FORAGING FLEXIBILITY IN THE PALLID BAT
(Antrozous pallidus)

David Stanley Johnston

A thesis submitted to the Faculty of Graduate Studies in partial fulfillment of
the requirements for the degree of

Doctor of Philosophy

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ABSTRACT

I analyzed fecal samples from tagged, individual adult male pallid bats (Antrozous pallidus) during the summers of 1993 and 1994 from a colony on the California coast and from a colony in Death Valley for the summers of 1994 and 1995. A comparison of pooled dietary data from individuals with the diets of these same bats treated as individuals suggested a generalist group with specialized individuals in the coast population and a generalist group with generalized individuals in the Death Valley population. Coastal bats did not significantly change their diets temporally during summer months, but the Death Valley bats did. Both groups ate different prey than arthropods caught in pit traps, suggesting both populations are selective foragers. I captured 6 of the individually-tagged bats from the coast and 5 of the individually-tagged bats from Death Valley, each with known dietary histories, to test for differences in learning abilities and foraging behaviour at the individual and population levels. Latency rates of learning and searching behaviour were measured for 3 foraging tasks in a laboratory situation for each of the subject animals. The coastal bats from an environment with more uniform prey had significantly faster latency rates of learning than the Death Valley bats from an environment with more patchy prey. Coastal bats did not show significant individual differences in latency rates of learning, but Death Valley bats did. 5 types of search behaviour were compared at the individual and population levels, and Death Valley bats spent more time roosting and spent less time on the ground during searches than coastal bats. Two behavioural foraging styles exist in the captive coastal bats which I correlated to dietary preferences. Bats from Death Valley did not show significant individual differences in foraging styles although there may be a weak relationship between diet and time spent crawling. I tested naive non-volant juveniles for an affinity to low frequency sounds, but my results suggested that adult bats' attraction to low frequency sounds is learned.

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Chapter I.

Introduction

Foraging Flexibility

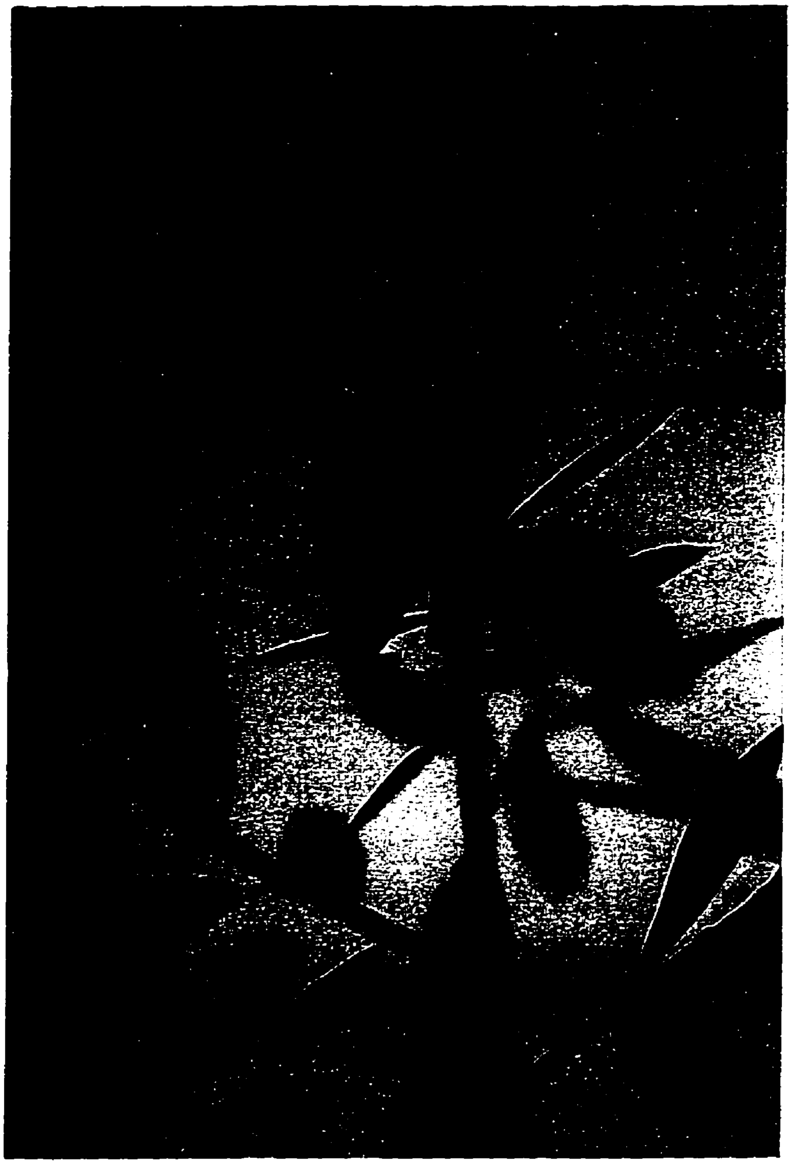
Aspects of individual foraging flexibility have been described in social insects (e.g., Heinrich 1979, Gordon 1991), in fishes (e.g., Dill 1983; Ehlinger, 1990; Kieffer and Colgan 1991; Magurran 1986), in birds (e.g., Greenberg 1983; Valburg 1992) and in some mammals (e.g., Henry 1986; Mills 1990; Terbourgh 1983). Most studies on foraging flexibility in bats have been limited to comparisons among populations of a species (Bell 1982; Belwood and Fenton 1976; Brigham 1989; Herrera et al. 1993) or laboratory studies comparing learning abilities in bats (Gaudet 1982). To avoid the confusion presented in the literature by different authors' use of the term flexibility in reference to adaptability in populations versus "flexibility" in individuals, I define foraging flexibility as the ability of an individual to increase its fitness by modifying its foraging behaviour through learning.

Bell (1982) observed some foraging flexibility in pallid bats (Antrozous pallidus) in the field while Gaudet (1982) tested some of their limits of flexible foraging behaviour in a flight room. While both authors have contributed to our understanding of the limits of flexibility in pallid bats, there has been little empirical work on the evolutionary basis for flexible foraging behaviour in bats. Today there is no systematic way of measuring flexibility although indices of dietary breadth have been suggested by Emlen (1974) and Fleming (1988). Therefore we need to know how to measure flexibility, which populations have developed flexibility, and what environmental pressures promote flexibility if we are to understand this evolutionary process.

Pallid bats (Antrozous pallidus) (**Fig. 1**) may be excellent candidates for the study of foraging flexibility because they are long-lived (e.g., longevity can exceed 11 years, Sidney pers comm.) and therefore, may be capable of learning new foraging strategies as a means to improve fitness (Kamil 1988). Pallid bats feed on different prey in different parts of their geographic range (e.g., sphingid moths in southwest New Mexico, Bell 1982; scorpions in Monterey, California, Orr 1954; Jerusalem crickets in San Jose, California, Johnston 1992). Do these differences in dietary preference result from genotypic selection in populations for different responses to environments, or do they reflect each individual's ability to learn in response to different prey types?

If the former is true, individuals from the same colony should all have the same dietary preferences since the environment should select a fixed genotype. A possible example where genotypic selection would operate in different directions in different adjacent patches is the slug-eating snake, Thamnophis elegans. An analysis of a slug-eating response by newborn T. elegans showed geographic variation in behaviour with a genetic basis (Arnold 1981). Two

Fig. 1. Male pallid bat (Antrozous pallidus pacificus) crawling down a willow (Salix lasiolepis) to gain access to prey.



conspecific populations of *T. elegans*, a coastal and an inland race, were tested for their response to different prey including the slug *Ariolimas californicus*. The coastal snakes were terrestrial foragers, eating mainly slugs; the inland snakes were aquatic foragers taking fish and amphibians. Although both populations were polymorphic for the slug-eating tendency, the slug-eating morph predominated in the coastal population, and the slug-refusing morph in the inland population. The slug-refusing morph starved to death if offered only slugs. In mollusk-rich environments in coastal California, where the slug-eating habit evolved, slugs constituted 90% of the diet (Arnold 1981).

If, however, the latter is true, then each member of a colony would exhibit phenotypic plasticity and eat according to learning experiences. An example where phenotypic plasticity allows an organism to forage on different prey in different environments is the common raven (*Corvus corax*) that exhibits exploring and learning ability to sample new foods in different environments (Heinrichs 1995).

When a species becomes adapted to feeding on a few select types of food, it is considered a specialist or stenophagic while food generalists are considered euryphagic (Emlen 1973). The red tree vole (*Arborimus longicaudus*), which occurs in California, feeds exclusively on the needles of Douglas Fir (*Pseudoseuga menzisii*) (Jameson 1988), and black-footed ferrets (*Mustela nigripes*) from the west central plains in United States eat only prairie dogs (*Cynomys* leucurus) (Seal 1989). Mammals with specialized food habits are also not restricted to small mammals. The giant panda (Ailuropoda melanoleuca) feeds solely on bamboo shoots, and the sperm whale (Physeter catodon) feeds almost exclusively on cephalopods (Vaughan 1972). Such species are obligate specialists and their populations are at much greater risk of crashing since they depend upon a narrow diet. For example the brant (Branta bernicla), a goose found along the east coast of North America, underwent a population decline of about 80% when its single food source, eel-grass, suffered from a blight in 1931-1933 (Moffit and Cottam 1941).

Food generalists such as the opossum (Didelphis virginianus) may eat anything they can find and digest (Vaughan 1972). Other mammals exhibit euryphagic behaviour even though their dentition might be generally classified as either carnivorous or herbivorous. Red foxes (Vulpes vulpes) seem to be very proficient at capturing small rodents, but they also take large numbers of insects, occasionally deer, birds and many species of plants (Henry 1986).

Emlen (1973) suggested the following possible evolutionary pathway for stenophagy: if one food is more available than another and both have equal nutritional value, a predator will probably eat more of the available food. As that food is eaten more frequently, the predator should become better at foraging on that item. The more one type of food is consumed, the more efficient the consumer will become at finding, handling (if necessary), and digesting the food item. As long as that food is available, the consumer will continue to specialize on it at the expense of efficiency in eating other items. Specialization has made one food item more valuable than another and thus the consumer will show a preference and will ultimately digest that item more efficiently (Emlen 1973, Hughes 1993).

Temporal heterogeneity is an important deterrent to the evolution of food specialization, but there are several ways organisms can overcome patchiness in food distribution over time or space. Specialists may survive where foods become abundant or rare over time by hibernating, aestivating, encysting or diapausing. Mobile vertebrates can migrate. An organism may change its food preference and distribution between patch types with the seasons as evident in exotic populations of Barbary Sheep (Ammotragus lervia) (Johnston 1980).

Pianka (1974) suggested that species that are food limited should seldom be food specialists. Regardless of the size of a species, it should broaden its diet as the environment becomes more heterogeneous. Animals inhabiting changing environments are less likely to be food specialists. Species should become generalists as their prey become increasingly patchy in time or space. As a population experiences unreliable food sources, it should become increasingly flexible in order to accommodate the changes in available food types. Consistent narrow specialization such as that found in black-footed ferrets or red tree voles should be rare because of initial nutrient imbalances, and the vulnerability it presents the species as an obligate specialist (Pianka 1974).

Greenberg (1984) found evidence in the foraging behaviour of warblers that suggested that foraging habitat neophobia may contributed to specialization by certain migrating warblers. Aversion to new situations by Chestnut-sided warblers suggested that this neophobia may present an evolutionary pathway for specialization Greenberg (1984). In contrast, Greenberg (1984) observed that Bay-breasted warblers were dietary generalists and showed little hesitation in approaching novel situations. The Bay-breasted warblers exhibited individual flexibility and Greenberg (1984) suggested that this allowed this species to overcome spatial patchiness in prey distribution. Having to learn to detect, capture, and handle prey could skew the relative currency value of prey items creating individual preferences for different prey (Hughes 1993).

In San Jose, California, I observed four dead chewed, exotic, slugs (Derocerus sp.) below a night roost of pallid bats (Johnston, 1992). Although slugs are a regular component of the diets of other vertebrates, (e.g., Corbet and Southern 1977, Boycott 1934, South 1980), slug eating has not previously been reported in bats. Slug capture by the San Jose colony of bats may help to provide some insight into the mechanisms responsible for the development of foraging flexibility. Does a given population of bats regularly take slugs? Is slug-taking a manifestation of flexible behaviour exhibited by inexperienced juveniles? Is retrieval and chewing slugs a normal behaviour for a certain age and sex of pallid bats to obtain an otherwise limited element such as calcium?

Pianka (1974) suggested that members of populations which forage on patchy prey populations should have phenotypic plasticity allowing them to adapt to whichever patch they are in at any given time. If pallid bats' dietary preferences reflect phenotypic plasticity, each member of a colony could develop individual preferences for specific prey types as a function of experience and learning, as suggested for other animals by Dill (1983), Hughes (1993), Johnston (1982), and Kamil (1987) in the aforementioned mechanism described by Emlen (1973). Now each individual that developed specialized diets could continue to improve specific foraging behavioural skills through the same mechanism. Ultimately, differences in foraging style may develop as in oystercatchers (Haematopus ostralegus)(Goss-Custard and Sutherland 1984) or in roof rats (Rattus rattus) (Terkel 1996) (See Chapter III). Since prey species for pallid bats (i.e., scorpions, moths, crickets, etc.) should require different handling skills, I would expect an animal exhibiting individually specialized diets to also develop different skills and methods of capture.

Perhaps pallid bats have a "sensory template" such as the song template described by Marler (1976). Such a template in pallid bats might include low frequency sounds made by terrestrial or flying prey. The flexibility to investigate each low frequency sound would ensure that the bat could take advantage of ephemeral populations of prey. As the bat becomes more hungry, motivation and flexibility increase as described by Dill (1983) in sunfishes and Gaudet (1982) in three species of North American bats. As long as the flexibility remains in the framework of the template, the bat is likely to exhibit foraging flexibility. This might help explain how the bats in San Jose started taking an exotic slug and why some bats in the laboratory, when hungry, try new prey types.

An example of a partly learned flexible behaviour was described by Marler (1976) who identified a developmental mechanism for songbirds such as the white-crowned sparrow. He found that exposure to a song model was required for normal song development but the model had to be a species-typical song or a close approximation; atypical songs were not learned. From an evolutionary point of view, such a mechanism may be expected because it protects the system from the consequences of responding to inappropriate environmental stimulations. Thus it is advantageous for a white-crowned sparrow to learn the song dialect of the community in which it was born, disadvantageous for it to inadvertently learn the song of some other community which would reduce its chances of subsequently finding a mate and reproducing (Baptista and Petrinovich 1984). In mammals, Garcia and Koelling (1966) observed a similar mechanism in Norway rats (Rattus norvegicus). Apparently, the rat's brain is only partially genetically "hard wired" for particular associations such as between taste and gastric illness so that learning for specific associations is facilitated

(Garcia and Koelling 1966). The template concept may be useful in describing bats' learning behaviour since this is not well understood in bats and little empirical work exists (Altringham 1996). In my search for such a mechanism in bats, I decided to investigate the possible affinity for low-frequency sounds by naive, volant juveniles.

In 1992, the California State Fish and Game Department listed pallid bats as a species of special concern. Olfert et al. (1993) suggested that it's important to maintain the psychological well-being of study animals when conducting behavioural research in a laboratory, but to my knowledge, there exists little if any information in the literature regarding the well-being of captive bats (See Appendix I). I therefore wanted to limit my impact on the bats' well-being as much as possible to reduce confounding variables and to successfully return them back into the wild. Since pallid bats in captivity for 6 years appeared unmotivated to complete tasks, I decided to test the latency rate of learning for these long-term captives to determine if learning ability decreases after long-term captivity.

The North American desert climatic regime is more variable than the Pacific Coast climatic regime (Felton 1951). In response, insect populations may be more ephemeral in more heterogeneous climates than homogeneous ones. I therefore chose to compare diets, learning abilities, and searching behaviours at the individual and population levels of a colony along central coastal California with a more uniform climate and a colony at Death Valley with a more patchy climate.

Hypotheses

I made 3 hypotheses about pallid bats diet and 4 hypotheses about their foraging behaviour.

In Diet:

1). Pallid bats with a uniform distribution of prey should be more specialized in their diet than pallid bats with a more patchy distribution of prey.

2). Pallid bats exhibit individual dietary preferences.

3). Naive pallid bats attempt slug eating, and reject the slug as unpalatable.

In Foraging behaviour:

1). Individuals within populations of pallid bats with more patchy prey will exhibit more flexibility (i.e., they will learn faster) than individuals within populations with more uniform prey.

2). Pallid bats show differences in individual foraging strategies (i.e., there will be measurable differences in the amount of time each bat spends in various types of searching behaviour).

3). Long-term captivity bats would have lower latency rates of learning than wild bats recently acclimated to a laboratory situation.

4). Naive, volant juvenile pallid bats will investigate low frequency sounds when searching for food.

Natural history of species

Pallid bats have forearm lengths of 48-60 mm, weigh from 14 g.to 24 g., and females are larger than males. Pallid bats occur in most of the Sonoran life zones in the southwest United States, north to southern British Columbia, south to the states of Jalisco and Queretaro in Mexico, and from the Pacific coast east to Oklahoma. They are most common in desert regions with rocky outcroppings and water (Orr 1954). Hermanson and O'Shea's (1983) summary of roost data indicated that pallid bats roost in small colonies in rock crevices and man-made structures.

Like other vespertilionids, pallid bats are heterothermic, so their body temperatures approach ambient temperature when they are inactive (Licht and Leitner 1967; Trune and Slobodchikoff 1976). Trune and Slobodchikoff (1976) found that pallid bats at low temperatures showed a decrease in metabolism, and Brown et al. (1978) reported a hearing sensitivity decrease and shift toward lower frequencies for pallid bats at lower temperatures. Licht and Leitner (1967) found that pallid bats exhibit stable body temperatures of 36° - 38.5° C in ambient temperatures of 35° - 36°C. Although Licht and Leitner (1967) reported that pallid bats can maintain their body temperatures at 40° to 41.5° C at ambient temperatures of 39° C, they did not investigate bats producing their own heat through an activity such as flying. Prolonged exposure to temperatures of 43.5 C and above is lethal (Licht and Leitner 1967). Chew and White (1960) found that pallid bats, tested at higher metabolic rates, lose twice as much water when wings are extended as when they are folded.

Copulation begins in October and continues through December (Orr 1954), and in some populations until February (Barbour and Davis 1969). Mating occurs both on horizontal surfaces and when bats are hanging upside down (Orr 1954). Sperm is stored in the uterus through the winter, and ovulation and fertilization occur in early spring. Gestation is influenced by local climate and ranges between 53-71 days (Orr 1954), so that parturition tends to occur in May and June in the southwest U.S. (Hermanson and O'Shea 1983). Findley et al. (1975) reported an average of 1.8 newborn per litter in New Mexico whereas Orr (1954) and Twente (1955) reported two young per litter in northern California. Triplet embryos have been recorded by Hall (1946) and Orr (1954).

Lactation occurs from early May through mid-August (Martin 1974). Foraging females leave the young behind but return frequently to attend to them (Beck and Rudd 1960; O'Shea and Vaughan 1976). Young are weaned between 6 to 8 weeks of age (Brown and Grinnell 1980), and Orr (1954) reported that captive young began to accept insect food at age 6 weeks, the age of development for permanent dentition and the ability to fly.

The ears and eyes of newborn pallid bats are closed. Neonates do not respond to auditory stimuli (Brown et al. 1978). The pinna unrolls and the tragus is abducted from the external ear opening at 8 to 10 days (Orr 1954). Auditory evoked potentials cannot be detected in bats younger than 6 days and do not begin to resemble adult patterns until 8 to 12 days of age (Brown et al. 1978). The authors explain that only low frequency sounds within the range of female communication calls elicit responses from 6 to 8 day-old bats, but by 12 days of age, the frequency range of responsiveness approaches that of the adult resolution and is developed by the time of first flight. In the wild short flights begin at 4 to 5 weeks of age and echolocation calls are similar to those of adults but with lower frequency elements (Brown et al. 1978). By 5 to 6 weeks, the echolocation calls of young and adults are indistinguishable, and by 7 weeks nocturnal activity patterns are similar (Brown and Grinnel, 1980).

Pallid bats have been observed to feed on the following prey: scorpions (Vejoridae), ground crickets (Gryllacrididae). Jerusalem crickets (Stenopelmatidae), solpugids (Solpugida), darkling ground beetles (Tenebrionidae), scarab beetles (Scarabaeidae). predaceous ground beetles (Carabidae), carrion beetles (Silphidae), short-horned grasshoppers (Acrididae), cicadas (Cicadidae), katydids (Tettigoniidae), praying mantis (Mantodea), long-horned beetles (Cerambycidae), and sphingid moths (Sphingidae) (Hermanson and O'Shea 1983). In addition, there are rare accounts of vertebrates being taken in the wild. Bell (1982) observed a pallid bat carrying a pocket mouse (Perognathus flavus) and O'Shea and Vaughan (1976) reported an iguanid (Phrynosoma douglassi) as prey.

