nights (Table 1). Levels of bat activity

were quantified by recording the time spent by the bat in an area and the number of feeding buzzes. A single foraging bout was defined as the time a bat spent feeding continuously in one location. In addition to sampling the six study sites, behavioural observations began in early May and continued throughout the summer.

In order to examine further intraspecific spacing of individuals I attempted to capture and remove bats from their feeding sites (Fig. 2). I used mist nets which were raised 10 m in the air and placed in the centre of a known feeding site. Nets were monitored continuously from dusk until 00:00 hours and captured bats were individually marked using coloured split plastic rings (A.C.Hughes) covered with reflective tape and placed on their forearms.

Observations were made 30 times at Gallagher Bluff and five times at McIntyre Bluff throughout the summer. Observations at the roosts began approximately 10 min before sunset when I would position myself at the base of the cliff and record cloud conditions, time and location of emergence and direction of departure of all bats within my hearing range. Observations also began 2 h before sunrise and the time and direction of return of each bat were recorded. The last bat was considered to have departed or returned to the roost if there was no activity for a 15 min interval.

I conducted a regional survey of Euderma distribution (Fig. 2) which included monitoring 47 sites on seven nights between 12 May and 7 August 1981. Because of the time constraints involved in sampling a large area and the results of preliminary observations (Fig. 7) I spent 10 min in "typical" (from the preliminary study) habitat. During this sample period I recorded presence, distance from the known roosts, and behaviour of observed bats.

Recordings

In order to gather a representative sample of Euderma echolocation calls I recorded vocalizations at four regularly used foraging sites, which were either open fields or Ponderosa pine clearings. The distance between the bat and the microphone varied between 20 and 50 m. Calls were recorded using a Bruel and Kjaer (B&K) 4133, 1/2 inch microphone, with a B&K 2209 sound level meter and a Racal/Lockheed Store 4D tape recorder, operated at 76 cm/second. The microphone used during taping sessions was mounted on a 10 m aluminium pole. Recording levels were monitored using a Tektronix 212 oscilloscope. A total of 37 individual calls, included within four search sequences, three approach, and two buzz sequences were slowed eight times and analyzed using a Princeton Applied Research 4513 Fast Fourier Transform

(FFT) real time spectrum analyzer. Sonagrams of representative calls were made on a Kay 7029 sonagraph. I have assumed that although the 37 analyzed calls were the "best" technically (i.e., the bat was close to the microphone) and not randomly chosen they will still represent typical calls.

Playbacks

I designed a series of playback experiments to test the hypothesis that Euderma uses the echolocation calls of conspecifics to space themselves in feeding areas. The taped calls used in the playback experiments were played on a Racal/Lockheed Store 4D tape recorder at 76 cm/s, amplified on a Realistic STA-7M amplifier and presented on KEF model T27 speaker mounted on a 10 m aluminium pole.

Playbacks were conducted between 21:00 and 05:00 on nine nights between 21 July and 20 August 1981. Presentations were made at three regular feeding sites. Since I could not identify individuals I have assumed that different bats were exposed to the playbacks at different sites. A foraging Euderma was presented with a taped call when it came within 50 m of the speaker and had been present for at least 1 min. The four 60 s presentations included: i) the echolocation call of a feeding conspecific played forward; ii) the same call

played in reverse; iii) background sounds, e.g., frog and cricket; and iv) three - ms sweeps from 15 to 9 kHz produced by an Exact 126 VCF sweep generator. The echolocation calls of feeding Euderma were recorded at study site 1 and represent the best 60 s section of a taped hunting sequence. To avoid biases due to presenting an individual with its own call or presenting neighbouring bats with a familiar call, playbacks were not conducted at site 1. In order to also avoid habituation by the bats I varied the sequence of stimulus presentations and never made more than four presentations in any session. Responses to the playbacks were recorded as i) initially positive, when the bat flew toward the speaker, ii) initially negative, when the bat flew away from the speaker, and iii) a zero response when there was no obvious change in behaviour.

Analysis of Data

The data about habitat use over the season were analyzed statistically using a Randomized Block Design (RB-3, Kirk 1968). Further analysis of seasonal differences, habitat use, and roost departures were computed using a One-Way Analysis of Variance (Sokal and Rohlf 1973). I used a χ^2 statistic to test for differences in response to playbacks, and a linear regression of feeding buzzes was determined as a function of bat time

by the method of least squares. Significance of the regression was tested using an F test. The effects of weather were analyzed using a BIOMED BMDP (Dixon 1981) computer program of multivariate regression. Standard deviations were calculated for mean values and are preceded by $\pm$ signs or are presented graphically as vertical lines on histogram bars.