Tocaloma Study Area

The Tocaloma colony is located in the small community of Tocaloma in Marin county, California (**Fig. 2**). The maternity roost is in an old home located along Mill Creek about 70 m from a bridge roost which at night is often 7° C warmer than ambient temperature. The Tocaloma colony numbers over 100 and consists presumably of females and first-year born. I found pregnant female pallid bats from early June to early July, and I observed a single young being carried by a mother on two occasions in this population. The only other recorded site with more than four individuals in a hibernaculum was reported by Twente (1955).

Plant communities within a 7 km radius of the observed Tocaloma population roosts include valley grassland, oak woodland, Douglas fir - redwood forest, coastal sage scrub, and riparian habitat. Grassland covers the majority of the Tocaloma study area (**Fig. 3**), and generally occurs on the deeper, heavier soils except on north slopes, where oak woodland or Douglas fir - Redwood forest predominate. Before overgrazing and the introduction of European grasses in the nineteenth century, the perennial purple needle grass (Stipa pulchra) and wild rye (Elymus glaucus) were probably the dominant species here. Oak woodland is distributed along first order riparian systems and on north slopes in the region. On southern exposures, grasses occur as an understory. There is no understory in

Fig. 2. Location of the two study colonies of pallid bats (A. p. Pacificus) at Tocaloma and (A. p. pallidus) at Caliente Mine.

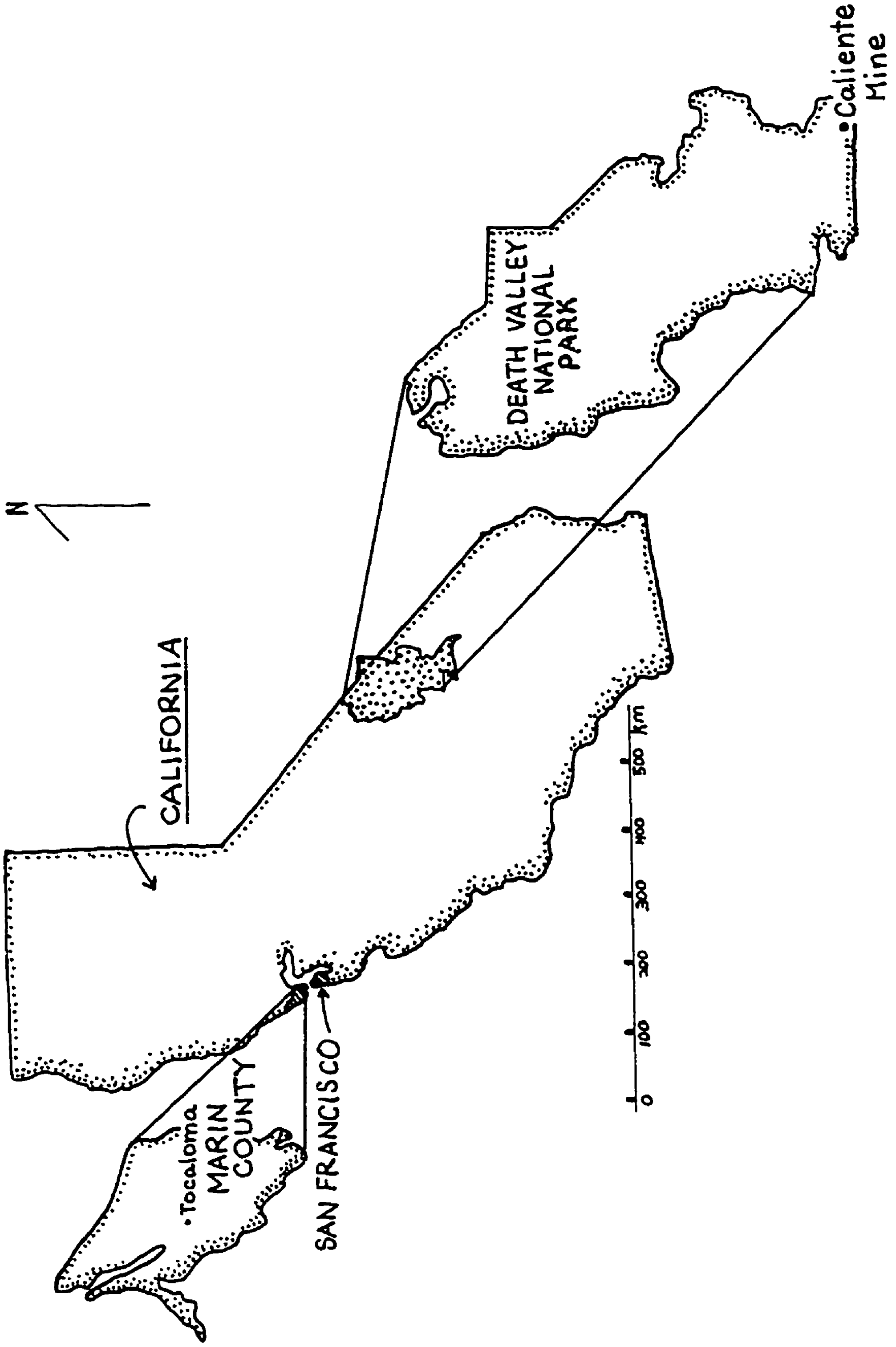

CALIFORNIA
N
DEATH VALLEY NATIONAL PARK
•Caliente Mine
•Tocaloma
MARIN COUNTY
SAN FRANCISCO
0 100 200 300 400 500 km

Fig. 3. Photograph of the predominant habitats of the Tocaloma study area.

the stream canyons, but forbs, shrubs, and some grasses occur under the oaks on the north slopes. Coastal sage scrub is found lining the insides of some coastal canyons on the lower slopes, but is usually limited to patches in the summer fog belt on rocky or thin soils. Species composition varies and there are pure stands of coyote brush. Douglas fir - coast redwood forest is found primarily on the western edge of the study area on north slopes. Mill Creek is a perennial creek flowing north through the study area forming a riparian community Rocky outcroppings among grasslands also become important foraging habitats for pallid bats. Table 1 provides a species account for plants found within these habitats.

The Tocaloma study site has a Mediterranean climate with wet, cool winters and warm, dry summers. The Pacific Ocean has a stabilizing effect on temperature and increases the precipitation with the aid of the Coast Ranges. Bolinas Bay is 8 km to the northwest, and Drakes Bay is 9 km to the southwest with Inverness Ridge between acting as a buffer to prevailing winds. A weather station 8 km to the east at Hercules Fire Station offers general information about the climate. Summer days were warm and evening temperatures consistently cooled down to 7° C to 12° C each night **(Fig. 4)**. Rainfall generally occurred during winter months October through May **(Fig. 5)**.

Caliente study area

The Caliente bat colony is located in the southeastern part of

Table 1. Plant species found in the Tocaloma Study Area

Valley Grassland
  Italian rye grass (*Lolium multiflorum*)
  soft chess (*Bromus mollis*)
  slender oat (*Avena barbata*
  fat oat (*Avena fatua*)
  false brome (*Brachypodium distachyon*)
  foxtail (*Hordeum sp.*)

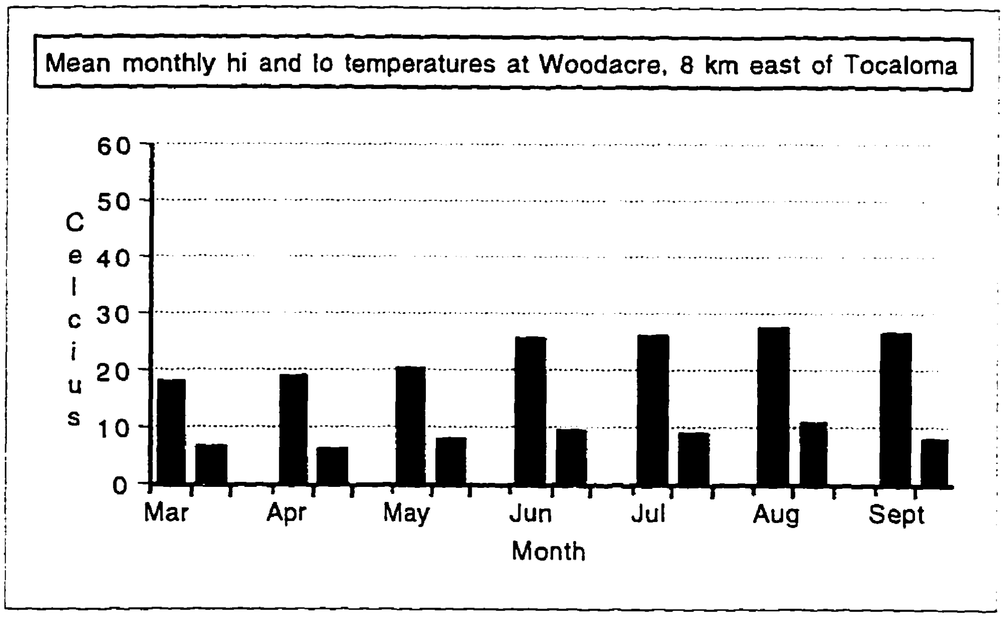
Oak woodland
  Coast live oak (*Quercus agrifolia*)
  valley oak (*Quercus lobata*)
  California laurel (*Umbellularia californica*)
  poison oak (*Toxidendron diversiloba*)
  gooseberry (*Ribes sp*.)

Coastal sage scrub
  California sage brush (*Artemesia californica*)
  coyote brush (*Baccharis pilularis*)
  California buckwheat (*Eriogonum fasiculatum*)

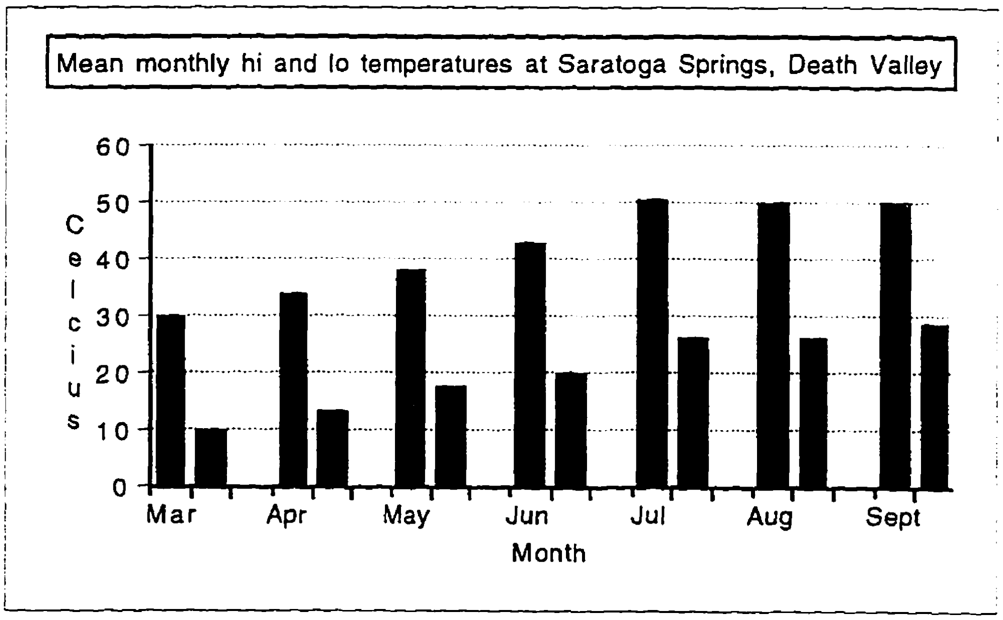
Douglas fir - coast redwood forest
  coast redwood (*Sequoia sempervirens*)
  Douglas fir (*Pseudotsuga menziesii*)
  tanbark oak (*Lithocarpus densiflora*)
  sword fern (*Polystichum munitum*)
  redwood oxalis (*Oxalis oregana*)
  western huckleberry (*Vaccinium ovatum*)
  redwood violet (*Viola sempervirens*)

Riparian community
  arroyo willow (*Salix lasiolepis*)
  box elder (*Acer negundo*)
  Oregon ash (*Fraxinus latifolia*)
  blackberry (*Rubus ursinus* and *R. procerus*)
  thimbleberry (*Rubus parviflorus*)
  western coltsfoot (*Petasites frigidus*)

Fig. 4. Mean monthly maximum and minimum temperatures from a), Woodacre, 8 km east of Tocaloma, std. 3.18° C night (lo) temperatures and b), Saratoga Springs 6 km west of Caliente Mine, std. 7.07° C night (lo) temperatures.

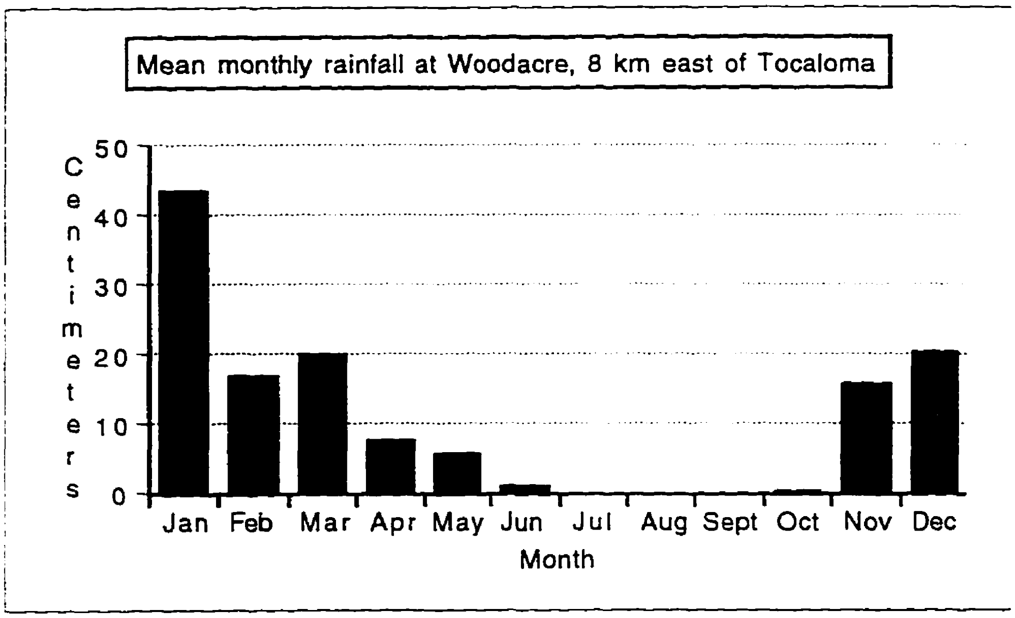


a.) Tocaloma

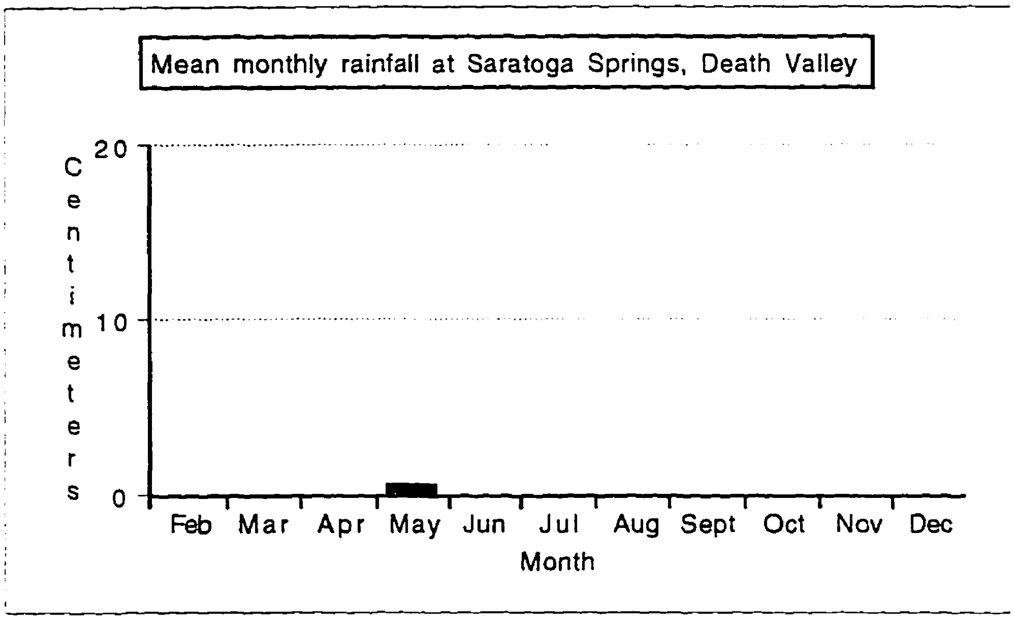


b.) Caliente

Fig. 5. Mean monthly precipitation from weather stations from three years, Jan. 1, 1993 through Dec. 31, 1995 for a.) Woodacre, Marin County and b.) Saratoga Springs, Death Valley.



a.) Tocaloma



b.) Caliente

Death Valley National Park at about 100 m asl elevation (**Fig. 2**). Most of the mines in the area including Caliente Mine and nearby Rainbow Mine were opened in the early to mid-twentieth century for hard talc formed by ancient lake sediments. Night roosts for these pallid bats occur in rocky crevices, in hollows, on man-made structures such as mining towers, and occasionally on sign posts. I only observed the Caliente pallid bats inhabit crevices within caves or mines for day roosts. These bats may night roost on steep rocky areas, although I never observed this. I did not establish locations for any hibernacula for this population, although I suspected they use crevices within mines. I caught pregnant females from April 9 through June at this site.

There are two plant communities within this study area not including Saratoga Springs 6 km to the east. The immediate area around the Caliente and Rainbow mine was creosote bush community, and the lower area included creosote and alkali scrub communities with nearby dunes and rocky substrate (**Fig. 6**). Table 2 provides a species account for plants found in these habitats. There was no rain in this area from 1992 through the winter of 1994 (Edward Baumunk, pers comm.) and until 0.02 inches of precipitation fell in spring 1994 (DV National Park Service). Plant productivity may have been lower than normal since the average rainfall for Death Valley is 1.66 inches/year. Ibex Dunes occur 0.5 km to the west of Caliente Mine and extend north and south for about 4 km, and a rocky ridge dominates the area east of the mine.

Table 2. Plant species found in the Caliente Study Area

- creosote bush community
  - creosote bush (*Larrea tridentata*)
  - desert holly (*Atriplex hymenolytra*)
  - false clover (*Oxystylis lutea*)
  - incienso (*Encelia fainosa*)
  - burrow weed (*Franseria dumosa*)

- saltbush community
  - four wing saltbush (*Atriplex confertifolia*)
  - creosote bush (*Larrea tridentata*)
  - desert holly (*Atriplex hymenolytra*)

- Saratoga Springs
  - arrowweed (*Pluchea sericea*)
  - yerba mansa (*Anemopsis californica*)
  - olney bulrush (*Scirpus olneyi*)

Fig. 6. Photograph of the predominant creosote bush community of the Caliente study area in the foreground with Ibex dunes in the background.

Saratoga Springs, 6 km from Caliente Mine, is the only source of water within about 16 km of the mine.

The Caliente study site has a hot desert climate with cold to warm dry winters and hot dry summers. A series of mountain ranges on both sides of Death Valley restricts the influence of the moisture and tempering effects from the Pacific Ocean to the west and the Gulf of Mexico to the southeast. The lowest point in the Western Hemisphere, Badwater, is about 40 km to the northeast. A weather station 4 km to the east at Saratoga Springs offers a picture of the climate. Summer days June through August were hot with daytime high temperatures from 28° to 56° C and evening low temperatures varied from 10° C to 31° C (**Fig. 4**). Rainfall is rare with the average for the Death Valley area at 1.66 inches/year (Felton 1954), which occurred on one day in the study area during the two year period from July 1, 1994 to June 30, 1996 (**Fig. 5**).

Chapter II

Dietary differences between two populations of pallid bats at the population and individual levels

ABSTRACT: I analyzed fecal samples from tagged, individual adult male pallid bats for the summers of 1993 and 1994 from a colony on the California coast and from a colony in Death Valley for the summers of 1994 and 1995. An analysis of fecal pellets suggests that dietary analysis by culled parts will bias results by underestimating smaller prey. A comparison of pooled dietary data from individuals with the diets of these same bats treated as individuals suggest a generalist group with specialized individuals in the coast population and a generalist group with generalized individuals in the Death Valley population. Coastal bats did not significantly change their diets temporally during summer months, but the Death Valley bats did. Both groups ate different prey than arthropods caught in pit traps suggesting both populations are selective foragers. Although I observed dead chewed slugs at the bottom of a night roost, only 4 of 11 naive male bats ate a slug when offered one in captivity suggesting individual foraging flexibility.

Introduction

Pianka (1974) suggested that 1) species that are food limited should seldom be food specialists, and 2) species should become generalists as their environment becomes increasingly patchy in time or space. Optimal foraging theory suggests that animals will feed selectively or not selectively according to the availability of prey. An animal should therefore choose more profitable prey as long as there is a relative abundance of prey. When prey are scarce, the predator should accept all potential food as long as the location, capture, and handling times do not exceed the energy gained by ingestion (reviewed in: Pyke 1984, Hughs 1993). My first hypothesis was that pallid bats in uniform environments should be more specialized than pallid bats in patchy environments.

Heinrich (1976) suggested that specialization should occur when the quality of preferred prey becomes marginally profitable due to competition and subsequent depletion of larger items. Hughes (1979) suggested that specialization would be likely where prey types 1) vary widely in quality, 2) require different effort, techniques and experience to obtain, manipulate and consume, and 3) when prey value can be increased by learning to handle or recognize an item more efficiently. Therefore, individuals skilled in acquiring preferred prey could maximize foraging success, while it is not profitable for inexperienced individuals to specialize on the same prey type. My second hypothesis was that pallid bats exhibit individual dietary preferences.

Slug eating was not reported in bats before my observations of dead slugs at the bottom of a pallid bat evening roost (Johnston 1992). Live slugs were only found in landscaped areas of newly built homes, and were not observed in the surrounding valley grassland dominating the area, so slug taking may be a behavioural response to a new food type. Since slugs were observed chewed but discarded at the bottom of a roost, I made the assumption that only naive bats attempt to eat slugs. My third hypothesis was that naive volant pallid bats attempt slug eating, and reject the slug as unpalatable.

Materials and methods

Adult male pallid bats were captured at a night roost at the Tocaloma bridge over Mill Creek, and at the Caliente Mine site near Saratoga Springs in Death Valley National Park (**Fig. 2**). I caught the bats between 23:00 h and 01:00 h, and placed each bat in a separate clean bag and held it for at least one hour. Upon release, each male bat was banded with a numbered U. S. Fish and Wildlife lip band and released at the site of capture. Most bands were filed smooth to remove burrs that may have caused irritation to animals. Fecal material was recovered from each cloth bag and placed in a labeled straight-sided glass vial.

Parts of orthopterans and other arthropods collected at each site were photographed for use as reference material. I used Kodak 160 ASA tungsten film with a Wild Leitz 6x - 50x dissecting scope coupled with a Wild Leitz 35 mm camera and a Cannon Ftb 35 mm camera mounted on a Bausch and Lomb 10x - 30x dissecting scope.

Fecal samples were soaked in 70% isopropyl alcohol for a minimum of 8 hours and then placed in a petri dish with additional

70% alcohol and teased apart with insect pins for identification using a 16x - 40x Leitz dissecting microscope. Drawings were made of prey body parts and identification was based on specimens and photographs of invertebrates from the study site, reference collections from the Gordon Edwards Museum of Entomology at San Jose State University, the Youth Science Institute, and Death Valley National Park as well as reference books (Powell and Hogue 1979, Borrer et al. 1977, and Dindal 1990), and a survey of Death Valley species (Riley 1893).

An analysis of feces from bats that ingested slugs revealed that some of the slug mantle and internal shell survived the bat's gastrointestinal track. Since sand often occurred in pallid bat feces, and it appeared similar to the remaining fragments of internal slug shells I found in fecal samples of captive bats, I distinguished shell fragments from sand particles since only the $CaCO3$ shell fragments dissolved when treated with dilute HCl.

Dissected fecal pellets were initially kept together to record the total proportions of prey types, since this permitted identification of loosely associated pieces of chitin as suggested by Belwood and Fenton (1976). Prey such as centipedes made it difficult to ascertain the actual number of prey consumed. Therefore I used the volume of total sample rather than actual numbers of prey consumed as a quantitative measurement of each prey type represented. Total percentage of prey consumed per bat per sample was then calculated. The percent frequency of occurrence for each prey type was also reported as suggested in Kunz (1988).

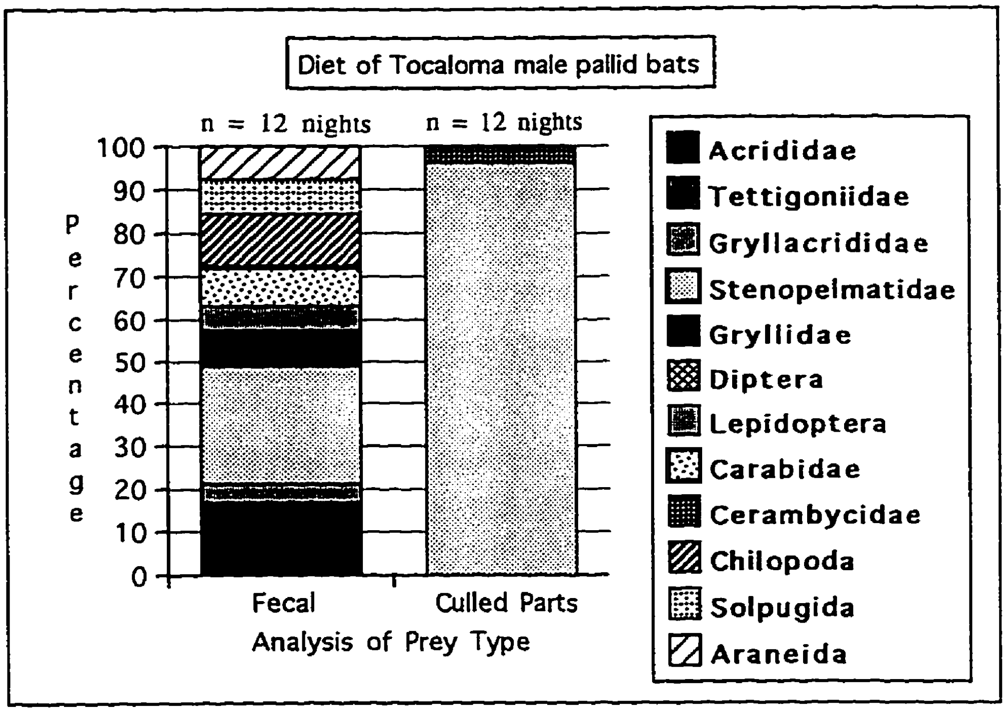
I collected 149 samples of feces from individual male bats from the Tocaloma site between 6 August 1993 and 15 August 1995 and 39 samples from the Death Valley site between 18 July 1994 and 26 September 1995.

My comparisons between dietary determination by culled parts at the bottom of a roost and by fecal analysis contradicted the reports by Black 1974, Easterla and Whitaker 1972, and Ross 1967, since all reported that fecal material and stomach analysis agrees with culled fragments from night roosts. I found through careful fecal analysis for two seasons that small prey such as Carabidae and Diptera, and soft prey such as Chilopoda, Solpugida, and Araenida are entirely ingested without culled parts by both A. p. pacificus and A. p. pallidus (Fig. 7) as predicted by Hermanson and O'Shea (1979). Therefore I only used fecal analysis for dietary data.

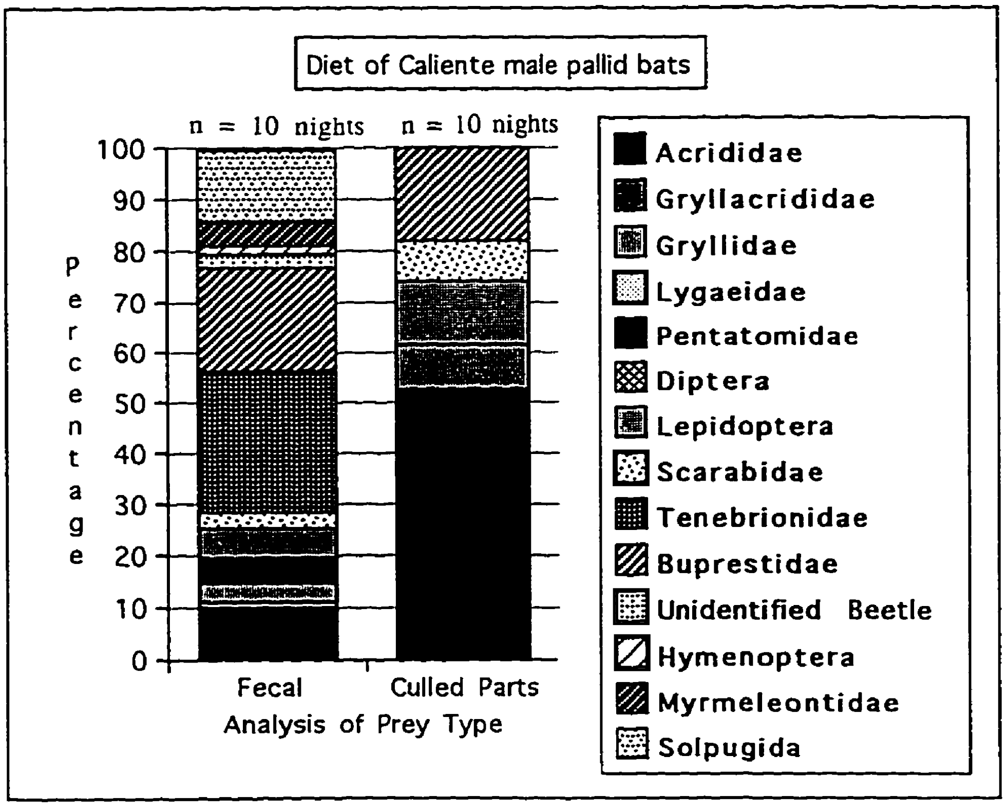
To quantify prey availability, I set out 20 pit traps at each of the study areas per sample night, or approximately on each sample night, as described by Kunz (1988). Pit traps were made by cutting the bottom out of plastic cups 10 cm high and 12 cm wide and inserting them into 26 cm high and 12.5 cm wide plastic cups to trap any invertebrates that could crawl up the sides of the base cup.

Collecting by black light was limited but was conducted at each study area to assess flying prey availability. A black light powered by a 12 v car battery with a converter was positioned above a 26 cm high by 12.5 cm wide plastic cup with 2 cm of alcohol in the bottom.

Fig. 7. Comparison of dietary analysis for Tocaloma and Caliente pallid bats by fecal pellets vs. culled parts at the bottom of the roost.



a.) Tocaloma



b.) Caliente

In addition, a 0.5 sq. m white cloth caught the ultra violet lighting, and the apparatus was set from about 21:00 h to 01:00 h. My experience at Tocaloma, and general knowledge from the literature. steered me away from light traps to assess prey availability for pallid bats. In August 1995 I found that some of the prey species at Caliente were only found in light traps. Subsequently, only field work in Death Valley for September 1995 has light trapping data.

The total volume of each prey represented was transformed to the arcsin of percentage estimates as suggested by Kunz (1988) since many proportions of samples are not normally distributed, ranging between 0% to 30% and from 70% to 100%. Fecal samples for each individual bat at Tocaloma were treated as a separate group and compared for differences in each prey type with a one-way anova.

Species diversity indices were calculated using the Emlen's index of diversity $D = \sum_{i=1}^{S} p_i e^{-p_i}$ to compare fecal sample groups of prey as in other dietary studies on bats (Anthony and Kunz 1977). Then the difference between the Emlen's species diversity index for each individual sample was subtracted from the index value for each month or time period for each site, and a Mann Whitney test was used to determine if there was a difference in the degree of specialization between the Tocaloma and the Caliente bats.

After male bats were acclimated to captivity and were 5/6 of their original weight (see chapter III - Materials and methods), each was offered a slug (Zocoleus sp. or Derocerus sp., depending on availability) in the petrie dish where they normally found meal worms. Bats were given slugs on successive nights until they completely ignored the slug. The behavioural response from each of 7 male bats from Tocaloma, 4 bats from Arivaca Junction, Arizona and two long-term captives originally from Big Bend National Park, Texas was then recorded.

Results

Dietary analysis of colonies over time

A comparison of the diet of a colony of pallid bats from the coast with the diet of a colony in the desert suggested that the coastal bats had a more uniform (temporally homogeneous) diet than those from the desert. Both colonies of pallid bats were generalists, as groups, with high indices of prey species diversity. Within the generalist colonies, the individual coastal bats were more specialized than the individuals from the desert colony.

Mature male pallid bats caught at Tocaloma ate a range of prey (**Table 3a** for species; **Fig. 8a** for percentages of groups and Emlen's Species Diversity Index). Moths and flies were not regular prey items for most members of the Tocaloma population but bats 009, 011, 017, and 028 each took small numbers ($\leq 5\%$ of a sample) of 4 mm to 9 mm long flies during July. I compared 4 time periods of 1 week each during the summer months and found Jerusalem crickets to be the preferred prey type for each time period. The changes in the volume of preferred prey were insignificant during the four time periods (One-way ANOVA, df = 3, F = 2.03, p = 0.14).

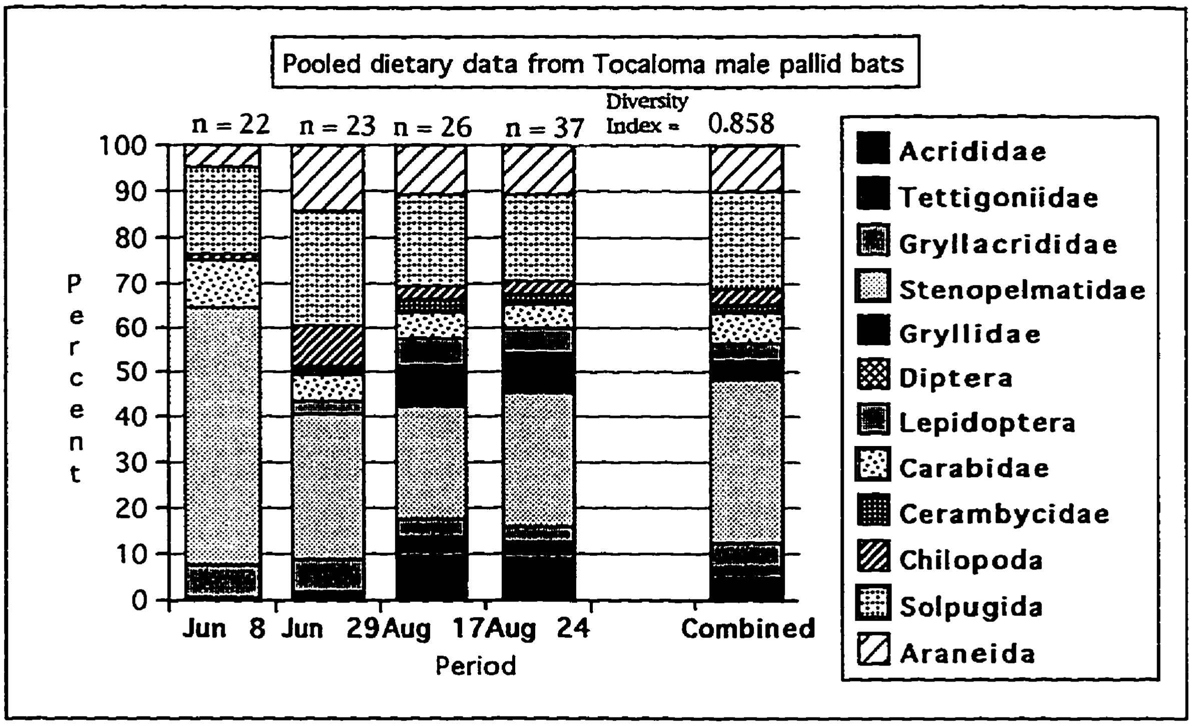
Table 3a. Diet of the Tocaloma pallid bats, *A. p. pacificus*. n = 149.

	% Vol.	% freq.
Insecta		
Orthoptera		
Acrididae, Grasshoppers	16.1	4.9
Gryllacrididae, (*Ceuthophilus californianus*)	4.7	6.1
Gryllidae, (*Gryllus sp.*)	8.3	4.9
Stenopelmatidae, (*Stenopelmatus fuscus*)	27.6	26.3
Tettigoniidae, (*Microcentrum rhombifolium*)	0.6	0.8
Diptera	0.2	1.6
Lepidoptera	5.8	4.9
Coleoptera		
Carabidae	8.4	7.3
Cerambycidae, (*Prionus californicus*)	1.0	3.2
Chilopoda	11.8	8.1
Solpugida	7.8	18.2
Araneida		
Lycosidae	7.8	13.8

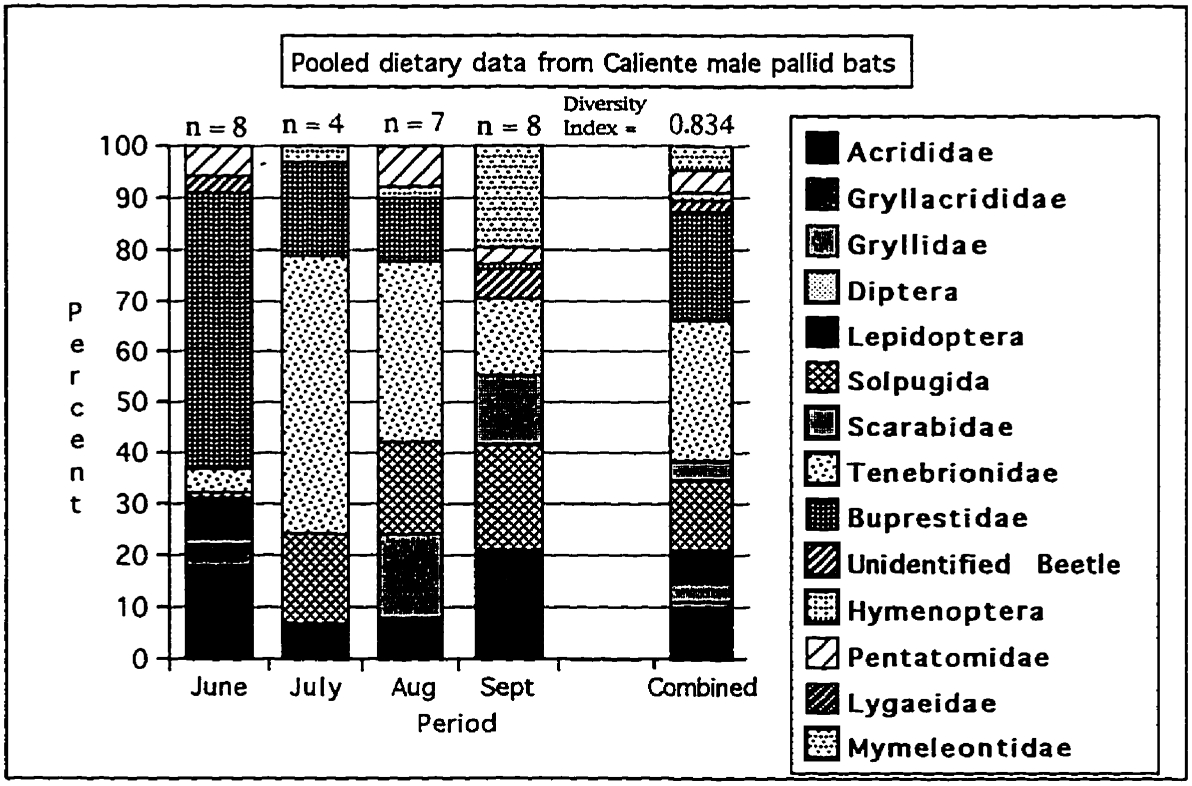
Table 3b. Diet of the Caliente pallid bats *A. p. pallidus*, n = 30.