RESULTS

Activity

Habitat Use

The time spent by the bats in each of the sites was compared in order to determine whether habitat use was random or whether bats foraged in some areas preferentially. Results indicated that Euderma spent significantly more time over the old field and the hayfield ($F=7.20$, $p<0.05$, Fig. 8). The remaining time presumably involved transient bats recorded as they travelled through the areas, rather than feeding. All feeding buzzes occurred at these sites and the results of a linear regression indicated a positive correlation between the number of feeding buzzes and time spent by the bat (Fig. 9). Although this linear regression is significant, the feeding buzz rate decreases with time. When these data were divided at 10 min there was a significant linear regression between feeding buzzes and time spent by the bat for time 1 - 10 min ($F = 20.1$, $p<0.01$), with a correlation coefficient (r) of 1.0. However, the linear regression between time spent and feeding buzzes from time 10 - 40 min was not significant ($F = 9.33$, $p>0.01$). The consistent use of open fields and Ponderosa pine clearings was evidenced throughout the summer during other aspects of this study. There was no

significant difference in habitat use with the season ($F=.546$, $p>0.05$, Fig. 10). When the mean times spent by the bats per month in the old field and the hayfield were combined there was no significant difference ($F=1.37$, $p>0.05$) in activity levels among the months of June, July, and August. However, when taken separately there was a significant difference ($F=9.75$, $p<0.05$) in the mean time per month spent by the bats in the old field, with a trend toward reduced foraging time per feeding session during August (Fig. 10).

Nocturnal Activity

To compare relative levels of Euderma activity throughout the night in all habitats the mean numbers of feeding buzzes and the mean bat time were determined for each hour of the night (Fig. 11). Bats were active from sunset to sunrise and there appeared to be a peak in foraging activity from 00:00 to 02:00 that accounted for 50% of the total nightly activity. Bats were active throughout the night when activity was analyzed by month to examine patterns across the summer (Fig. 12).

Environmental Effects

There was no evidence of a significant environmental or lunar effect on activity patterns of Euderma ($p>0.05$, Table 2). Bats were observed foraging over a range of

night temperatures, spanning 14°C ($4.4^{\circ} - 18.3^{\circ}\text{C}$) and were active in light to moderate showers but not heavy rain. Because the sound of the rain reduced my ability to hear the echolocation calls, this may be an artifact. Activity was not apparently affected by differences in cloud cover or wind. There was, however, little variation in wind conditions over the summer, with zero to light breezes prevailing. Euderma was active through all phases of the moon.

Foraging Behaviour

Euderma spent 68.8% (N=70) of the total observed foraging time flying in an elliptical orbit 10 m above the ground. The orbits ranged from 40 - 70 m long and from 20 - 30 m wide. The bats spent most of the foraging period flying in this manner with occasional digressions from the orbit. This feeding pattern was most obvious in May (33 of 70 observations) but did continue until the end of July. For the remainder of the total foraging time (31.2%) the bats adopted a less predictable feeding pattern, moving over a larger area and spending little time in any one spot. This pattern became most obvious in August.

The duration of each foraging session and the mean feeding buzz rate per minute was variable (Table 3), and although there appeared to be a reduction in the length

of a foraging session in August there was a corresponding increase in the feeding buzz rate.

I heard 263 feeding buzzes and never saw Euderma land on the ground, but at least 20% of the recorded feeding buzzes were accompanied by a dive to within 1 m of the ground. ^

Fifty-three percent of the time the bats stopped producing echolocation calls immediately after a feeding buzz for periods ranging from 5 - 65 s. This cessation of calls also occurred during search flight.

Intraspecific Spacing

Individual bats appeared to maintain exclusive feeding areas. Although individuals sometimes fed in the same general location, they were never observed within 50 m of one another. However, bats using adjacent areas did invade neighbouring areas when they were vacant. For example, an adult female was netted and removed from its feeding site for 2 h and during this time a second bat moved into this area and fed. The following evening the marked bat was back at the site. This invasion of feeding sites was recorded 10 times through the study period.

During the summer I observed 14 encounters between conspecifics; all of these occurred when the bats were closer than 50 m. These encounters were never between individuals on adjacent feeding sites, but rather

involved itinerant and foraging bats. In all cases one of the bats left the area, and during 71% of these interactions one or both of the bats produced what I have termed an "interaction buzz". This call involved an increase in the pulse repetition rate similar to a feeding buzz but of longer duration. Interaction buzzes continued until one of the two bats departed.

Observations at Roosts

The roost site at Gallagher Bluff was inhabited from May until August by a minimum of four and a maximum of 36 individuals. I first detected bats in McIntyre Bluff in June and never observed fewer than five or more than 11 individuals. The number of bats leaving Gallagher roost on a nightly basis was variable. However, means for May and June were similar, with a rise in numbers in July and a drop again in August (Table 4).

Euderma maculatum left the day roost an average of 48.6 min after sunset ($N = 30$, Fig. 13) and the light intensity at this time was such that I was unable to read without the aid of a lamp. All bats departed within 25 min and the departure was significantly ($F=4.55$, $p<0.05$) earlier on cloudy nights (47.0 ± 9.93 min after sunset, $N = 14$) than on clear nights (55.0 ± 5.9 min after sunset, $N = 9$). At dawn bats returned an average of 66.8 ± 12.8 ($N = 8$) min before sunrise and the time between the first

and last bat averaged 51 ± 18.9 min. Bats departed from many places on the faces of both cliffs and dispersed at 180° from the face.