	% Vol.	% freq.
Insecta		
Orthoptera		
Acrididae (*Tytthotyle maculata*)	9.9	12.5
Gryllacrididae	1.0	2.3
Gryllidae (*Gryllus sp.*)	4.0	1.1
Diptera	0.3	1.1
Lepidoptera	5.7	8.0
Sphingidae		
Coleoptera:		
Scarabidae (*Diplotaxis sp.*)	3.4	5.7
Tenebrionidae (combined)	27.8	19.3
Cnemodinus testanceus		
Edrotes ventricosus		
Cryptoglossa verrucossa		
Buprestidae (*Hippomelas sp.*)	21.0	10.2
Coleoptera (unidentified)	2.3	6.8
Hymenoptera		
Tiphiidae	1.5	4.5
Hemiptera		
Pentatomidae	4.3	3.4
Lygaeidae (*Geocoris sp.*)	0.1	1.1
Myrmeleontidae	4.9	8.0
Solpugida	14.1	15.9

Fig. 8a) Pooled dietary data for Tocaloma during 4, one-week periods (dates are the first day of 7 days). 8b) Pooled dietary data for Caliente diet during four months.



a) Tocaloma



b) Caliente

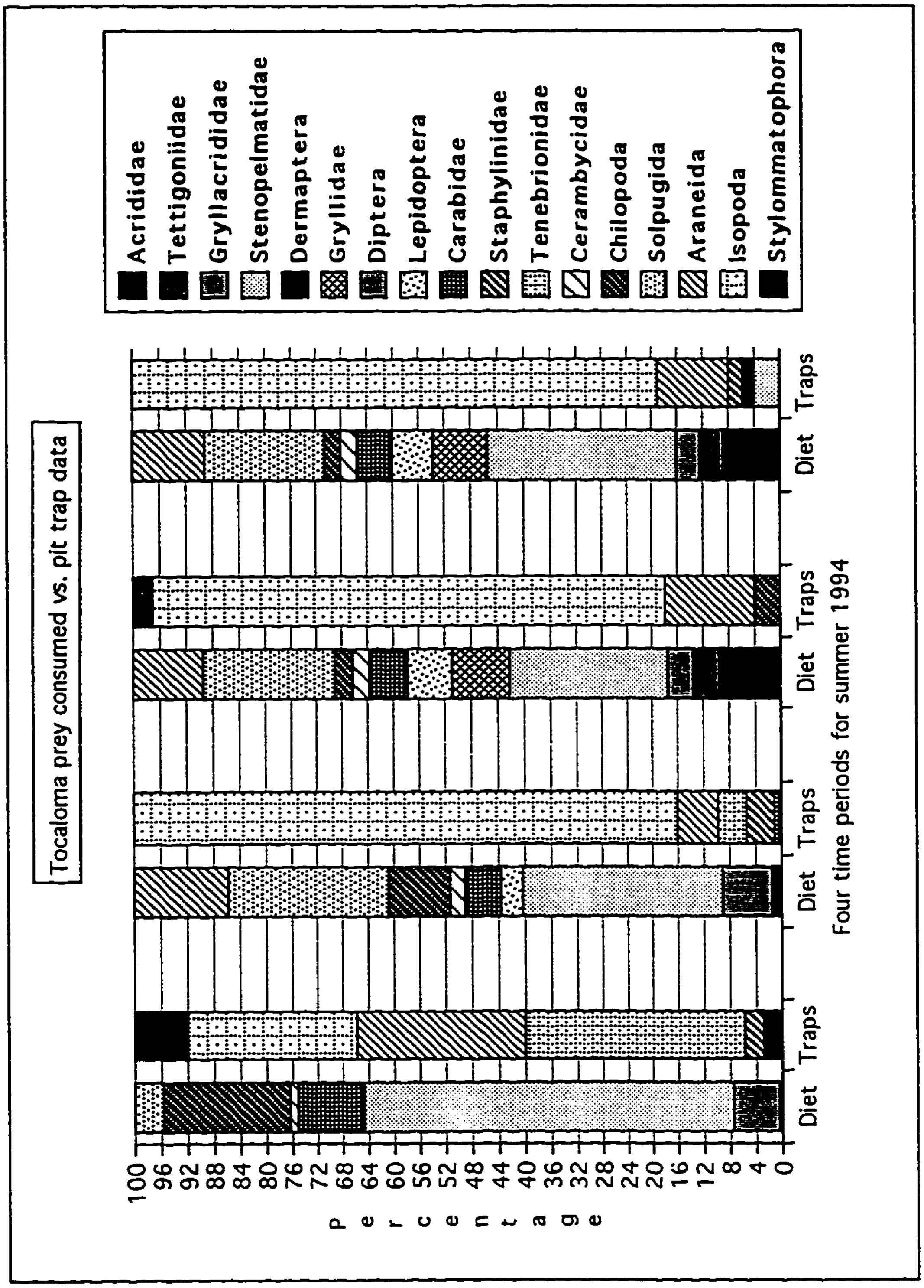
Although females and juveniles were not intentionally caught, I have reported dietary data for these groups since such data has not been reported in the literature. The small amount of data from females and juveniles at Tocaloma suggested juveniles had similar diets to mature males, and pregnant females ate more moths than mature males during August at Tocaloma (**Appendix 2**).

Mature male pallid bats caught at Caliente Mine ate a variety of prey (**Table 3b** for species; **Fig. 8b** for percentages of groups). Pallid bats captured about 6 km southwest of Caliente Mine near Saratoga Springs, in the presence of year round standing water, also consumed predacious diving beetles (Hydrophilus triangularis) and dragon flies (Odonata). Male pallid bats within 16 km of Sheep Springs also ate Scorpionida, and sphingid moths (Sphingidae) and a Banded Gecko, (Coleonyx variegatus). I pooled data from each summer month and found changes in preferred prey were significant. During the month of June, buprestids were found in 7 out of 8 samples, and consumption was significantly greater in this month (One-way ANOVA, df = 3. F = 18.11, $p < .001$). In July and August, a flying tenebrionid 6-8 mm long (Cnemodinus testanceus) was the predominant prey and was consumed in significantly higher amounts during these months (One-way ANOVA df = 3.F = 17.06, $p < .001$). In September, several species of mymeleontids made up the predominant prey followed by solpugids. Mymeleontids were eaten in significantly higher amounts in this month (One-way ANOVA, df = 3, F = 3.61 p = .028) although solpugids were not. The Caliente bats' diet changed significantly over time and was therefore more patchy than the Tocaloma bats' diet.

The high species diversity index for each of the colony's combined dietary data revealed that both colonies were generalists, although my pit trap data suggested that both colonies were also selective feeders. Out of 149 samples of fecal pellets from Tocaloma, there was no evidence that pallid bats ate some of the relatively abundant species found in pit traps (i.e., isopods, tenebrionids (stink beetles), staphylinids (rove beetles) and stylommatophoras (land slugs) **(Fig. 9)**. While 20 pit traps per night may not adequately sample the environment for prey availability for gleaning bats, I still observed low numbers of common prey such as Jerusalem crickets and centipedes in my pit traps. Several families of spiders were caught in pit traps but only lycosids (wolf spiders) were found in fecal samples suggesting that pallid bats selectively eat species of a single spider family.

Smith (1929) found Jerusalem crickets crawled on the ground or in pit traps in western U.S. states all months of the year except summer months when they burrowed into the ground, but my data suggested bats ate Jerusalem crickets as their primary prey throughout the summer. Weisman (pers. comm.) suggested that Jerusalem crickets may not burrow into the ground in more humid areas along the coast of California, and may be available all year long. Weisman (pers. comm.) suggested that field crickets are also available throughout the summer months and throughout the entire

Fig. 9. Tocaloma prey consumed vs. pit trap data for one week periods starting June 8, June 29, August 17, and August 24.

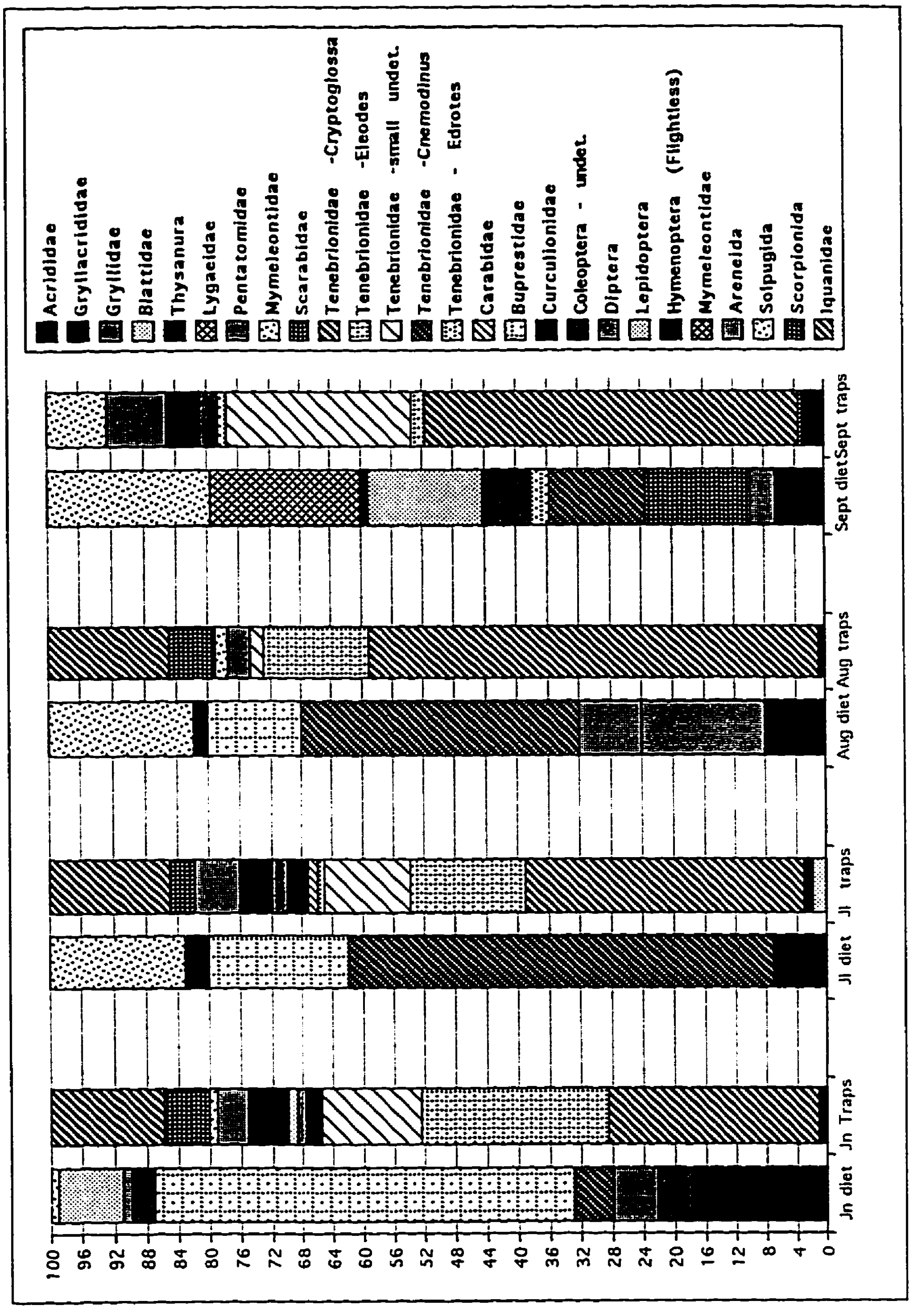

Tocaloma prey consumed vs. pit trap data
Percentage
100
96
92
88
84
80
76
72
68
64
60
56
52
48
44
40
36
32
28
24
20
16
12
8
4
0
Diet
Traps
Diet
Traps
Diet
Traps
Diet
Traps
Four time periods for summer 1994
Acrididae
Tettigoniidae
Gryllacrididae
Stenopelmatidae
Dermaptera
Gryllidae
Diptera
Lepidoptera
Carabidae
Staphylinidae
Tenebrionidae
Cerambycidae
Chilopoda
Solpugida
Araneida
Isopoda
Stylommatophora

year at least as sub-adult instars in coastal areas of California.

The availability of prey at Caliente Mine in Death Valley was measured by pit traps, light traps, and pooled data for 4 time periods. Pit traps offered information about what was available on sandy or gravel substrates but did not allow assessment of arthropods on rocky substrates. Therefore pit trap data was probably biased against the presence of arthropods that preferred rock habitat which I observed light-tagged pallid bats forage over.

Rarely consumed prey items sometimes appeared in large numbers in pit traps and light traps. On every visit during the summers of 1994 and 1995, one of the ground crawling tenebrionids, Cryptoglossa verrucossa, was the most common arthropod caught in pit traps throughout the summer months (mean %/month = 42% by volume, **Fig. 10.**). I wanted to observe any interactions between these two beetles, Cryptoglossa verrucossa, and Elodes sp. and pallid bats, so I captured two and allowed them to freely walk in the flight room after Death Valley bats were reduced in weight. I observed two pallid bats crawl up to each of these beetles and both bats stopped investigating them when their head was approximately 2 cm away. Each bat possibly smelled the beetle although the beetle did not have its abdomen in the air in the typical defensive posture (as though it were releasing a defensive gas). In addition to spraying the offensive odour, these beetles produce quinonoid secretions which are believed to make them unpalatable (Powell and Hogue 1979). Nonetheless, out of a total of 44 fecal samples, one fecal

Fig. 9. Diet of Caliente population vs. pit trap data for four months. Data combined into months for summers 1994 and 1995.


100
96
92
88
84
80
76
72
68
64
60
56
52
48
44
40
36
32
28
24
20
16
12
8
4
0
Jn diet
Jn Traps
Jl diet
Jl traps
Aug diet
Aug traps
Sept diet
Sept traps
Acrididae
Gryllacrididae
Gryllidae
Blattidae
Thysanura
Lygaeidae
Pentatomidae
Mymeleontidae
Scarabidae
Tenebrionidae -Cryptoglossa
Tenebrionidae -Eleodes
Tenebrionidae -small undet.
Tenebrionidae -Cnemodinus
Tenebrionidae - Edrotes
Carabidae
Buprestidae
Curculionidae
Coleoptera - undet.
Diptera
Lepidoptera
Hymenoptera (Flightless)
Mymeleontidae
Areneida
Solpugida
Scorpionida
Iquanidae

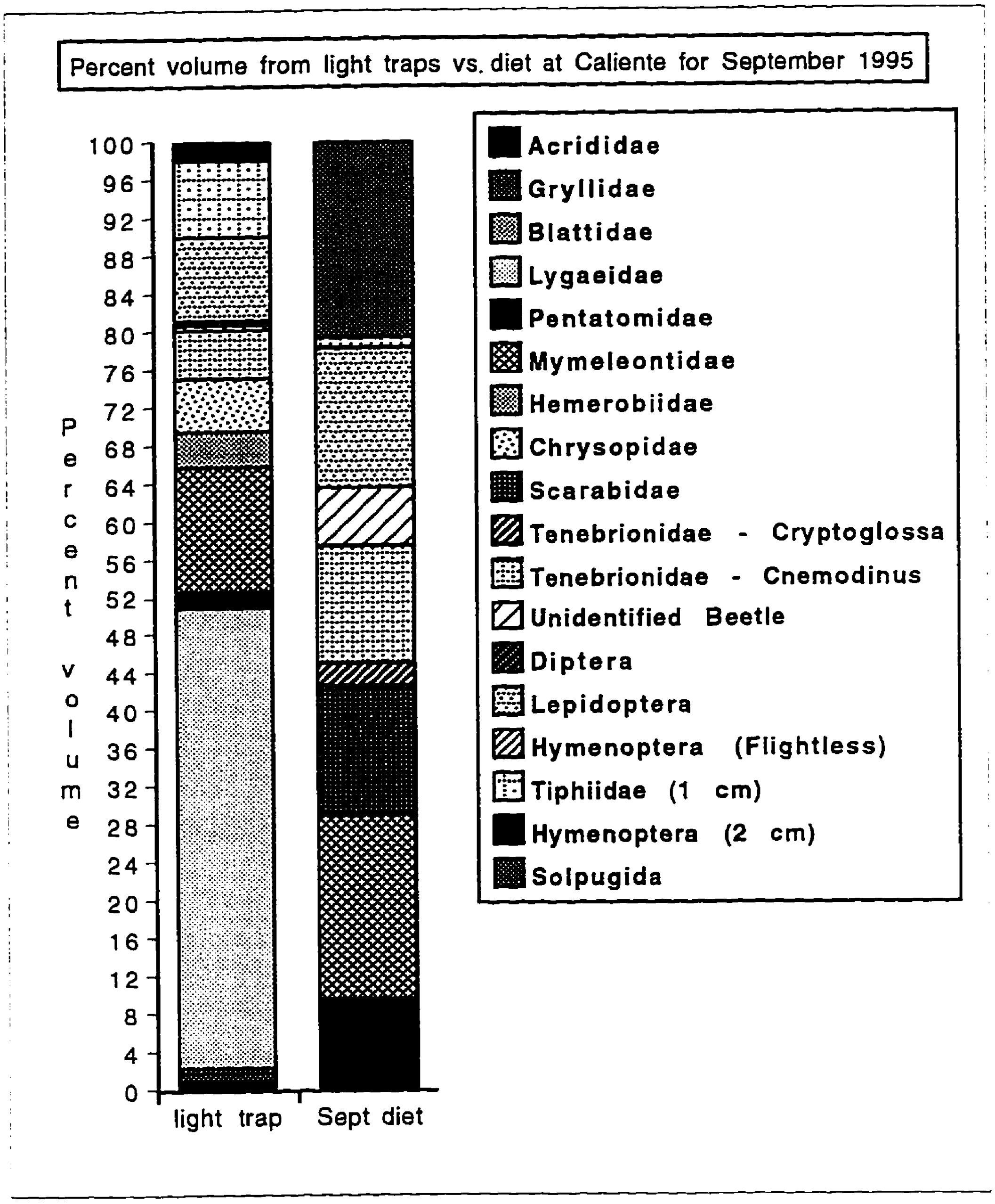
sample had evidence of Cryptoglossa verrucossa.

On 13 September 1995, the light trap caught 85 tiphiid wasps making approximately 15.7% of the total volume of insects in the light trap that night and yet only one bat, #100, had this tiphiid in a fecal sample the same night. On the 13th and the 25th of September 1995, approximately 3,000 Big-eyed bugs, Geocoris sp. (Lygaeidae), were caught each night in the light trap making 49.3% of the total volume of insects caught that night in the light trap. Three of these small, 4 mm long, hemipterans occurred in fecal samples for those two nights. Dipterans also occurred in very small numbers in the samples **(Fig. 11).**

Foraging activity normally diminishes as temperature drops probably due to lower densities of arthropods and increased energetic costs since more energy is required to maintain a homiothermic body temperature. In addition to energy constraints for flying at low temperatures on some spring nights, bats at Death Valley may also have energy constraints associated with flying at higher temperatures. On nights with temperatures exceeding some tolerable level, the real availability of arthropods may be nil, even though arthropod traps may suggest high densities of prey were available.

I found some evidence that pallid bats at the Caliente Mine site did not forage on hot nights. On 18 July 1994 I captured four male pallid bats at 01:00 in the mine portal. I palpated each of their stomachs and felt no evidence of prey consumption so far that

Fig. 11. Diet of Caliente population vs. insects caught in a light trap for September 1995.


Percent volume from light traps vs. diet at Caliente for September 1995
Percent volume
100
96
92
88
84
80
76
72
68
64
60
56
52
48
44
40
36
32
28
24
20
16
12
8
4
0
light trap
Sept diet
Acrididae
Gryllidae
Blattidae
Lygaeidae
Pentatomidae
Mymeleontidae
Hemerobiidae
Chrysopidae
Scarabidae
Tenebrionidae - Cryptoglossa
Tenebrionidae - Cnemodinus
Unidentified Beetle
Diptera
Lepidoptera
Hymenoptera (Flightless)
Tiphiidae (1 cm)
Hymenoptera (2 cm)
Solpugida

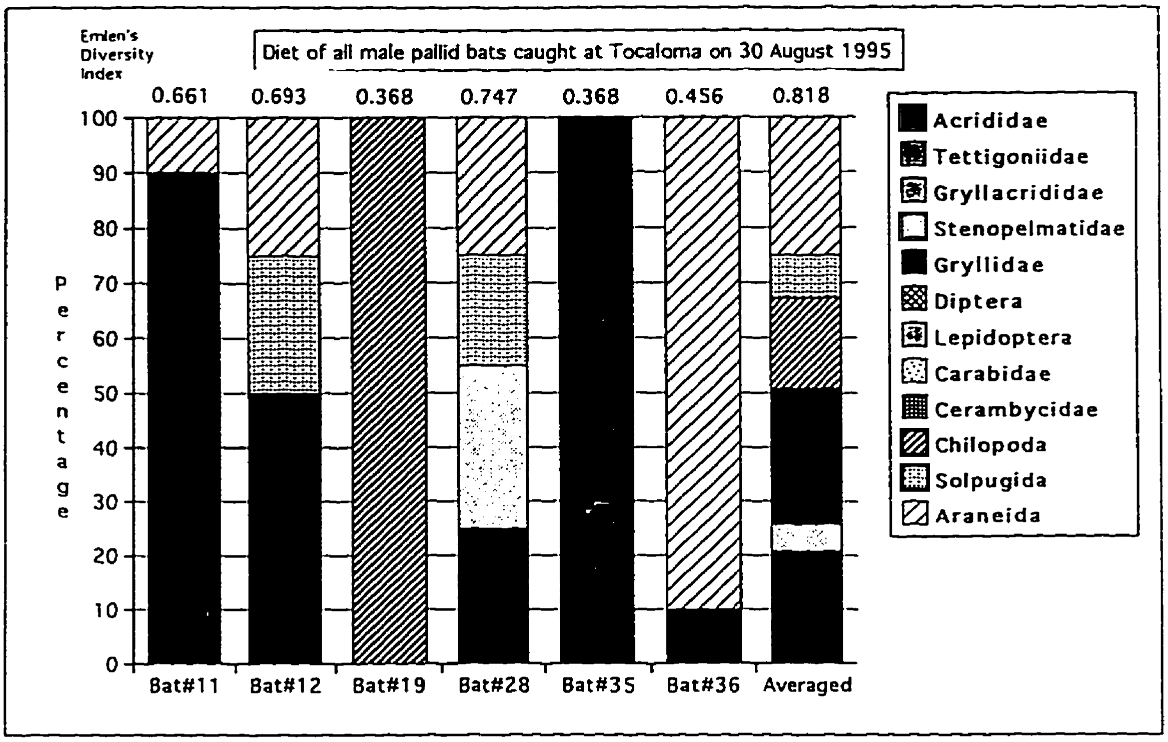
evening. After two hours in cloth bags with no fecal samples produced, I released them outside the mine with standard numbered lip bands. One week later I found two of the banded bats in Caliente mine, dead and emaciated. The outside daytime temperatures exceeded 50° C but cooled down on that night to 39° C by 03:00.

My observations suggest that pallid bats do not forage when temperatures exceed their ability to maintain a tolerable body temperature and water balance while flying. I suspect that two of the bats I caught on 18 July 1994 died because I encouraged or forced them to forage at temperatures exceeding the normal limit for foraging. The Death Valley pallid bats were never observed foraging when the outside temperature was 39° C, suggesting these bats aestivate or choose not to forage in these higher temperatures. Frequent high winds in Death Valley were often accompanied by sand storms which seemed to preclude foraging. Aestivation in Chiroptera is also reported by Beausseau (1941) in an emballounorid in Libya.

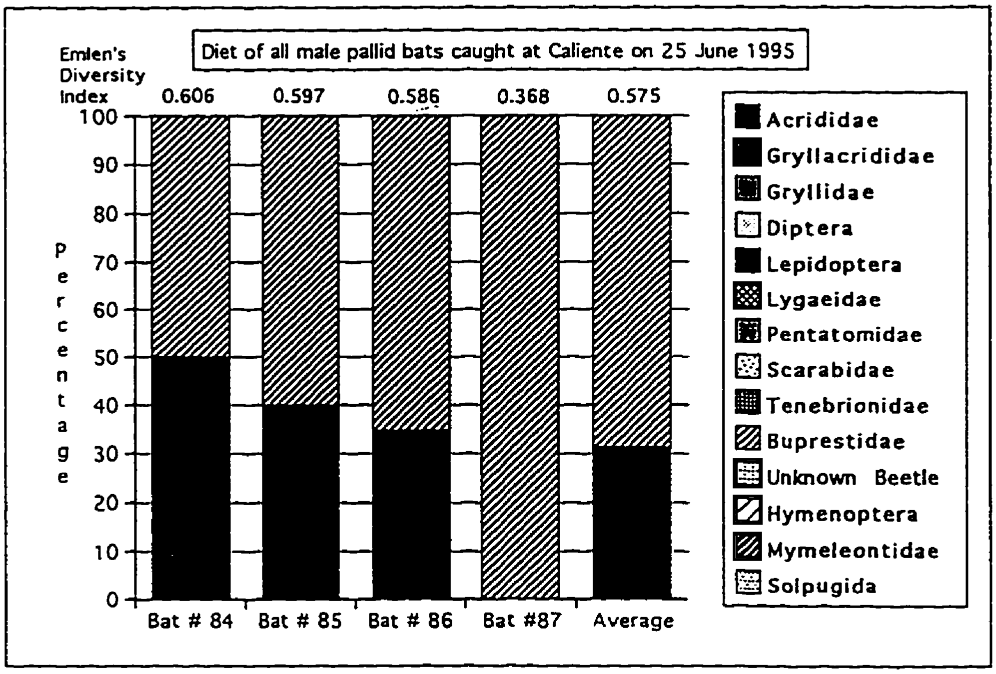
Differences in individual dietary specialization between bats at Tocaloma and Caliente

A comparison of the total diet of each group compared with the diet of each individual for a specific time period revealed that individual Tocaloma bats were more specialized than individual Caliente bats. On any given night or period of time, individual bats from the Tocaloma colony rarely ate the same items, so the species

Fig. 12a.) Diet of all male pallid bats caught at Tocaloma on 30 August 1995. b.) Diet of all male pallid bats caught at Caliente on 25 June 1995.



a) Tocaloma



b) Caliente

diversity for the group was greater than for any individual (**Fig. 12a**). In contrast, individual bats from the Caliente colony often ate the same prey types, so the species diversity for the group often matched the mean for the individuals. On June 25, 1995 mature males consumed the same two prey, metallic wood-boring beetle Hippomelas sp. (Buprestidae) and furnace heat lubber, Tytthotyle maculata (Acrididae) (**Fig. 12b**). Based on differences between group and individual indices of species diversity, Tocaloma bats were significantly more specialized than the Caliente bats (Mann Whitney, $p < .001$). An analysis of the distribution of these values revealed that 20 samples were highly specialized with a difference in Emlen's species diversity index of 0.5 whereas none existed this high from the Caliente samples (**Fig. 13**).

Individual variation within the colony

My data suggested that within the Tocaloma group, individuals had different dietary preferences. I made relatively few recaptures, possibly because bats learned to avoid the net on successive nights of mist netting, but I analyzed data for 8 bats, each with at least 4 samples. Out of 12 prey types, any individual bat fed on only 2 to 7 types (mean = 5.25), and no overlap in prey types existed between Bat # 34 and Bat # 48. Bat #34 had significantly greater amounts of tettigonids than other bats (One-way ANOVA, df = 7, F = 3.53, p = 0.007) and never ate Jerusalem crickets, the preferred prey for other Tocaloma bats (**Fig. 14**). This suggested the Tocaloma colony had a

Fig. 13. Distribution of the differences of Emlen's species diversity indices between individuals and pooled data for each month or time period.

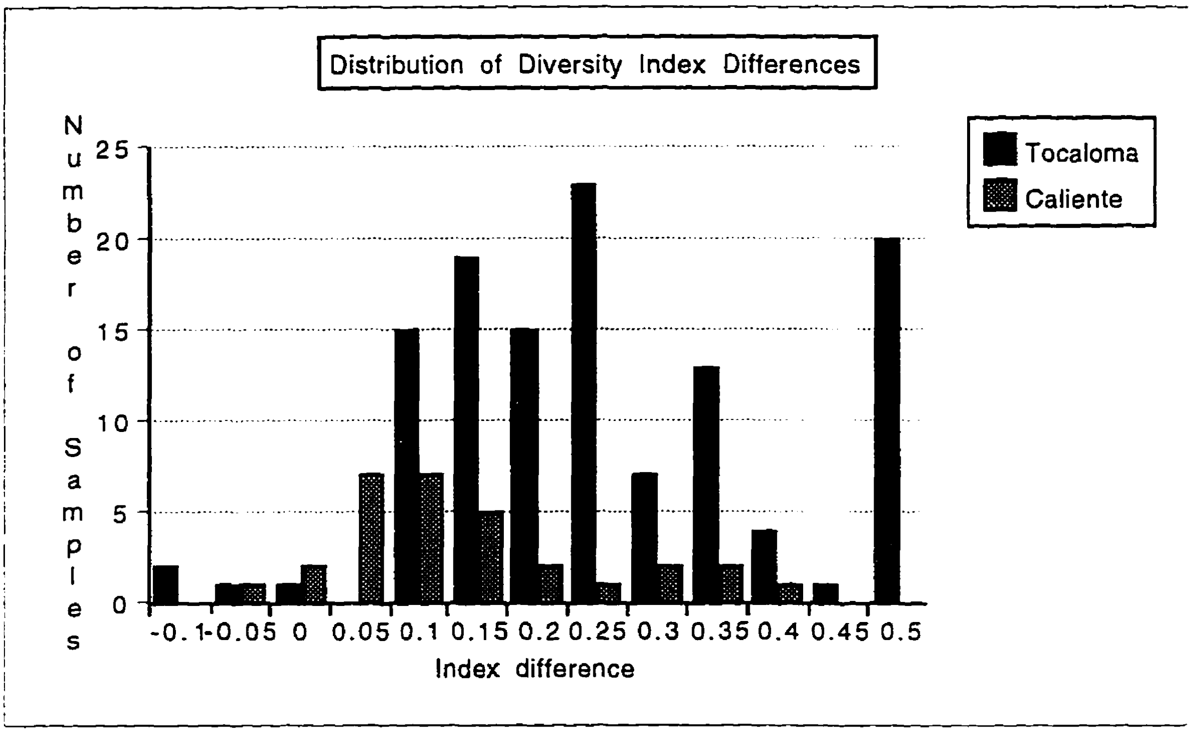
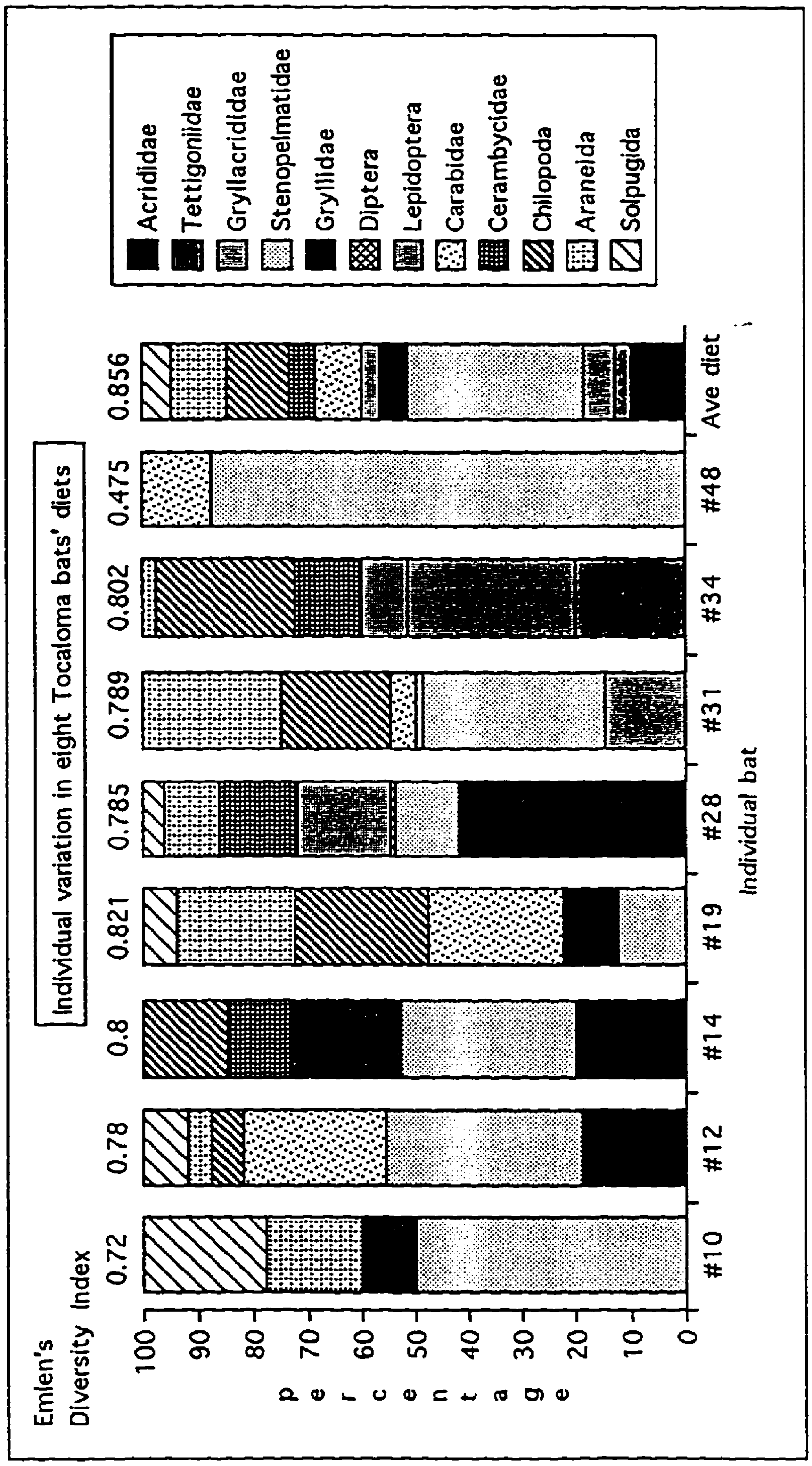

Distribution of Diversity Index Differences
Number of Samples
25
20
15
10
5
0
-0.1
-0.05
0
0.05
0.1
0.15
0.2
0.25
0.3
0.35
0.4
0.45
0.5
Index difference
Tocaloma
Caliente

Fig. 14. Individual variation in the diets of eight Tocaloma adult male pallid bats during the 1993 and 1994 summers. For Bat # 10, n = 4; Bat # 12, n = 8; Bat # 14, n = 5; Bat # 19, n = 4; Bat # 28, n = 7; Bat # 31, n = 4; Bat # 34, n = 4; Bat # 48, n = 4.


Individual variation in eight Tocaloma bats' diets
Emlen's Diversity Index
0.72
0.78
0.8
0.821
0.785
0.789
0.802
0.475
0.856
percentage
100
90
80
70
60
50
40
30
20
10
0
#10
#12
#14
#19
#28
#31
#34
#48
Ave diet
Individual bat
Acrididae
Tettigoniidae
Gryllacrididae
Stenopelmatidae
Gryllidae
Diptera
Lepidoptera
Carabidae
Cerambycidae
Chilopoda
Araneida
Solpugida

generalist diet within which individuals show some specialization, and no two individuals in the Tocaloma colony had the same diet.

I recaptured too few bats at Caliente to attempt comparing individual's diets. (I only caught 40 mature males, and of these, several did not produce a fecal sample, reducing my sample to 30.) However, I caught bat # 88 once in June and twice in September, and its diet matched the generalized diet of the colony closely for each night (**Fig. 15**). Furthermore, the differences between the species diversity for each individual and for the group also suggested that individuals appeared to follow a diet resembling the colony's generalized diet.

Slug eating in wild and captive bats

Four of 11 naive male pallid bats from three sites, Tocaloma, Calif., Big Bend, Texas, and Aravaca Junction, Arizona, ate slugs (Derocerus sp. or Zocoleus sp.) in captivity (**Table 4**). There was no evidence that slugs occurred at Aravaca Junction in the Sonoran Desert of Southern Arizona, but slugs of several species occurred in the Tocaloma area. I did not visit the Big Bend site; however, the description of this site (Krull 1990) suggested that it was too dry to support populations of slugs. Bat # 42 died (with emetica covering parts of its head and body) two days after ingesting a Derocerus sp. slug, an exotic found in the Toronto area. Subsequently I abandoned this test and did not offer slugs to any of the captive bats from

Fig. 15. Comparison of pooled data for Caliente colony and Bat #88 for June and September.

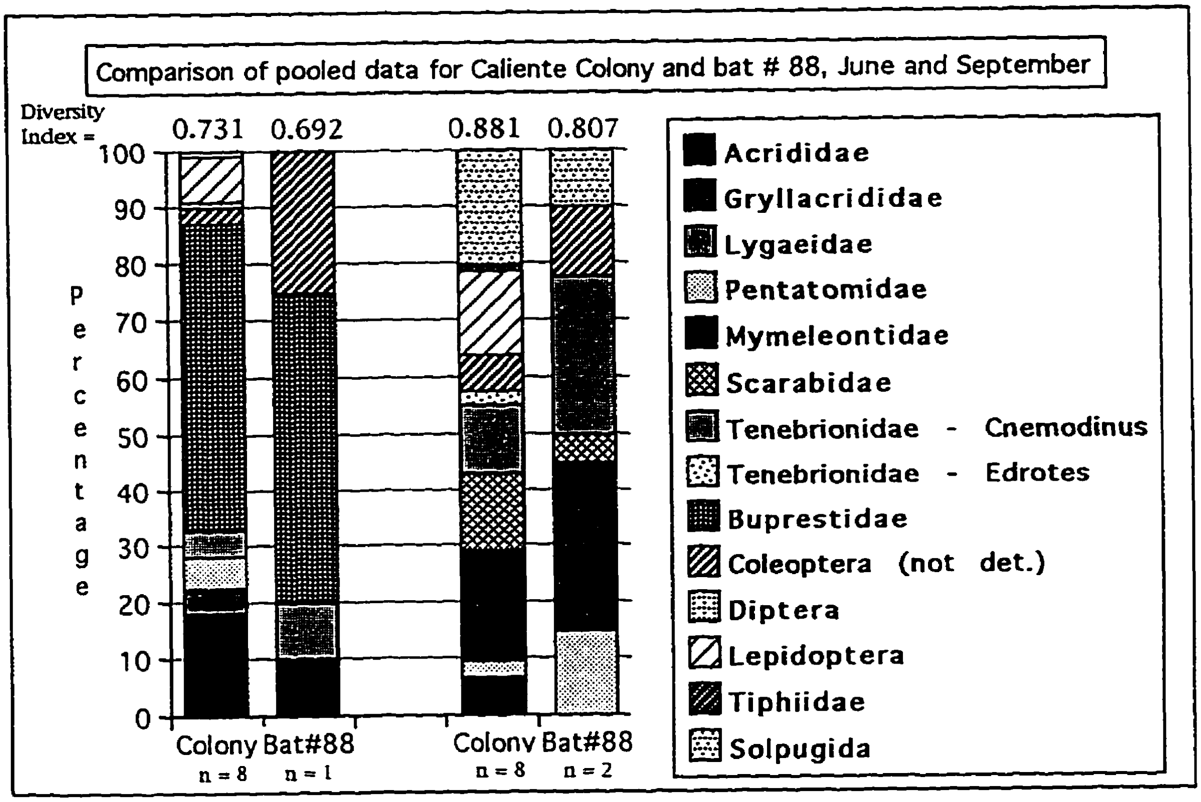

Comparison of pooled data for Caliente Colony and bat # 88, June and September
Diversity Index =
0.731
0.692
0.881
0.807
Percentage
100
90
80
70
60
50
40
30
20
10
0
Colony
n = 8
Bat#88
n = 1
Colony
n = 8
Bat#88
n = 2
Acrididae
Gryllacrididae
Lygaeidae
Pentatomidae
Mymeleontidae
Scarabidae
Tenebrionidae - Cnemodinus
Tenebrionidae - Edrotes
Buprestidae
Coleoptera (not det.)
Diptera
Lepidoptera
Tiphiidae
Solpugida

Table 4. Behavioural response to slugs as prey by 11 male pallid bats.

Population	Bat #	Age class, sex	Takes 1st slug	Chews 1st slug	Eats 1st slug	Eats 2nd slug
Tocaloma, Calif.	# 02	adult, m	+	+	-	-
Tocaloma, Calif.	# 04	adult, m	-	-	-	-
Tocaloma, Calif.	# 05	adult, m	+	+	+	-
Tocaloma, Calif.	# 06	adult, m	-	-	-	-
Tocaloma, Calif.	# 08	adult, m	+	+	+	-
Arivaca Jct., Ariz.	# 38	juv, m	-	-	-	-
Arivaca Jct., Ariz.	# 40	adult, m	+	-	-	-
Arivaca Jct., Ariz.	# 41	adult, m	+	+	-	-
Arivaca Jct., Ariz.	# 42	adult, m	+	+	+	-
Big Bend, Texas	# 601	adult, m	-	-	-	-
Big Bend, Texas	# 602	adult, m	+	+	+	-

Bat #	Comments 1st slug	Comments 2nd slug*
# 02	chewed slug several times before rejecting it	ignored slug
# 04	appeared to smell slug, touched slug with mouth, and then ignored it	ignored slug
# 05	ate slug in petrie dish	ignored slug
# 06	ignored slug	ignored slug
# 08	quickly took slug to roost and ate it	ignored slug
# 38	appeared to smell slug, touched slug with mouth, and then ignored it	ignored slug
# 40	took slug and flew, but dropped it without making chew marks	ignored slug
# 41	rejects slug after initially chewing it	ignored slug
# 42	took slug to roost and ate it, died 2 days later	ignored slug
# 601	ignored slug	ignored slug
# 602	ate slug in petrie dish	ignored slug
		*presented day after 1st slug

Caliente.

I dissected a slug 23 mm long and isolated a hard calcium carbonate shell 5.5 mm x 3.5 mm and about 0.3 mm thick. The fact that nearly all of the internal shell dissolved in the digestive tract of these bats suggested that the calcium was made available to the bats after ingestion. Although I observed 4 dead, chewed slugs at the bottom of a pallid bat roost in San Jose, I did not find any slug mantle or internal shell fragments in the Tocaloma bats' fecal samples to suggest that wild adult male pallid bats ate slugs.

Discussion

Optimal Foraging Theory

Optimal Foraging Theory (OFT) probably was first introduced by two original papers by MacArthur and Pianka (1966) and Emlen (1966). These authors proposed a means to predict how natural selection shapes the patterns of foraging behavior. They made the general assumption that an animal would promote its fitness by foraging in ways that maximize the net rate of energy gain (E/T). Thus OFT and the subset, Optimal Diet Theory (ODT), is based on the primary prediction that a forager should always accept the most profitable food type, and that it should accept successively less profitable types only when encounter rates with higher-ranking types fall below critical levels (See Pyke 1979 for a review of early OFT models).

Hughes (1993) summarized the assumptions made for the basic

Optimal Diet Theory as follows: 1) the forager can evaluate the profitability in terms of yield per unit handling time, for each food type encountered and rank this relative to the profitability of other types; 2) the forager can estimate and remember the average profitability of food types encountered; 3) the forager can measure encounter rates with different food types; and 4) the forager uses all this information to decide which encountered items to accept and which to reject.

Early empirical studies tested Optimal Foraging Theory for: 1) diet, 2) patch choice, 3) when to leave a patch, 4) movement, and 5) central place foraging which deals with situations in which an animal has a central foraging base such as a roost or nest (Orians and Pearson 1979). There exist many OFT models, and critics of OFT and ODT often point out that most models appear to be designed to meet specific situations and species. Nearly all of the early models assumed a constant handling time and an instantaneous prey recognition time. Later, investigators (e.g., Oaten 1977, Caraco 1980, and McNamera 1982) took into account that many variables, such as the amount of energy obtained from a single individual prey, are random variables (i.e., there are stochastic or variable parameters taking different values with certain probabilities). The first models addressing this problem used mean values for the various parameters. Animals that prefer lower variance are termed "risk averse," while animals that prefer higher variance are "risk prone" (Caraco 1980). The fitness of a foraging animal is a function, not only of the mean values of the various parameters, but also of their variances (Pyke 1984). For this situation Pyke (1984) argues that an animal should make its foraging decisions on the basis of these variances as well as the means. Smith and Sweatman (1974) suggested that animals should devote time to sampling their environment in order to obtain necessary information for subsequent foraging decisions since the environment is theoretically always changing. If the quality of two food patches switched from time to time, then an animal that can feed in either patch should spend some time in what might be the worse patch so that it could switch appropriately when conditions change. Hughes (1979) probably developed the first OFT model to incorporate components of making these switches and thus, the cost of learning to forage, as an integrated part of the model.