Distribution

Euderma maculatum occurred throughout the southern Okanagan Valley (Fig. 2) and were observed at a maximum distance of 14 km from the known roosts. With one exception all observations were in open fields or Ponderosa pine clearings (i.e., in typical Euderma habitat). On one occasion a single bat was noted on a ridge of Douglas fir between the Okanagan and Similkameen Valleys.

Echolocation Calls

The echolocation calls of Euderma maculatum during a hunting sequence can be divided into search, approach, and terminal (feeding buzz) phases based on the categories defined by Griffin et al. (1960). The duration, power, and interpulse intervals varied with the phase in the hunting sequence (Table 5).

Search Phase

I recorded two types of search phase calls, one a single note (Fig. 14A) and the other a double note (Fig. 14B). Both were steep frequency modulated calls, with multiple harmonics in the single note call and the first

note of the double note call. There was some variation in call structure (Fig. 14).

Approach Phase

As with the search calls, the approach calls took two forms. The first was similar in structure to that shown in Fig. 14A and was a multiharmonic FM sweep, and the second a two note, FM pulse (Fig. 14C). Approach calls typically occurred immediately prior to a feeding buzz.

Terminal Phase

These calls were steep FM pulses (Fig. 14D) and the harmonics of earlier calls were dropped during this sequence.

Playback Response

Responses to the four categories of acoustic stimuli differed significantly ($\chi^2 = 28.5$, $p < 0.01$, Fig. 15). The bats' responses to the foraging call played forward were significantly different from their responses to the background noise ($\chi^2 = 27.2$, $p < 0.01$). One-third of the positive responses to the foraging call forward appeared to be aggressive displays, with the bat circling within 1 - 2 m of the speaker and producing an interaction buzz. The remainder of the positive responses were less dramatic and involved an initial approach toward the speaker upon presentation of the call.

Responses to the artificial call and the foraging call in reverse were not significantly different ($\chi^2 = 0.42$, $p > 0.05$). The responses to these presentations differed from those to the foraging call forward by the strong negative response ($\chi^2 = 10.4$ and 8.4 , respectively; $p < 0.05$, Fig. 15). However, only the responses to the foraging call in reverse differed significantly from those to the background noise ($\chi^2 = 7.91$ and 4.71 , respectively; $p < 0.05$).

DISCUSSION

Activity

Habitat Use

Information concerning habitat use by Euderma has been based on limited observations and trapping records. The bat has been netted in Lower Sonoran Life Zones (Easterla 1973; Poche and Ballie 1974; Poche 1975, 1981) and Ponderosa pine forest (Jones 1961; Findley and Jones 1965; Woodsworth et al. 1981). Results of this study indicate that these bats forage in open areas surrounded by Ponderosa pine. This relationship may be an artifact based on the abundance of these trees in this area. However, the fact that the bat did not use the open burnout area suggests the importance of the Ponderosa pine. This association may be based on i) the tendency for insects to be associated with Ponderosa pine, or ii) the use of trees for a temporary roost in which to eat food items too large to manage in flight and/or digest prey after a foraging session (Black 1974). Because Euderma did not actually forage among the trees it seems unlikely that the association between the bats and the trees was due to an aggregation of insects. However, the regular cessation of production of echolocation pulses during the hunting sequence may correspond to the bat alighting in a tree to consume prey. Such use of

temporary night roosts between feeding sessions has been observed in many temperate insectivorous bats (Cross 1965; Hirshfeld et al. 1977; Anthony et al. 1981). When one considers that many bats subsist on marginal energy budgets (Kunz 1980), and that flight metabolism for small insectivorous bats is estimated between 5 (Griffin 1958) and 30 (Studier and Howell 1969) times basal, it would be energetically more efficient if Euderma stopped near its feeding grounds rather than returned to a distant roost. The use of adjacent night roosts would also allow the bats increased foraging time over commuting time. Thus the use of Ponderosa pine as night roosts could provide a considerable saving to the bats.

Nocturnal Activity Patterns

Euderma were active over all hours of the night, with a peak between 00:00 and 02:00. Reports from the literature generally support these data, although a peak as such has not been observed. In previous studies Euderma have been netted and observed from shortly after sunset (Jones 1961; Ruffner et al. 1979; Poche 1981; Woodsworth et al. 1981) to early morning (Constantine 1961; Easterla 1973; Ruffner et al. 1979). Bell (1980) reported similar activity patterns in a community of insectivorous bats in a desert environment. Many insectivorous species have very discrete foraging peaks

(Cockrum and Cross 1964; O'Farrell and Bradley 1970; Fenton et al. 1977) however, usually coinciding with insect activity patterns (Swift 1980). In general, nocturnal insects show increased flight activity beginning before sunset and peaking near midnight, with a decline in activity after this point (Williams 1935; Morgan and Waddell 1961; Taylor and Carter 1961). Williams (1935) reported that the maximum flight activity for moths occurred near midnight. This may account for the peak in Euderma activity at this time.