The individual pallid bat as a specialist

Although OFT models are used to predict optimal diets, they do not explain why individuals within species select different kinds and amounts of forage [e.g., in herbivores, (Provenza and Balph 1988, 1990), in otters, (Lyons 1990), and, as suggested, in little brown bats (Myotis lucifugus) (Anthony and Kunz 1977)]. Furthermore, some individual conspecific vertebrates [(e.g., herbivores (Grovum 1988), and otters (Lyons 1990)] do not necessarily select the highest energy-efficient food.

Schoener (1971) stated that an optimal diet should not exclude any prey types more valuable than those included in the diet. However there was no overlap between the diets of two Tocaloma bats, and one bat ate none of the other bats' preferred prey. Emlen (1966) suggested that predators may choose common, less valuable prey to less common, more valuable prey, especially if prey differed widely in value. The arthropods taken by the Tocaloma bats did not differ widely in caloric value/mass (Cummins and Wuycheck 1971) although their densities, distribution and handling costs could have. Each bat should have had an equal chance at each prey type since they roost together, but only if it's assumed that had the same learning experiences and individual physiologies were not significantly different.

Partridge and Green (1985) suggested that the evolutionary basis of foraging behaviour is only generally considered by OFT (i.e., only a model creates the "average animal"). Estes et al. (1981) and Lyons (1991) revealed that the "average" sea otter didn't exist, as evidenced by their studies on the great variability in diet within a single colony and therefore deviation from a predicted optimum diet. Since the individual Tocaloma bats only took from 2 to 7 prey items out of the total of 12 for the colony as a whole, an "average" pallid bat also did not exist at Tocaloma.

Learning and Optimal Foraging Theory

Lyons (1991) suggested that learning may play a role in the currency of each prey type for sea otters. If the search time and handling time for each prey type requires specific learning, then an individual should continue to lessen the cost of a specific prey type as it specializes on that prey (Pianka 1974). Partridge (1976) found individual differences in handling times for prey in great tits (Parus major) which suggested that individual dietary differences were due to individuals' different profitabilities for specific prey types. Such a mechanism may work in the Tocaloma colony, especially if prey are consistently available so that individuals can continue to learn and specialize, therefore reducing the time for detection, capture, and handling.

Hughes (1979) provided a model incorporating learning costs as a part of OFT and thus introduced a mechanism for transposing the rank of prey types by switching from a specialized diet of one prey type to that of another. Although Hughes (1979) suggested that individuals skilled in acquiring preferred prey could maximize foraging success (while it is not profitable for inexperienced individuals to specialize on the same prey type) he fell short of providing a mechanism for a predator to develop such skills in the first place. If predators require different skills in detection and handling, and these skills need to be learned at high costs, learning may potentially be a critical factor in the fitness of the individual. Kunz (1987) and Tuttle and Stevenson (1982) correlated low temperatures, strong winds, heavy rain, fog, and drought with low foraging success for bats, and therefore affecting the development and survivorship of young, but I know of no studies that specifically investigated learning ability as a factor in young volant bat mortality. Further research needs to be investigated to determine the role learning may play in the survivorship of young.

Perhaps an individual's first prey types are introduced through matrilines, and other prey are taken through a combination of socially dependent and independent mechanisms. O'Shea and Vaughan (1977) reported that young pallid bats were often in close association with mothers in July and August although there was no evidence that the two or three bats flying together were related or if young learn from their mothers. Perhaps an OFT model can be made to predict individual specialization within a single colony if learning costs and rewards are weighted enough to accommodate skewed values of prey associated with their learning costs.

Provenza and Balph (1987) found that wild and domestic ungulates introduced into new foraging environments were less efficient than conspecifics reared in the same environment. A review by Griffith et al. (1989) suggested that naive ungulates spent more time foraging, ingested less forage, spent more time walking, walked for greater distances, suffered more from predation and malnutrition, and ingested more toxic plants than experienced animals (reviewed by Griffith et al. 1989). Provenza et al. (1992) suggested that naive animals learn about the new environment through trial and error, which is less efficient than learning from social models.

Galef and Beck (1991) suggested that individual learning is inadequate to ensure that rats selected a nutritionally sound diet from a "cafeteria of choices" available in the wild. Empirical studies suggested that several processes worked together to promote social transmission of diet choices facilitating young rats to feed on the same foods as adults in any certain colony. Galef (1976) found that suckling rats acquired food preferences through flavours transmitted through their mother's milk, and young rats also learned about the foods they smelled on the mother's fur. Galef (1990) also found chemical smells from the breath of adult rats transmitted information about safe foods.

Slugs, flies, and big-eyed bugs

Individuals from Tocaloma and Caliente took small numbers of aberrant prey, and flies were also eaten by pallid bats from Waterdog Lake in British Columbia (**see Appendix 3**). Based on my observations of bats in captivity, I do not believe these field observations represent regularly taken prey. I assume the bat from the lower Sonoran Desert that ate a slug in captivity and died two days later made a mistake just as the wild Caliente bat that ate a stink beetle (Cryptoglossa) The difference, of course, is that only the survivor could benefit from learning.

Since one of the major assumptions of OFT is that a forager can evaluate the profitability of each food type encountered and rank this relative to the profitability of other prey types (Hughes 1993), I believe more investigations are needed to better understand how the forager is so capable. Ward (1992) argued that satisficing is a valid alternative to OFT (i.e., organisms do enough of whatever is required to survive and reproduce). Hughes (1993) suggested that animals are not perfect and may mistake the identity of some prey before capture. Hughes (1993) mathematically demonstrated why a predator should proceed to eat the "sub optimal" prey instead of discarding it, even after mistaking its identity. While this may in fact work for pallid bats eating 3 or 4 mm flies, assuming only energy is involved and not minerals or vitamins, it alone does not account for pallid bats capturing slugs and discarding them after chewing them. I believe an important element in the flexibility of bats is the testing of different prey, learning what is palatable immediately and through nutritional feedback, and remembering specific events surrounding the detection, capture and consumption of prey. Buchler (1976) suggested that little brown bats made "intentional mistakes", and I suggest that the taking of aberrant prey is critical to maintaining fitness for the individual. Perhaps fitness for the colony is maintained through a combination of individual and matrilineal learning.

Possibly aberrant prey types that do not follow an OFT model based on energy, may be critical to a bat's diet. As an alternative hypothesis, slugs, flies and even the stink beetle may be eaten as important sources of limited nutrients. Male slugs concentrate calcium in reservoirs below the mantle just prior to becoming a female and laying eggs (Fournie and Chaetail, 1982). It is possible that lactating females extract calcium from these slugs by chewing on male slugs with aqueous reservoirs of calcium. I observed discarded slugs only during the mid to late summer when young bats are volant and females are lactating. An alternative hypothesis is that the slugs are captured by lactating females because extra calcium is needed for milk production. Barclay (1993) found that calcium may be a limited resource in some species of bats. Bell (pers. comm.) commented that the Peragnathus captured by a pallid bat (Bell 1982) was observed in mid-summer when females may lactate. I also observed lizard remains and dead slugs at the bottom of a roost in early August when females were lactating.

The role of dietary feedback in learning

Foraging experiments have shown that there are two ways that learning provides the feedback necessary for animals to change behaviour to accommodate changing food resources; animals learn from post-ingestive feedback, and they learn from conspecifics (review by Provenza and Cincotta 1993). Diet selection, in part, is the result of post-ingestive feedback from nutrients and toxins. Rats (Rattus norvegicus) increased their food intake compensating for low caloric foods (e.g., Booth 1985, Gibson and Booth 1989) and for nutritional deficiencies (e.g., Baker et al. 1987, Zahorik et al. 1974, Baker and Booth 1989), and for the recovery from post-ingestive distress (e.g., Green and Garcia 1971). Provenza et al. (1983) also found that cattle develop a preference for supplemental protein blocks when ingesting forage low in protein.

Williams (1978) argued that individual humans are distinctly different in every anatomical and physiological particular, and that this was the basis of individuality in people:

> "Stomachs, for example, vary in size, shape and contour...They also vary in operation.... A Mayo Foundation study of about 5000 people who had no known stomach ailment showed that the gastric juices varied at least a thousand fold in pepsin content. The hydrochloric acid content varies similarly....Such differences are partly responsible for the fact that we tend not to eat with equal frequency or in equal amounts, nor to choose the same foods..."

Few studies have been conducted on the intraspecific variation in responses to toxins, but Keeler et al. (1988) found that while some sheep fed a high (2.5x) level of Galega officionialis failed to show clinical symptoms of toxicolosis, other sheep were killed by a low (1.0x) dose. Keeler et al. 1992 also found a similar individual variation in susceptibility to toxins in Verbesina enceliodes in sheep. Goats vary in their ability to ingest condensed tannins in Blackbrush (Coleogyne ramoissima), a shrub comparatively low (0.67%) in nitrogen (Provenza et al. 1990). Such different responses are possibly due in part to differences in concentration of the many enzymes required for detoxification and digestion (Provenza and Cincotta 1993).

My data suggested that individuals from the Tocaloma population are more specialized than individuals from Caliente. For both populations, I assumed the same aforementioned conditions that Hughes (1979) suggested are important for specialization to occur (i.e., 1) prey types for both populations vary widely in quality, 2) both sets of prey require different techniques and experience, and 3) learning can increase their value in both populations). I also assumed that Heinrich's (1976) suggestion that specialization is expected when the quality of preferred prey becomes marginally profitable due to competition and subsequent depletion of larger items also occurs in both populations. The striking difference between the two populations' environments is the amount of evenness in the diet. If an assumption is made that bats will only change their diet as a result of the availability of their prey, then my data suggests that both diet and prey availability are more uniform in the Tocaloma bats than in the Caliente Mine bats. Fenton and Morris (1976) and Bell (1982) used an artificially created foraging patch and also found evidence that desert bats fed opportunistically and selectively.

Spatial Efficiency and Optimal Foraging Theory

When the cost of sharing a home range is decreased and when dispersal is risky, individuals should do better to remain and share food resources within their natal home range (Waser and Jones 1983). Day roosts and night roosts can be a limiting factor for most bat species (Kunz 1982), and habitat and roosts are diminishing for pallid bats in coastal California, (pers. comm. Pierson). Assuming this is true for Tocaloma bats, the distance from a prey patch to the roost should be a currency constraint. Therefore, each bat can improve its fitness by specializing on specific prey while coexisting within a certain area which becomes the home range. Such a mechanism can increase the efficiency of a colony when individuals effectively take more kinds of prey in a smaller area. Otherwise, diminishing densities of prey, and therefore, intraspecific competition, could force the colony to forage over a greater area, increasing costs to the averaged individual (Orians and Pearson 1979).

Assessing availability of prey

Whitaker (1994) suggests that there are three problems relating to determining the availability of food to insectivorous bats. First, investigators often assess insects where they can trap with their collecting devices; second, bats may have foraged elsewhere before being caught where "availability" is being assessed; and third, at least some species of bats, such as Plecotus, fly to their specific or preferred feeding sites where high concentrations of specific prey exist.

This latter concern could be addressed by radio tracking individual bats over time to map specific foraging areas. Krull (1990) investigated foraging habitat types used by A. pallidus pallidus and found that desert pallid bats, at least, use a variety of habitats including open ground, shrubs, and air space. Light tagged individuals from the Tocaloma colony were observed foraging over valley grassland, coastal sage scrub, rocky meadows, as well as over Mill Creek suggesting that all open habitats are used as foraging areas by the colony. Radio tracking each individual in the colony with dietary data was beyond the financial scope of my investigation, but this work is important. Pierson (Pers. comm.) observed the same pallid bat foraging in the same area in two successive years.

Whitaker's (1994) first two problems associated with assessing availability of prey are more difficult to address than the third aforementioned problem. If sampling is not biased for habitat, several methods should be employed for pallid bats. In addition to the use of pit traps to assess ground and litter/detritus dwelling prey, sticky traps should be used for samples on rocky outcroppings, sweep nets for foliage, and sticky or Malaise traps (Kunz 1988) for airborne insects.

Ultimately, the most complete assessment of what prey is available to an individual bat is perhaps an averaged diet based on pooled data collected from a sample of the same members of the colony at a specified roost during a specified time period. This is made with the assumption that each area or habitat within the home range of the colony is equally accessible to each individual.

Controlling for sex and age class

Some studies suggest that reproductive fitness is responsible for individual variation in diet. Pierotti and Annett (1987) found that some gulls with specialized diets within a colony may have based prey choice on maximizing the intake of limiting nutrients to increase reproductive fitness. Brigham et al. (1992) and Rolseth et al. (1994) found no significant differences in prey choice among four reproductive and age classes (pregnant, lactating, post-lactating, juvenile) for Yuma bats (Myotis yumanensis); however, other studies that reported on North American bat fauna found dietary differences in age and reproductive classes for other species. Wilkinson (1993) reported that differences may exist between the diets of males and lactating females in big brown bats (Eptesicus fuscus), and Rolseth et al. (1994) found that juvenile hoary bats (Lasiurus cinereus) consumed significantly fewer Odonata and more Chironomids than adults from the same area. Incidental data I collected suggested lactating females ate more moths than males or juveniles; however, not enough data was collected to analyze. I excluded young males as described by Davis and Hitchcock (1965) thus controlling for these variables by sampling only mature males. This practice also ensured that maternity colonies were not disturbed during parturition. Since I controlled for age class and sex, other variables must be examined to predict an OFT model for the specialization of individuals.

Conclusion

Many species of arthropods not eaten by pallid bats were found in pit traps , and some prey species were found in only small numbers in traps at Tocaloma and Caliente. Although assessing the availability of prey was difficult and some biases were unavoidable

(Whitaker 1993), my data suggested that both colonies were selective feeders. For determining the availability of prey for each individual bat, the best indicator should be the diet of the colony as a whole for any given period of time. My data revealed that individual pallid bats are more specialized in dietary preferences in a colony where the diet was more uniform in distribution than in a colony where the diet was more patchy. in distribution. Furthermore, my data suggested that the bats from Tocaloma showed individual dietary differences. Spatial efficiency, individual nutritional needs, high costs associated with learning different skills necessary for the detection, handling of prey, and social learning through matrilineal lines may all contribute to individual dietary preferences. Individual bats from both colonies ate small numbers of unusual prey both in the wild and in a laboratory situation, but more work is needed to determine if this is part of a learning mechanism or if this is related to limited nutrients since energy alone from these prey types cannot support energy-based Optimal Diet Theory models. Radio tracking studies are needed to help determine if specialization occurs through individuals' spatial loyalty to specific prey patches with different densities of prey types. Finally, more research is needed to understand the mechanism of maintaining dietary specialization, that is, what is the role socially dependent and independent learning plays, and if there is an OFT model that can predict individual specialization.

Differences in searching and learning behaviour at the individual and population levels

ABSTRACT I captured 6 individually-tagged bats from a colony of Pallid bats (Antrozous pallidus) from the California coast and 5 individually-tagged pallid bats from a colony from Death Valley, California, each with known dietary histories determined by fecal analysis, to test for individual and population differences in learning abilities and foraging behaviour. Latency scores and searching behaviour was measured for three foraging tasks in a laboratory situation for each of the subject animals. The coastal bats from an environment of more uniform prey had significantly faster latency rates of learning than the desert bats from an environment of more patchy prey. Coastal bats did not show significant individual differences in latency rates of learning, but desert bats did. Since the study animal was listed as a California threatened species, I tested a small number of captive pallid bats and big brown bats (Eptesicus fuscus) for the effects of long-term captivity on latency rates of learning, and my data suggested that long-term captivity does not affect this type of learning ability. I compared 5 types of search behaviour between individuals and populations, and I observed that desert bats roosted more time and spent less time on the ground during searches than coastal bats. Two behavioural foraging styles exist in captives which I correlated to dietary preferences. Bats from the desert population did not show significant individual differences

in foraging styles although there may be a weak relationship between diet and time spent crawling. I tested naive non-volant juveniles for an affinity to low frequency sounds, but my results suggested that adult bats' attraction to low frequency sounds is learned.

Introduction

Learning is a mechanism that enables an individual to adapt to changes in its environment. Levins (1968) suggested that it makes sense that the evolution of learning occurs in heterogeneous environments allowing this phenotypic plasticity to increase the fitness of individuals. Stephens (1991) used genetic population models and suggested that individuals need some uniformity in the environment to develop learning, but that in an absolutely fixed environment, only a fixed genetic pattern of behavior should evolve. Recent genetic population models using fixed and "plastic" alleles (Anderson 1995, and Bergman and Feldman 1995) suggested that learning is always a favored state in a uniform environment, but environments in an intermediate state between a uniform and a patchy state are the best situations to allow learning to evolve.

Hughes (1979) suggested that individual differences in foraging style may develop when learning facilitates taking prey with different handling and detection skills. Within a single colony female sea otters demonstrate individual prey preferences, and the same females live within the same or overlapping home ranges (Lyons

1991). This author suggested that preferences are learned by juveniles through matrilinear means. If pallid bats' dietary preferences reflect individual flexibility, each member of a colony could develop individual preferences for specific prey types as a function of experience and learning as suggested for other animals (summarized by Kamil 1987), and groups of individuals within a population could develop different foraging styles as described by Goss-Custard and Sutherland (1984) in oystercatchers or in roof rats (Rattus rattus) by Terkel (1996). Goss-Custard (1984) found that oystercatchers in the same population exhibit two different ways of opening mussels. Certain individuals opened mussels underwater while other oystercatchers opened these mollusks only above water; each situation required a different technique which was learned from a parent (Goss-Custard 1984). A similar matrilinear mechanism is responsible for two different techniques that roof rats apply to open pine cones for seeds (Terkel 1996). Krull (1990) observed pallid bats in many habitats taking prey requiring various skills (i.e., moths in air, insects on shrubs, arthropods on the ground). If learning is necessary to detect, capture, and handle very different kinds of prey such as is found in the diets of pallid bats, then there may be different skills to develop to optimally forage on certain prey types.

Baldwin (1896) proposed how learning can be advantageous to individuals whose behavior is only partially genetically determined. Baldwin (1896) explained that learning allowed an individual to complete a partially programmed behaviour, thus increasing the chance for survival. This individual advantage of learning, stated Baldwin, "guides evolution so that ontogenetic adaptation in the earlier generation is kept in existence and utilized more widely in the subsequent generation". This process that allows learning to assist in the integration of genetic components of behaviour into the gene pool is now referred to as "genetic assimilation" or the "Baldwin affect" Maynard-Smith (1987). To my knowledge there is little known about foraging skills learned by juvenile bats. Brown et al. (1978) reported on the development of hearing in juvenile pallid bats, but we do not know if the foraging skills are inherent, or learned; or a combination of both. We do know that bats develop skills as they mature as suggested by the change in diet to potentially more desirable prey (Anthony and Kunz 1988) and the ability to discern objects through echolocation Brown et al. (1978). Perhaps there is inherited information that bats can use as a base or "template" to then "fine tune" through learning for specific situations.

My hypotheses are therefore:

1) Individual pallid bats from populations with a more uniform prey distribution will learn faster than pallid bats from a more patchy prey distribution.
2) Pallid bats will show individual differences in time spent for searching behaviours when tested on foraging tasks in a laboratory situation.

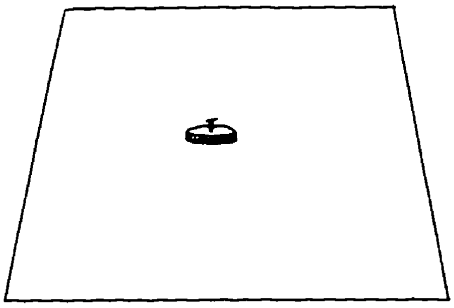
3) Long-term captive bats will have slower latency rates of learning than recently acclimated wild bats for foraging tasks performed in a laboratory.

4) Naive juvenile pallid bats demonstrate an affinity for insect-generated low frequency sounds as an inherited part of a prey detection mechanism.

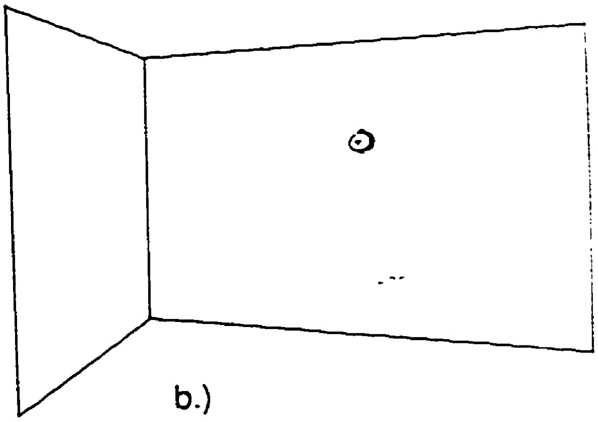
Materials and methods

In 1993, I captured 6 bats from the Tocaloma population to develop foraging tasks in a laboratory situation to test individual differences in learning abilities and foraging behaviour (**Fig. 16**). Then in 1994, I captured 6 bats from Tocaloma and in 1995, 5 bats from Caliente (see study areas Fig. 2), each with a known dietary history, to conduct laboratory studies on their specific learning and searching behaviour. I released all bats at the respective capture sites within 10 weeks of capture date. I used a latency rate of learning model from Dill (1983) to compare differences in foraging flexibility for each bat for 3 tasks (Dish, Tube, and Plant) that I chose out of the 7 tested in 1993. Each object for each of the tasks as described (Fig. 14) had a meal worm attached to a metal clip. I measured latency or time to first capture prey (Kiefer and Colgan 1991), and the intercapture interval or time between captures (Gotceitas and Colgan 1988) described by Kamil et al. (1987). Colgan (1991) and Johnston (1982) have commented on the importance of making foraging tasks similar to field situations, so

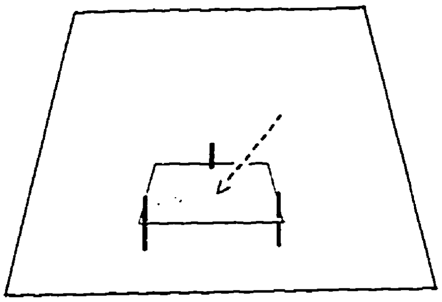
Fig. 16a-g. Seven objects, each with a meal worm, creating foraging tasks given to bats: a) petrie dish in center of room, b) petrie dish on vertical surface 1.5 m above floor, c) under cover positioned 20 cm above prey, d) bottom of inside of tube 8 cm diameter by 30 cm long, e) under cardboard pieces on floor, f) inside tomato or willow shrub 35 cm high, g) underside of tree branch 1.5 m high.
* Indicates task used for comparisons between individuals and populations. -------> Indicates placement of meal worm where not visible by experimental design.



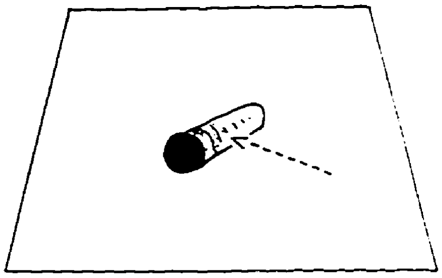
a.) *



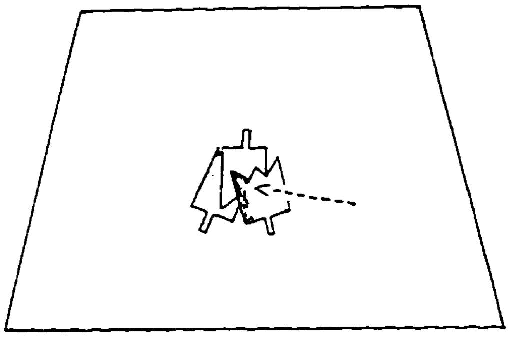
b.)



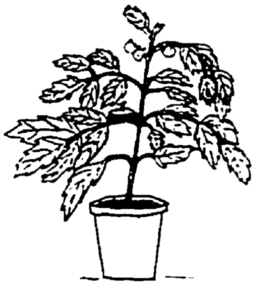
c.)



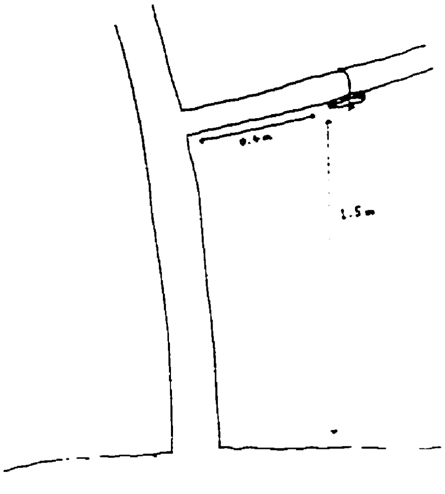
d.) *



e.)



f.) *



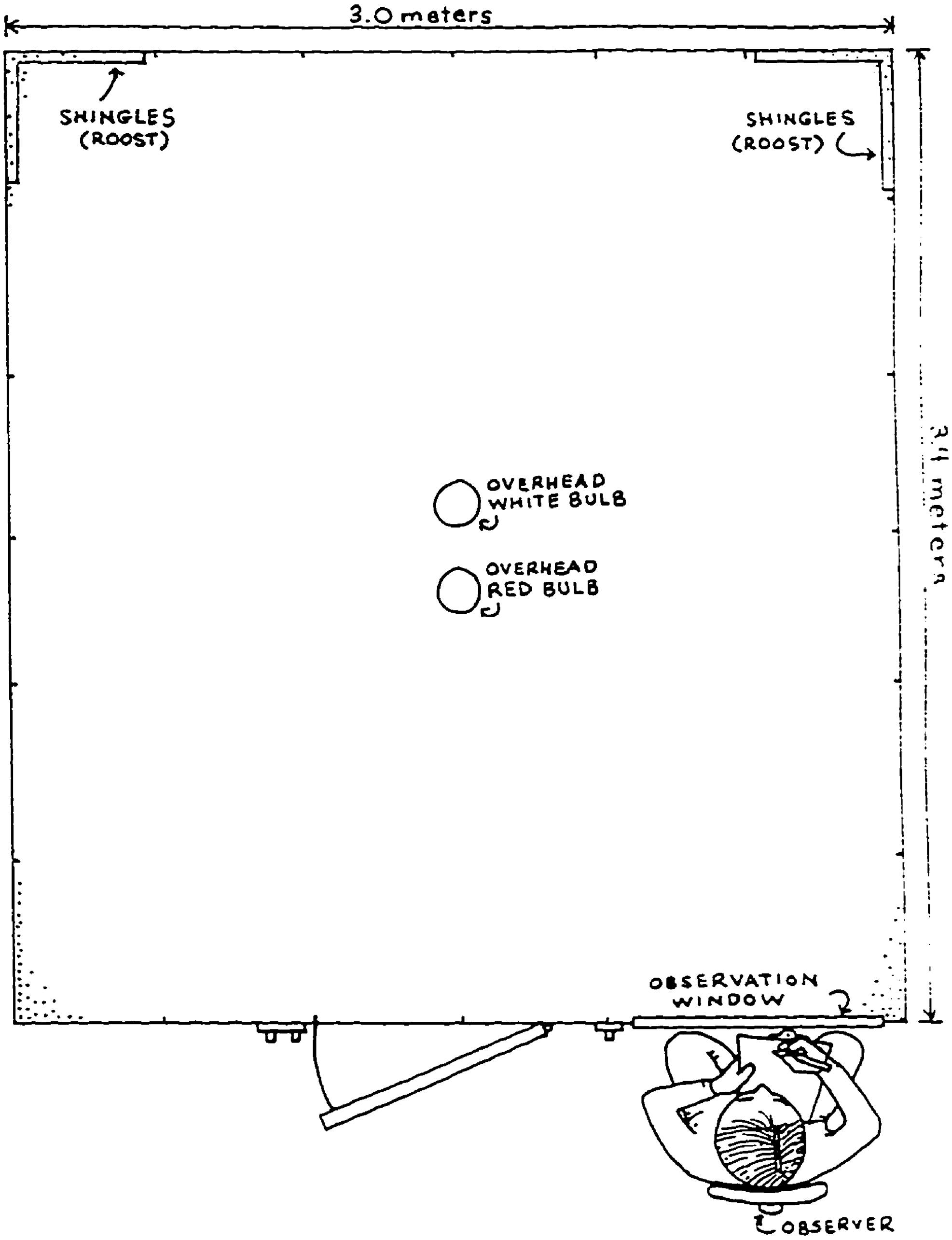
g.)

each of the three chosen tasks given to individual pallid bats represented a potentially real but new foraging situation.

The first task, making contact with a meal worm attached to the center of a plastic petrie dish on grid square B4, allowed full vision of the prey and access by crawling or flying to the prey site on open ground **(Fig. 16a)**. The second task, making contact with a meal worm attached to the bottom center of a tube on grid square C2, eliminated vision of the prey and required the subject bat to enter and crawl into the tube from either opening **(Fig. 16d)**. The third task, making contact with a meal worm attached to a plant stem on grid square D5, allowed vision of the prey but in a cluttered situation. This task required the subject bat to either land at the base or the top of the plant and then crawl up or down along the plant stem to the meal worm **(Fig. 16f)**.

I first tested foraging tasks in a 3 m x 3 m x 2.5 m screened tent erected outdoors. My results were possibly confounded by uncontrolled variables, so to control temperature, background noise, light and to make visual observations for subsequent experiments, I designed and built a flight room adjacent to the laboratory **(Fig. 17)**. The room was 3.0 meters wide by 3.4 meters deep and 2.5 meters high, with white and red lights on dimmers, two outlets, an exhaust fan, a portal for electrical wires and an observation window viewed from the lab. The walls and ceiling were constructed of wall board and painted white. The bottom had 3 cm of construction grade sand which recorded imprints of landings and crawling. The perimeter of

Fig. 17. Diagram of flight room used to observe foraging behaviour and measure latency scores.


3.0 meters
SHINGLES (ROOST)
SHINGLES (ROOST)
3.4 meters
OVERHEAD WHITE BULB
OVERHEAD RED BULB
OBSERVATION WINDOW
OBSERVER

the bottom of the walls had tick marks dividing the floor space into a grid with 36 equal rectangles each 50.0 cm x 56.6 cm. Observations in the flight room were illuminated by the red light and adjusted by rheostat to a constant 0.01 light candles per foot.

Mature male pallid bats from each population were captured and housed in a 35 cm x 35 cm x 49 cm aluminum screen and Plexiglas cage for about a week as a part of their acclimation to captivity as suggested by Gaudet (1982). Each bat was allowed to fly on most evenings in the flight room. Wilson (1988) was used as a guide for the care of captive bats. Each bat was weighed nightly and fed a controlled number of a single prey type, mealworms (Tenebrio molitor), to control for individual prey choice as suggested by Kieffer and Cogan (1991). Mealworms were fed oatmeal, sliced raw potatoes, celery, carrots, and spinach. In addition, mealworms were also often rolled in a vitamin and mineral powder before being fed to the bats. Gaudet (1988) recommended reducing a bat's weight to 2/3 of its weight at capture to ensure it is motivated to search for prey in captivity. My study bats, however, were motivated to forage at 5/6ths of their original capture weight, so I didn't continue to reduce their weight after this point.

At the end of the first two weeks in captivity, I placed each bat separately in the flight room with a petrie dish of mealworms, allowing each to learn that mealworms were available. The following night I placed each bat inside the tent or room on a spot 2 m above the floor on one wall. For each task, the bat was placed in the southeast corner roost and clocked from that moment until it left the site and again when it completed the task by making contact with the meal worm. For every trial for each task, a specific location was used, and the location changed for each task.

Since different bats left the starting site at different times and it appeared as though this affected the bat's level of comfort in the enclosure, search time started when the bat took flight the first time. To find each individual's rate of learning (Kamil et al. 1987), I repeated the process for each task 4 more times, once on each successive night. To control for a potential increase in latency period due to satiation of appetite and depreciation of motivation, I provided one "king" meal worm weighing approximately 0.5 grams each, once a night for five consecutive nights.

I recorded six different activities, including roosting, flying, hovering, land-listening, crawling, and jumping (**Table 5**). I used only the first trial of the tube to record various searching behaviours because subsequent trials (Days 2, 3, 4, and 5) were shorter with a minimum number of searching activities (e.g., roost for 1 second, fly for 7 seconds, and land on object with prey). Once a bat made contact with the prey, I stopped recording. Crawling made tracks on the sand which was recorded along with all landing prints on a foraging grid for first trials (**Appendix 4a - m**).

Three naive non-volant female juveniles 39 days old (pers. comm. Pat Winters) from California Bat Conservation Fund, a wildlife rehabilitation center, were tested to determine if naive juvenile

TABLE 5. Descriptions of searching behaviours

Roosting	Anytime a bat roosted in an upper corner of the flight room. Roosting included a variety of behaviour including grooming, resting and listening which I could not always separate.
Crawling	any quadrapedal motion on the floor or object in the flight room
Land-listening	anytime a bat was horizontal on the sandy floor of the flight room. Normally bats never "rested" on the floor, rather they appeared to actively listen for prey by moving their head and ears while remaining otherwise motionless. When bats landed, they left an imprint with their forearms which made an open V print on the sandy floor.
Flying	any volant activity with direction
Hovering	flight without any directional motion.

pallid bats had an affinity to the low frequency sounds generated by prey. Each bat was placed at one end of a Y maze three hours after their normal feeding time to help ensure they were motivated to eat. In order to ensure a constant sound, rather than using a live prey which may make low frequency sounds intermittently, I recorded the sound of a June beetle, a known prey item (Hermanson and O'Shea 1983) flying inside a paper bag using a Sony CSF 1000 cassette tape recorder capable of recording low frequency sounds. A speaker with a recording of the beetle inside a paper bag was placed at one exit and another speaker was placed at the other exit without being played. Position of the "beetle speaker" was randomly determined on each trial, and care was taken to attenuate the speaker to the approximate loudness of the live beetle although loudness was not actually measured. A total of 18 trials were run between the three bats. A score of 1 was given if the bat chose the side with the beetle sound, a score of 2 if they chose the silent speaker, and no value if they made no response or did not choose a side to exit. For a control, I used two adults, Bat # 23 from Tocaloma and Bat # 53 from Caliente and the experiment was repeated with 5 trials each. For a more normal situation for adults that would allow them to "forage" by flying as opposed to crawling in a Y maze, two closed paper bags were placed in the room, one with a moth and the other empty. Each bat was given another 5 trials.

Total search time was used for each successive trial to measure and graph the latency to complete each task for each subject animal.

A one-way ANOVA test for different declining total search time scores was used to determine if the bats were learning. Learning for each bat and each population was significant where the probability of the slope of a line did not equal 0. A repeated measures ANOVA (Zar 1984) was used to determine differences in the learning abilities between individuals, days and tasks. Roosting, flying, crawling, and siting and listening times in minutes between individuals were tested for significant differences by one-way or two-way ANOVA (Zar 1984). Since the sample sizes for the two groups of bats was unequal, scores for the same roosting and searching times between populations were tested using the nonparametric Mann Whitney U test (Sokal and Rohlf 1973).

Results

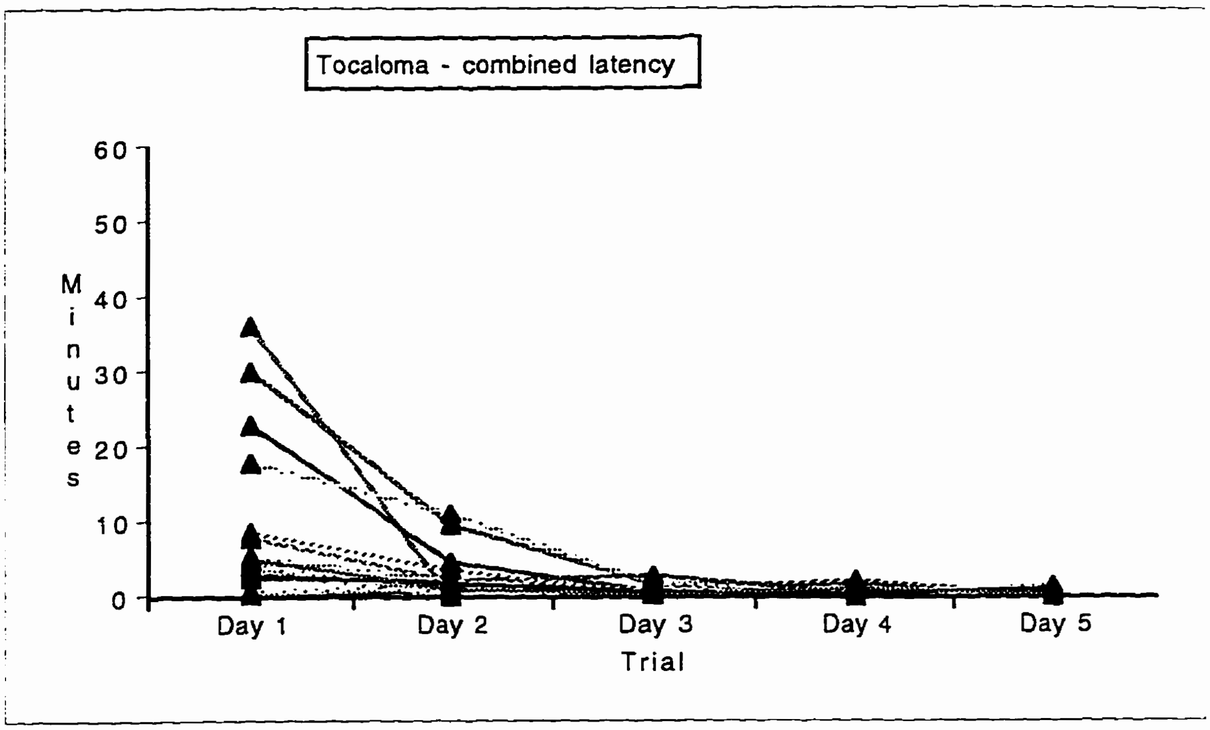
Latency scores

The data from the 5 bats from the Tocaloma population in summer 1993 showed a declining linear trend in time to complete a task for 6 of the 7 tasks (i.e., each successive trial demonstrated a faster recovery). Performance on the plant task did not reach statistical significance probably because one of the bats had difficulty completing this task on the second trial (one-way ANOVA, df = 4, F = 3.66, p = .079). For this task, most bats either jumped onto the base from the ground or flew on the plant. rather than attempt to crawl up the plastic sides of the container as Bat # 05 did. Scores for tasks not completed were not included in the latency rate of learning statistics. There was no significant difference between the scores of individuals (ANOVA, df = 4, F = 0.66, p = 0.64). From these tasks, I determined that some overlapped potential situations in the field, so I limited tasks for the ensuing tests to Dish, Tube, and Plant (**Fig. 16**).

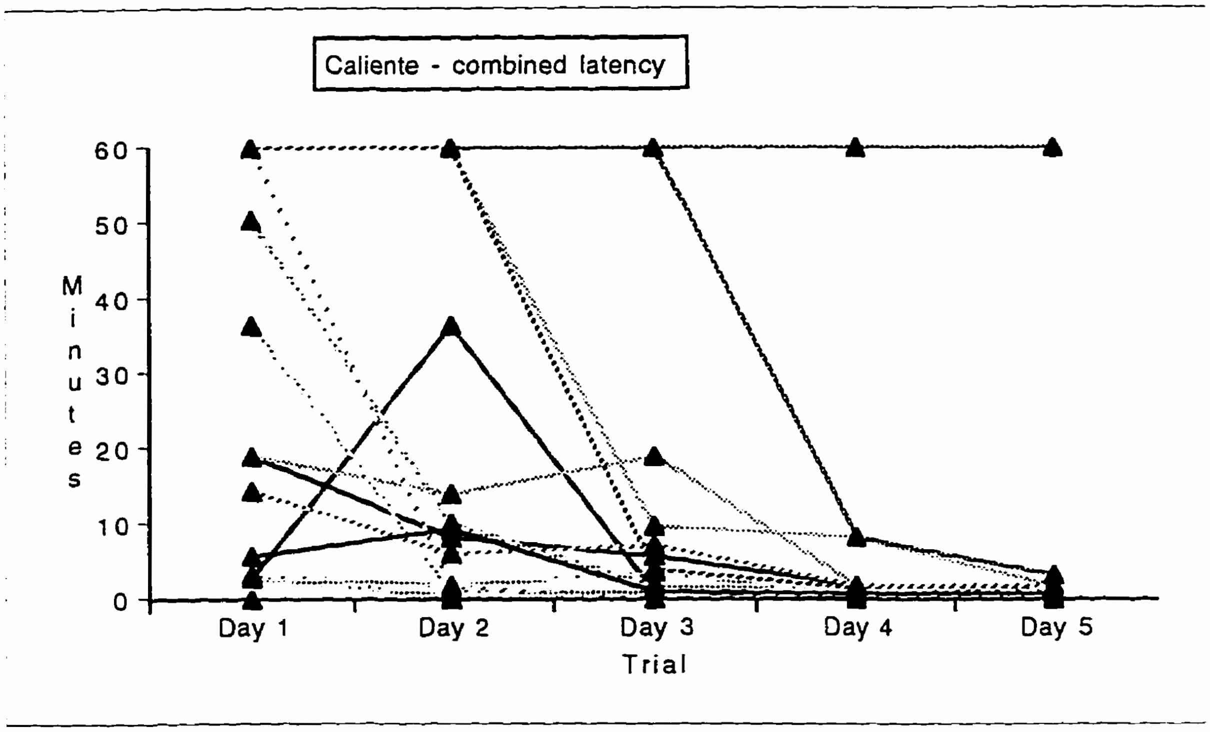
Data from 6 bats from the Tocaloma population in summer 1994 showed a strong declining linear trend in latency scores (ANOVA, df = 5, F. = 9.06; p < 0.001) (**Fig 18a**). The pooled std = 5.765 min. Data from 5 bats from the Caliente population in summer 1995 also showed a declining linear trend with significant latency scores (repeated measures ANOVA, df = 4, F. = 3.92; p = 0.006). The pooled standard deviation for Caliente bats was 20.79 min. (**Fig. 18b**).