Environmental Effects

I found no association between feeding activity and climatic or lunar changes. Continuing activity of Euderma over a wide range of temperatures has been noted by Poche (1981) who mist netted this species over temperatures of -3° - 28° C.

Although Euderma behaviour was not affected by wind, both O'Farrell et al. (1967) and Kunz (1973b) found reduced bat flight activity under heavy wind conditions. Because their studies relied on mist nets to assess activity, any reduction in capture success could have been due to bats avoiding billowing nets rather than to reduced activity.

Rainfall depresses bat activity under some conditions (Kunz 1974; Fenton et al. 1977), but because

many insects are active in the rain (Williams 1940; Fenton et al. 1977) reduction in activity levels may reflect negative thermoregulatory effects upon bats (Fenton et al. 1977), and in particular heat loss due to evaporative cooling. Based on behavioural (Poche 1981; this study) and physiological data (Poche 1981), Euderma appear to function well at relatively low temperatures. Through vasoconstriction of wing blood vessels the bat can reduce heat loss (Poche 1981). Because the highly vascularized wings serve as a large area for heat dissipation (Kluger and Heath) the ability to shunt blood away from this area will reduce the cooling effects of the rain and perhaps allow the bat increased foraging time.

Although Euderma were active throughout the lunar cycle, bright moonlight inhibits foraging activity in a number of tropical species (Crespo et al. 1972; Erkert 1974; Fenton et al. 1977; Morrison 1978). "Lunar phobia" is considered to be an adaptation to avoid increased predation risks from visual predators (Morrison 1978). This phenomenon appears to be less common in temperate zones (Kunz 1973b; Anthony et al. 1981) presumably because there are no known predators specializing on bats in these areas (Anthony et al. 1981). In the Okanagan, owls represent the only potential volant nocturnal predator of Euderma. At least eight species of owls occur

in the area (Godfrey 1974) but none are known to specialize on bats (Sparks and Soper 1970; Fisher 1974). I also observed no evasive tactics by the bats when I heard or saw owls in a feeding area, further suggesting that these birds do not prey on the bats on a regular basis. For this reason there may be no predation pressure on Euderma to reduce foraging activity during bright moonlight.

Foraging Behaviour

Generally, Euderma spent less time per feeding session as the summer progressed; however, a corresponding increase in the feeding buzz rate resulted in comparable feeding buzz numbers per session for each of the four months. Although the bats spent less time per feeding session in August they apparently contacted as many prey items as earlier in the season, suggesting changes in the density, distribution, and/or species of insects selected by the bats. The results of the linear regression of feeding buzz as a function of time spent by the bat, in addition to the decrease in feeding buzz rate per session suggests that fewer prey items are contacted after a certain time in the patch indicating a possible depletion of prey. The foraging pattern also changed from an elliptical orbit in the first three months to a less predictable pattern in August. This is in contrast

to the results of Woodsworth et al. (1981) who suggested Euderma switched from a rapid trapline approach in spring to spending more time per site later in the summer. Because chiropteran foraging behaviour is influenced by many factors (environmental conditions, distribution and abundance of prey, physiological state, etc.), behavioural changes can occur on a nightly basis (Fleming and Heithaus 1977; Vehrencamp et al. 1977; Racey and Swift 1981) making predictions concerning "typical" behaviour very unreliable.

Although Poche and Ballie (1974) reported a spotted bat dropping to the ground to capture a grasshopper, I saw no evidence of Euderma taking prey from the ground. My data show that the generalization relating large ears in bats to gleaning (Ingles 1949; Barbour and Davis 1969; Findley 1972) is not uniformly applicable and although large-eared Euderma does not appear to glean. Recently an alternative explanation has been advanced (Simmons pers. comm.) concerning the significance of pinna size in bats. Simmons has found a positive correlation between the length of the pinnae and the lowest fundamental frequency in the echolocation call. Thus, Euderma with proportionately the largest ears in the Chiroptera also have an extremely low frequency component. According to Simmons then, pinna size is related to the structure of the echolocation call rather than to a particular

foraging strategy. This discovery does not necessarily exclude the possibility that large ears may also serve to localize prey sound and thus be advantageous to gleaning species.

Diving by this species in association with a feeding buzz is a particularly interesting behaviour in light of the literature concerning moth hearing (Roeder 1967). Tympanate moths are capable of detecting and responding to some sounds produced by bats and will go through a series of evasive tactics culminating in a dive to the ground (Roeder 1966; Fullard 1979). It then seems possible that the drop towards the ground by the bat is an attempt to capture a diving moth. Since data from stomach and faecal analyses (Ross 1967; Poche 1981) revealed extensive use of moths by this species, such a suggestion may be valid. Not all feeding buzzes were accompanied by a drop, this suggests that either the moth did not detect the bat or the bats also feed on other insects that could not detect their calls.

Roosting Activity

Euderma appear to roost alone (Pöche 1975; Poche and Ruffner 1975) in crevices in high cliff faces (Easterla 1969; Woodsworth et al. 1981). My data confirm these reports as bats departed from many locations on both cliff faces.

If this species matures at a rate comparable to most vespertilionids (Jones 1967) the increase in numbers leaving the roost during July corresponds to the emergence of the newly volant young. The ensuing drop in August may involve the departure of females from nurseries, this would reduce competition for available resources (Stebbins 1968; Kunz 1974) or increases in density pressuring the young to disperse and find unoccupied feeding sites.

Light intensity is important in controlling the time of emergence of bats from day roosts (Erkert 1978; Swift 1980). Data from this study imply that times of emergence are related to light levels as emergence and return changed according to the time of sunset and sunrise. Thus, as Erkert (1978) suggested, the duration of the activity period is related to the length of the night. Dense cloud cover reduces light intensity by a factor of 10 (Erkert 1978) and could account for the earlier emergence observed on cloudy evenings.

Sunset related timing of emergence may be an important anti-predator strategy (Erkert 1978). That is, by emerging and returning when light intensities are low the bat reduces the time of contact with diurnal predators. Easterla (1973) observed an American Kestrel (Falco sparverius), Peregrine Falcon (Falco peregrinus), and a Red-tailed Hawk (Buteo jamaicensis) attempt to

capture a Euderma released during daylight. Black (1976) also released a single Euderma during daylight hours and observed an American Kestrel attack and capture the bat. This author noted no avoidance response by the bat and suggested that the large ears which are held forward in flight may hinder visual perception. Therefore, the emergence and return of Euderma at low light levels may be a mechanism to avert such contact.

Survey

Although the survey was limited, it indicated that the bats had dispersed at least 14 km from the known roosts. Generally, this is a rather extensive travelling distance (Bateman and Vaughan 1974; Fleming et al. 1977; Heithaus and Fleming 1978; Racey and Swift 1981) though Myotis grisescens, bats smaller than Euderma, have been sighted foraging 14 km from a roost (LaVal et al. 1977). Based on aspect ratio and wing loading, Euderma is considered to be a slow flier (Poche 1981). Thus, it seems unlikely that this species would travel 28 km on a nightly basis, suggesting the existence of other roost sites. Because the Similkameen and Okanagan Valleys have similar habitats, the presence of other populations in this area, though not verified, seems possible.

Echolocation Calls

In general, the FM structure and multiple harmonics used by Euderma during the search and early approach phase provide greater resolution in perceiving target features and locating the target position (Simmons et al. 1979; Simmons and Stein 1980). It is, however, the low frequency component that is most interesting as it distinguishes the echolocation call of Euderma from those of most of the Microchiroptera. Several factors may have contributed to the design of such a call. For instance, the wavelength, which is a function of the frequency of the call, will determine the size of prey a bat can best detect. The fundamental frequency of the call encompasses wavelengths from 27 mm (12 kHz) to 48 mm (7 kHz). Theoretically, a bat can best detect targets one-third the size of the wavelength of their call (Griffin 1958); 9-16 mm in this instance. These values correspond well to reports of Euderma feeding on moths with body lengths of 5 - 12 mm. Thus it appears the longer wavelength of this species closely approximates the size of prey in its diet. Perhaps the ability to detect relatively large insects has enabled Euderma to exploit a size class unavailable to competitors with high frequency calls and thus shorter wavelengths.

The low frequency, moderate intensity call of Euderma may also have evolved as a means of countering

detection by tympanate moths (Fenton and Fullard 1981). Bats using echolocation calls with frequencies below 20 or above 65 kHz are less conspicuous to tympanate moths (Fenton and Fullard 1981). For example, results from moth audiograms indicate the echolocation calls of Euderma would not be detected by the moth until the bat was 2 m away (Fullard pers. comm.); whereas, Myotis lucifugus, a high frequency, high intensity echolocator, can be detected at over 40 m. The low frequency call of the spotted bat may be an example of a selective pressure exerted on a bat's echolocation by the moth's ability to hear the higher frequencies (Fenton and Fullard 1981).

Finally, low frequency calls are less directional and less subject to atmospheric attenuation than high frequency calls (Griffin 1971) and therefore are well suited for long range communication purposes. For instance, the 40 kHz (frequency of maximum energy) call of Myotis lucifugus would be attenuated by 1.64 db/m whereas the 10 kHz call of Euderma would lose only 0.20 db/m. Based on atmospheric conditions, call intensity and frequency, and behavioural response, Barclay (1981) calculated that M. lucifugus could detect the echolocation calls of conspecifics up to 50 m away. Behavioural results from my study indicated that Euderma could hear other individuals within 50 m and, because the calls were audible (to me) up to 250 m away, it seems reasonable to

assume the bats were capable of hearing this distance. The greater directionality of a high frequency sound would increase the signal-to-noise ratio, yet it would be advantageous only if the signaller knew the approximate location of a potential receiver (Wiley and Richards 1978). A low frequency call would be ideal for communicating in many directions at once. If the call of Euderma does have a role in the spacing of individuals, selection should favour a call that is widely broadcast.

Just as a bat becomes more conspicuous to its neighbour, so could it alert potential predators. This may be especially important to bats such as Euderma with easily detectable calls. Although this does not appear to be a problem in the Okanagan Valley, it would be interesting to know whether the structure of the echolocation call would be similar in areas where the species was exposed to predation pressures.

There are a number of selective forces involved in the design of an echolocation call. Thus, the low frequency call of Euderma may have been shaped by a combination of social, environmental and prey pressures.

Territoriality: Observational and Experimental Evidence

Wilson (1975,p.256) suggested that "a territory was an area occupied more or less exclusively by an animal by means of repulsion through overt defense or advertisement." Defense of the resource is the diagnostic feature of most definitions. The cost to the territory owner are in defense of the area, while benefits accrue from access to a particular resource, such as mating and nesting sites or a food supply.

Because bats are volant and thus could respond quickly to intruders the defense of an area is less costly than that for terrestrial mammals. In all likelihood this defense would be similar in both cost and style to that of birds (sensu Brown and Orians 1970).

The Euderma I studied consistently maintained exclusive feeding areas, and their behaviour during encounters of conspecifics was suggestive of territoriality. Mutual avoidance, like territoriality, also achieves an even animal dispersion pattern but, does so without aggression (Myers et al. 1981) and involves no investment in time and energy (c.f., defense). That the behaviour displayed by Euderma may be more than mutual avoidance was implied by the production of an apparently aggressive vocalization during conspecific encounters and the retreat of one individual during these interactions.

Similar vocalizations have been reported for a number of bat species during territorial defense (Phillips 1922; Wallin 1961; Bradbury and Vehrencamp 1976). The notion of territoriality is further supported by the response of the bats during the playback experiments; and in particular by the seemingly aggressive response by some individuals to the taped foraging call of a conspecific. Non-territorial Euderma avoiding a potential encounter with a territory owner may account for the negative responses.

Although an isolated observation, the invasion of a vacated feeding site and the return of the individual originally using the site to the same area further supports the idea of territoriality.

Several studies have shown that feeding territory defense should occur when resources are uniformly dispersed and are predictable in time and space (Horn 1968; Kruuk 1972; Davies 1976). Theoretically, if food is patchily distributed and unpredictable a clumped dispersion is more efficient energetically, and in particular it may allow individuals to utilize the knowledge of the group to find food (Wilson 1975). Defense should also occur at intermediate resource densities (Gill and Wolf 1975; Carpenter and MacMillen 1976). That is, if food density is low it is energetically inefficient to defend an area lacking the

necessary resources. Alternatively, if food is superabundant the animal can obtain its energetic requirements without excluding others.

Euderma prey predominately on moths (Ross 1967; Poche 1981), a food source that is commonly dispersed (Peck pers. comm.), predictable, and abundant throughout the summer (Black 1974). According to theories of territoriality the most efficient use of such resources would result in the regular spacing of individuals. Based on the behaviour of bats during encounters and the characteristics of their probable food source one may predict that Euderma maculatum defends individual feeding territories.

The Use of Echolocation in Spacing

Most importantly, the results of the playbacks imply that the echolocation call, presumed to serve in detection of obstacles and prey, also plays a role in spacing individuals in feeding habitat. Bats are neurally capable of hearing the echolocation call of a conspecific while simultaneously receiving and processing their own echolocation pulses (Barclay 1981; Simmons pers. comm.). Therefore, the use of the echolocation pulse of another bat is not only possible but may confer advantages such as providing information about the location of food and roosts (Barclay 1981) or the maintenance of space (this

study). One could envisage the echolocation call of Euderma functioning in a number of ways.

The call of an individual should be easily perceived by a distant bat because of its relative immunity to atmospheric attenuation and its non-directional nature. The vocalizations may then serve as long range warning signals to advertise the presence of the bat on its territory in a manner similar to use of song by territorial birds (Peek 1972; Davies 1981) and insects (Morris 1971; Otte and Joern 1975). However, unlike the situation in both birds and insects, there is no loss of time and energy to advertisement as the bat is foraging simultaneously. Such signalling is energetically less costly than a chase and should discourage a potential intruder most of the time. Occasionally, however, an active defense of the territory would be required (Davies 1981). Such was apparently the case during intraspecific encounters of Euderma. A foraging bat could also hear the echolocation call of a conspecific and thus detect intruders in its area. The ability to use the echolocation call in this way would surely prove advantageous in a situation in which visual acuity is reduced.

In addition, if this prediction is correct and individuals repeatedly use the same feeding sites, owners should be able to recognize the calls of neighbours

versus the calls of strangers, as birds do (Emlen 1971; Brooks and Falls 1975; Kroodsma 1976). That bats are capable of individual recognition has been suggested by a number of authors (Mohres 1966; Bradbury and Emmons 1974; Findley and Wilson 1974; Fenton 1977). If a bat could distinguish between familiar and unfamiliar calls it could save time and energy otherwise spent in chasing adjacent bats that had already established a feeding territory. Such possibilities are suggested by the fact that intraspecific interactions were between foraging and itinerant Euderma and not between bats in adjacent feeding areas. This hypothesis could be tested by marking individuals and presenting a known bat with the taped echolocation calls of a neighbour and of a stranger. If this prediction is true, the bat should respond more strongly to the call of a stranger than that of a neighbour.

Finally, in a reverse sense, if an intruder were capable of finding food by listening to sounds produced by the prey (Fiedler 1979; Bell 1982; Fenton et al. 1982) and thus reducing its use of echolocation, it may then be able to exploit another's area without detection.

Communicative Function of Echolocation

Animal communication has been defined by Wilson (1975,p.176) as "an action on the part of one organism that alters the probability pattern of behaviour in another organism in a fashion adaptive to either one or both of the participants." The definition proposed by Dawkins and Krebs (1978) is more stringent and requires that the sender is "intentionally" attempting to manipulate the receiver for its own benefit.

Because echolocation involves a passive reradiation of sound rather than an active reply by a second animal, its use for orientation and prey capture is not considered communication (Griffin 1977). The question is then whether the use of an individual's echolocation call by a conspecific constitutes communication. Proving the existence of conscious intention on the part of the sender is obviously impossible in this situation. Thus for the purposes of this discussion I will assume that communication involves a response that is adaptive to one or both individuals. In the case of Euderma, avoidance of energetically costly interactions and the maintenance of feeding areas are no doubt adaptive for both, and thus constitute communication by Wilson's (1975) definition.

Clearly, in a low light situation an animal may depend on acoustic communication. Bats, with their ability to echolocate, present an unique situation in

which orientation and food detection are also acoustic. For this reason, the incorporation of two functions (i.e., communication and orientation/prey detection) into one signal seems feasible. In fact, because both can be carried out simultaneously, such a system should be energetically efficient. This may be especially advantageous to a territorial species, which could forage and advertise at the same time.

The dual nature of a signal has also been recognized in many species of electric fish. The electric signals emitted by these fishes were originally thought to function solely in orientation and object location, but further research revealed a communication component used in territory defense (Black-Cleworth 1970) and mating (Hopkins 1974).

Many of the communicative sounds of bats are non-echolocative vocalizations. Thus, it is generally assumed that information transfer between individuals occurs only in this context. Because most bats echolocate and they also tend to be gregarious animals, I suspect that the communicative capacity of the echolocation call is widespread throughout the Microchiroptera. In light of recent studies (Barclay 1981; this study) it would be interesting to examine the social role of echolocation in other species. Although unknown, one would predict that such a system may be well

developed in those species that forage in structured groups (Howell 1979) or maintain group feeding territories (Wallin 1961).

Euderma maculatum is one of few vespertilionids known to consistently maintain exclusive feeding areas. Such a spatial distribution is not often encountered in small insectivorous species. This rather unusual spacing pattern is presumably based on the diet of this species which appears to specialize on dispersed insects. More detailed information concerning spacing in these animals will depend on capturing and marking individuals.

The use of echolocation for social purposes has long been neglected (Sales and Pye 1974) and this study represents the first demonstration of its use in the spacing of individuals. The discovery of this additional function of the echolocation call enhances our knowledge of this complex system and encourages further investigation into the role of echolocation.

CONCLUSIONS

1. Euderma maculatum foraged in open areas characterized by Ponderosa pine and roosted in high cliff faces.
2. There was no significant change in foraging time between May and August.
3. Euderma foraged throughout the night and activity was not significantly affected by moonlight, temperature, wind, or rain.
4. Individuals maintained exclusive foraging areas and may defend feeding territories.
5. Echolocation calls have search, approach, and terminal phases typical of insectivorous bats. Calls are of low frequency (12-7 kHz) and may be the result of a combination of selective pressures.
6. Euderma always responded to presentations of taped foraging calls of conspecifics, suggesting a communicative function for the echolocation calls perhaps related to spacing of individuals.

TABLES

Table 1

Tabular representation of the habitat sampling schedule.

Hours of the night	<u>Study Sites</u>					
	1	2	3	4	5	6
21:00 - 22:00	A	A	B	B	C	C
22:00 - 23:00	A	A	B	B	C	C
23:00 - 24:00	C	C	A	A	B	B
00:00 - 01:00	C	C	A	A	B	B
01:00 - 02:00	B	B	C	C	A	A
02:00 - 03:00	B	B	C	C	A	A
03:00 - 04:00	A	A	B	B	C	C
04:00 - 05:00	A	A	B	B	C	C

Two sites were sampled simultaneously for 30 min. The total sampling period took three nights. A = night one, B = night two, C = night 3.

Table 2

Correlation coefficients for the effects of climatic and lunar variables on foraging time of Euderma maculatum.

Temp.	Wind	Cloud Cover	Precip.	Lunar Phase
-0.071	-0.019	-0.061	-0.014	-0.014

Critical r value ($r_{.05}$) = 0.115, df = 281.

Table 3

Mean length of foraging bouts and the mean number of feeding buzzes per minute by month for Euderma maculatum.

Month	N	Mean FD	N	Mean FB rate/min
May	37	11.6 $\pm$ 10.6	37	0.379 $\pm$.114
June	23	11.0 $\pm$ 8.4	23	0.305 $\pm$.209
July	31	10.1 $\pm$ 8.9	19	0.440 $\pm$.224
August	19	6.9 $\pm$ 5.3	12	0.632 $\pm$.412

FD = length in minutes of a continuous feeding session

FB = feeding buzz

N = sample size

Table 4

Mean number of individuals leaving Gallagher Roost
per month

Month	N	No. of bats	Range
May	11	12.0 ± 9.7	(4 - 30)
June	8	16.4 ± 7.9	(11 - 36)
July	5	23.6 ± 3.8	(18 - 27)
August	3	10.3 ± 3.2	(8 - 14)

N = number of observations.

Table 5

Mean time and major power peaks for the call of Euderma
maculatum

Call	N	Duration (ms)	N	Power Peak (kHz)	N	Interpulse Interval (ms)
Search (Single)	7	6.75 $\pm$ 0.42	7	9.8 $\pm$ 0.27	15	365 $\pm$ 3.09
Search (Double)	7	a) 7.87 $\pm$ 0.627 b) 5.99 $\pm$ 1.1	7	a) 10.8 $\pm$ 0.71 b) 9.1 $\pm$ 0.23	6	320 $\pm$ 2.98
Approach (Single)	11	4.32 $\pm$ 1.2	11	8.3 $\pm$ 0.34	5	180
Approach (Double)	8	4.7 $\pm$ 0.47	2	8.8	2	128
Terminal	4	3.4 $\pm$ 0.45	4	8.63	3	60

When results did not vary standard deviation was not recorded. The double-note calls in the approach phase were identical. N = number of calls analyzed.

FIGURES

Figure 1

Portrait of the study animal, Euderma maculatum.

Figure 2

Map of the study area.

Numbers refer to study sites 1 through 6, X represents all sites where Euderma was observed, and O the general vicinity of surveys.

GR = Gallagher Roost, MR = McIntyre Roost and N = netting sites.

The darkened lines represent roads.

Inset: ★ location of the study site.

Figure 3

Photographs of study site 1, the old field and study site 2, the forest.

1

2

COLORED PICTURES
Images en couleur

Figure 4

Photographs of study site 3, the burnout, and study site 4, the hayfield.

3

4

COLOURED PICTURES
Images en couleur

Figure 5

Photographs of study site 5, the orchard, and study site 6,
the Okanagan River.

5

6

COLOUR PICTURES
Pages en couleur

Figure 6

Photographs of the roost sites. (a) Gallagher Bluff, the main roost, (b) McIntyre Bluff.

a

b

COLOURED PICTURES
Images en couleur

Figure 7

Histogram representing the interval of time between the arrival of the observer at a site (time 0) and the arrival of a bat. This information is based on 73 sightings from 5 to 30 May 1981 and is a sum of the total number of bats arriving in each time interval. The points joined by the line represent the total number of bats recorded at time 0, 5, 10, etc.

Figure 8

Patterns of habitat use by Euderma maculatum. Bars represent the relative time spent in the six habitat types. N_1 = total number of observations, N_2 = total number of times a bat was observed (this refers to the presence of the bat only and is not indicative of time spent).

Percent time is the percent of the total time spent by Euderma in the six sites.

OF = old field, HF = hayfield, R = river, BO = burnout, F = forest, and O = orchard.

Figure 9

Relationship between the number of feeding buzzes and the time spent foraging in minutes by Euderma maculatum. The correlation coefficient is significant ($p < 0.01$, $N = 62$).

Figure 10

Levels of Euderma activity by month. Each bar represents the percent by month of the totaled mean times, in min, spent by the bats in the six study sites (N = 18).

Inset: percent by month of the mean time spent by Euderma in the old field (Site 1).

Figure 11

Nightly activity patterns over the season. The bars represent the mean number of feeding buzzes ($N = 64$) and the mean time spent, in min ($N = 55$) for each hour of the night for all sites, from May until August. $N =$ the number of observations.

Figure 12

Nightly activity patterns per month. A bar represents the mean time spent, in minutes, for each hour of the night for all sites from May until August.

▲ = sunset and sunrise

TIME SPENT

Figure 13

Relationship between sunset time and the time of emergence of the first Euderma (N = 30).

N = the number of observations made at the ro~~cks~~ts.

- = overcast
- ◐ = partly cloudy
- = clear

Figure 14

Tracing of sonograph of representative calls of the search phase (A,B), the approach phase (C), and the terminal buzz (D), echolocation calls of Euderma maculatum.

Inset: represents the variation (two forms) found in the structure of the fundamental note of calls A and B.

Figure 15

Comparison of responses to sound presentations by Euderma maculatum. Each histogram represents the percent of responses that were initially positive , initially negative , and a zero response .

BN = Background noise, FF = Foraging call forward, FB = Foraging call backwards, A = Artificial call.

Percent resp. = Percent response, N = the number of responses.

Inset: results of statistical analysis. Numbers represent sound stimuli and X responses were significantly different and NS responses were not significantly different, using a χ^2 test.

	1	2	3	4
1	—	X	X	NS
2		—	X	X
3			—	NS
4				—

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