Bats from an environment with a more patchy prey distribution did not perform faster than bats with more uniform prey distribution. Clearly, the 6 Tocaloma bats completed tasks in significantly less time than the 5 Caliente bats (**Fig. 18a, b**). A comparison between all scores for both populations of bats suggested that bats from Tocaloma have shorter latency scores (one-way ANOVA (df = 10, F = 23.39, p < .001). Distribution of the means for 11 pallid bats for all trials from Caliente and Tocaloma populations shows a greater variation in scores among the Caliente bats (**Fig. 19**). Using all scores, mean times and standard deviations for Tocaloma bats: N = 90, Mean = 2.68, std 5.78; and for Caliente bats: N = 75, mean = 14.53, std 22.37.

Fig. 18a, b.) Pooled data for latency scores for 6 Tocaloma bats and 5 Caliente bats.



a) Tocaloma



b) Caliente

To control for results that may be skewed from some Caliente bats potentially inclined to hibernate because of the proximity of testing time to hibernation time (see discussion), I eliminated tasks for bats that did not complete the first trial (i.e., tasks for each bat with a score of 60 minutes) and compared only scores for Day Five for all remaining trials. With this modified data set, the Tocoloma bats still performed in less time than the Caliente bats (Mann Whitney U, $p = 0.049$).

There was no significant difference in the Tocaloma bats between the three tasks (two-way ANOVA, $df = 2$, $F = 0.94$, $p = 0.54$) or between individual's combined latency scores (two-way ANOVA, $df = 5$, $F = 1.52$, $p = 0.199$). Bat # 10 and Bat # 31 first completed two of the tasks in less than a minute, and therefore did not show a significant decrease in time (**Fig. 20a, e**). With only slightly higher first-day times, Bat # 19 also did not significantly decrease the time required to complete each task (**Fig. 20d**). This data was consistent with my initial data on Tocaloma bats using 7 tasks suggesting that individual differences between bats' latency scores only approached significance.

There were significant differences between latency scores for 5 individual Caliente bats for three tasks for five-day trials (repeated measures ANOVA, $df = 4$, $F. = 5.14$; $p = 0.002$) and between the three tasks (repeated measures ANOVA, $df = 4$, $F = 3.27$, $p = 0.044$) (**Fig. 21a-e**) (See **Appendix 5** for means and standard deviations). Bat # 102 and Bat # 103 had poor success at

Fig. 19. Distribution of the means for 11 pallid bats for all trials from Caliente and Tocaloma populations.

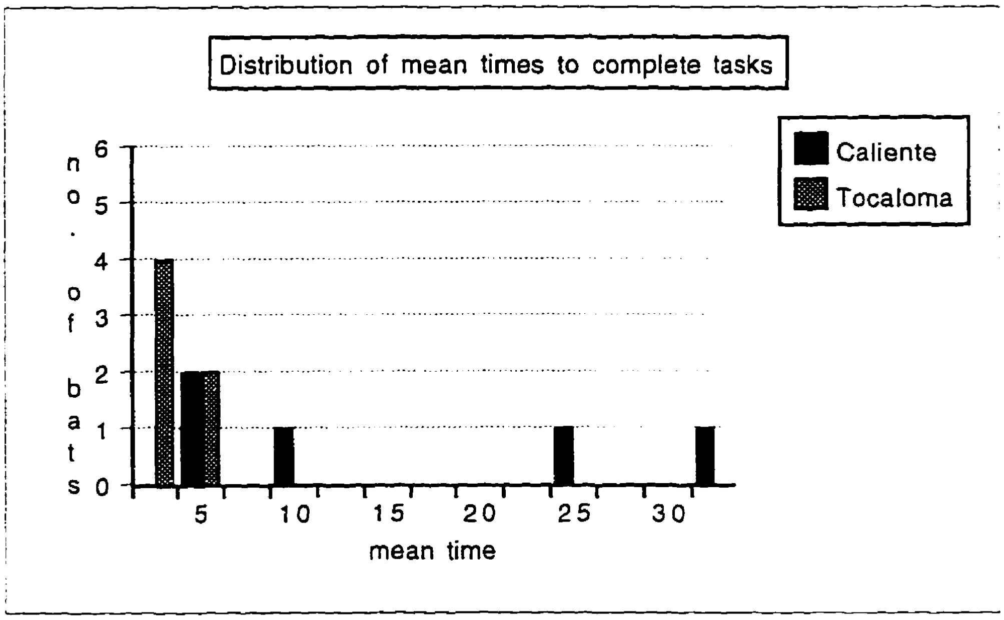
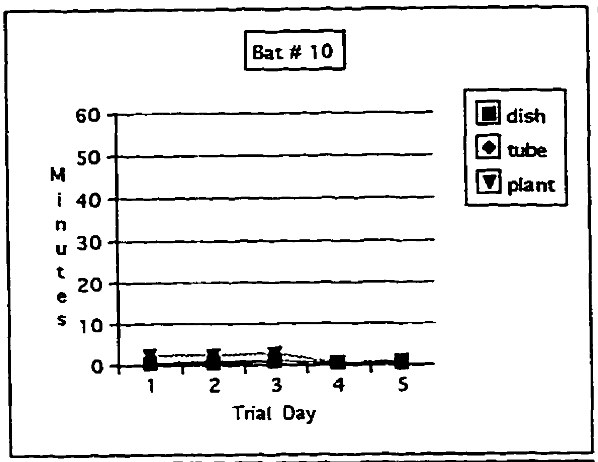
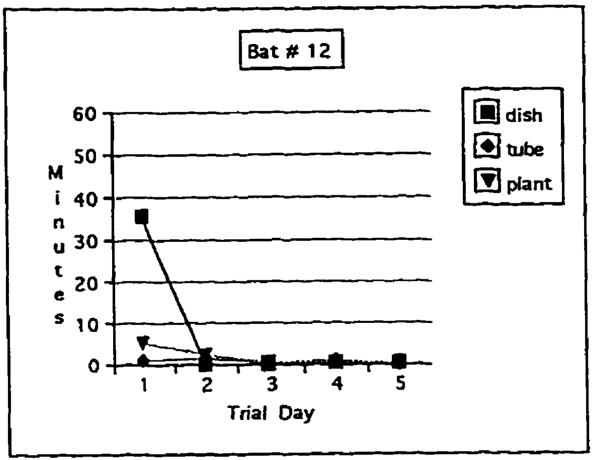
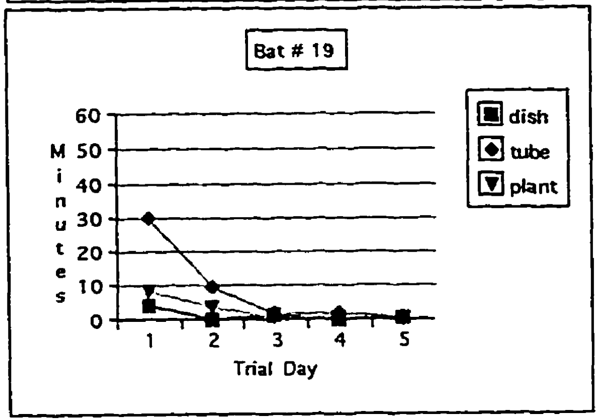
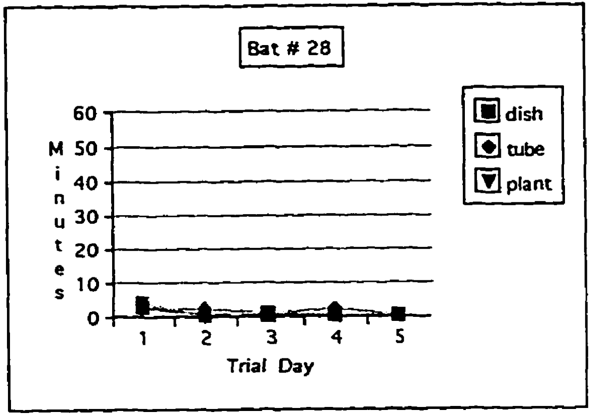

Distribution of mean times to complete tasks
Caliente
Tocaloma
no. of bats
0
1
2
3
4
5
6
5
10
15
20
25
30
mean time

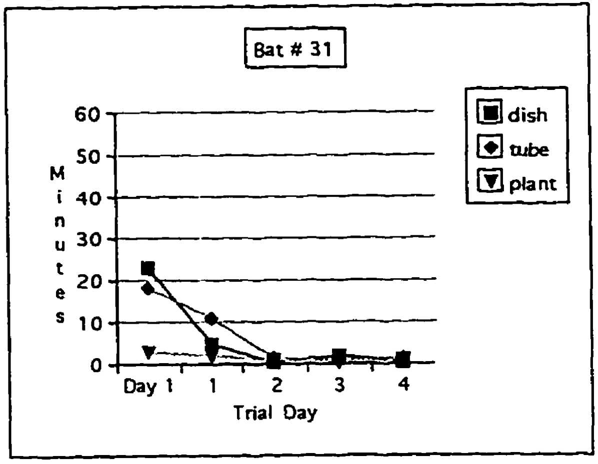
Fig. 20a - f. Latency scores for 3 tasks for 6 Tocaloma bats over the course of 5 trials.

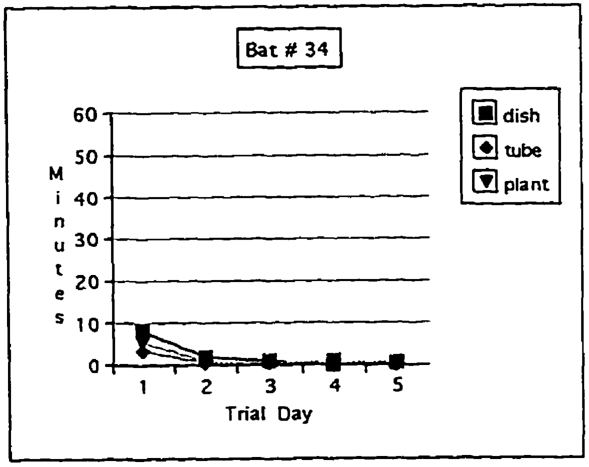

Bat # 10


Bat # 12


Bat # 19


Bat # 28


Bat # 31

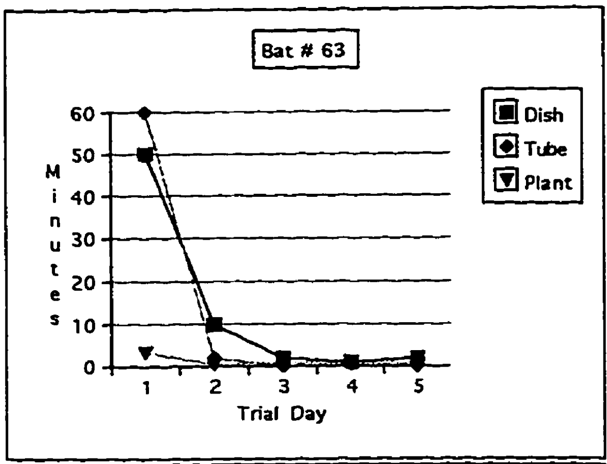

Bat # 34

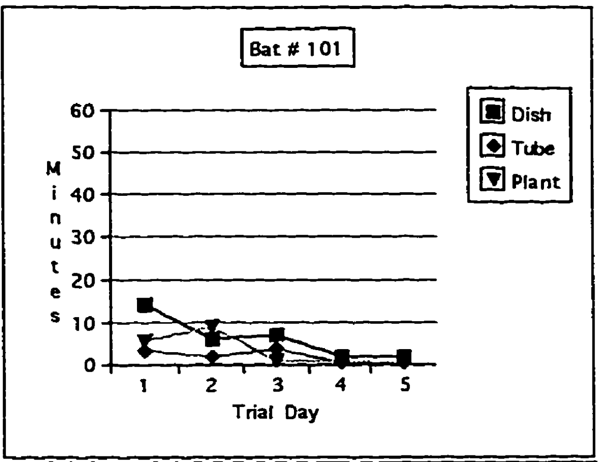
completing tasks, particularly the tube task which Bat # 103 never completed, giving the highest possible scores of 60 minutes for each of five tube trials. Trials to recover the meal worm that exceeded 60 minutes were scored as 60 minutes and the bat was then placed back in his cage. Complications arising from bats possibly entering long-term torpor could have skewed results, although temperatures were increased in the flight room from 22° C to 27° C and 29° C. to increase bats' metabolic rate (Trune and Slobodchikoff 1976).

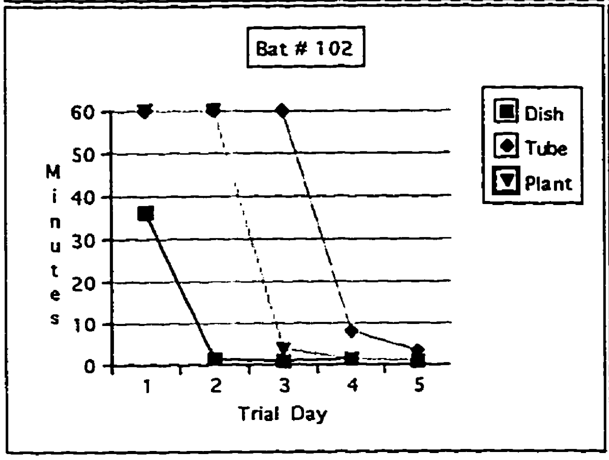
Although scores were significantly higher for the tube task, I observed bats repeatedly landing in the front of the tube with some reluctance to enter (i.e., the bat would land-listen in front of the tube entrance, but fly off again repeating this cycle until it finally crawled into the tube and ate the meal worm. If the first time a bat landed on or near the tube counted as a capture, there would be no significant difference between combined scores for each of the tasks.

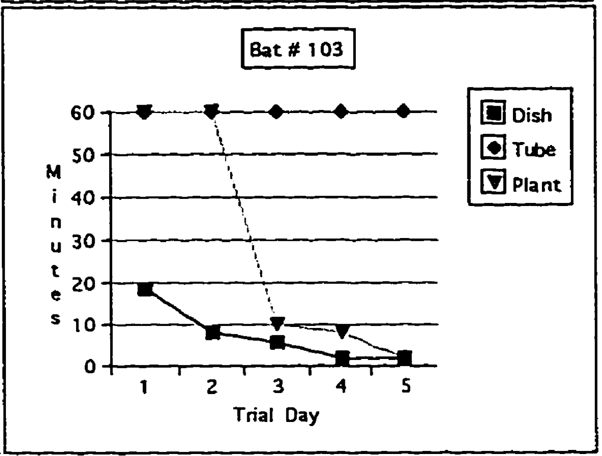
There was no difference between the latency rates of learning scores in long-term captive bats and recently acclimated wild bats. Although there was a significant difference in scores between the old and physically handicapped pallid bat (Bat # 602) and the other three long-term captives (one pallid bat, Bat # 601, and two big brown bats, Bat # 701 and Bat # 702), there was no significant between these three long-term captives and the acclimated wild pallid bats (**Fig. 22**). Three of the captive bats in five trials for the dish significantly reduced the amount of time it took them to complete the second task over the course of five days (one-way

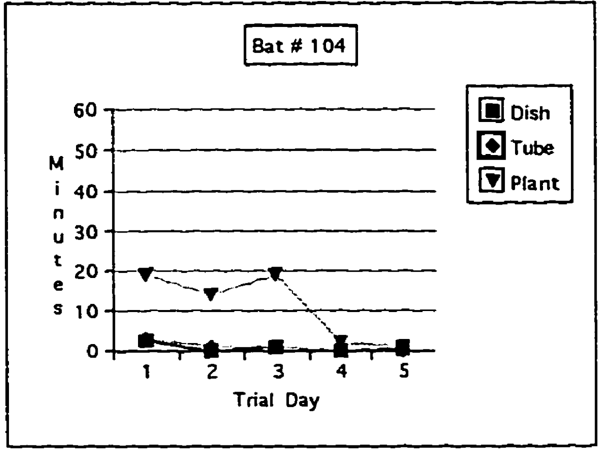
Fig. 21 a-e. Latency scores for 3 tasks for 5 Caliente bats over the course of 5 trials.


Bat # 63
Dish
Tube
Plant
Minutes
0
10
20
30
40
50
60
1
2
3
4
5
Trial Day


Bat # 101
Dish
Tube
Plant
Minutes
0
10
20
30
40
50
60
1
2
3
4
5
Trial Day


Bat # 102
Dish
Tube
Plant
Minutes
0
10
20
30
40
50
60
1
2
3
4
5
Trial Day


Bat # 103
Dish
Tube
Plant
Minutes
0
10
20
30
40
50
60
1
2
3
4
5
Trial Day

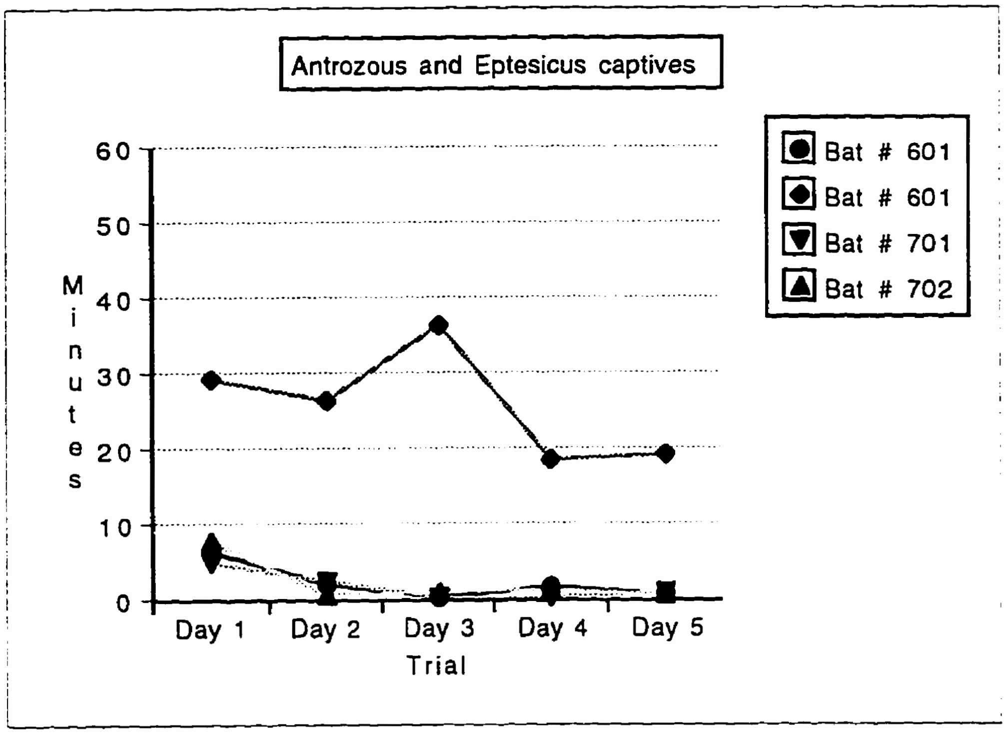

Bat # 104
Dish
Tube
Plant
Minutes
0
10
20
30
40
50
60
1
2
3
4
5
Trial Day

ANOVA, df = 4, F. = 24.5; $p < 0.001$). However, there was no significant difference in the scores for Bat # 602 who has gout according to Scott Sims DVM (Pers. comm.), and dermatitis as a result of his inability to groom himself thoroughly. Bat # 602 was fully ambulatory (see foraging grid, Appendix 4m), and completed tasks without flying. Although Bat #602 responded to sounds generated by other bats eating, his hearing and memory may have been impaired. The data for Bat # 602 suggested that this bat randomly found the meal worm on each successive trial. There was no significant difference between the other long-term captive pallid bat and big brown bats. Three of the captive bats significantly reduced the amount of time it took them to complete five trials for tasks (two-way ANOVA, df = 4, F. = 24.5; $p < 0.001$), and one disabled pallid bat # 602 did not (two-way ANOVA, df = 4, F = 0.02, $p = 0.89$).

Searching behaviour

Of the five types of searching behaviour, bats rarely hovered after acclimating to finding prey in captivity, unless confronted with an unusual situation such as a visitor to the flight room. Jumping behaviour was only observed during the branch task with prey on the underside of a limb 1.5 m high although Tocaloma bats regularly tried jumping out of their cage since the Plexiglas front prevented them from crawling out. Roosting was not considered a searching behaviour since I could not always assess when bats listen for prey at the roost. Bats usually made many passes over prey as described

Fig. 22. Latency scores for tube task trials for 2 captive pallid bats (A. p. pallidus) (Bat # 601 and Bat #602) and 2 captive big brown bats (Eptesicus fuscus) (Bat # 701 and Bat # 702).

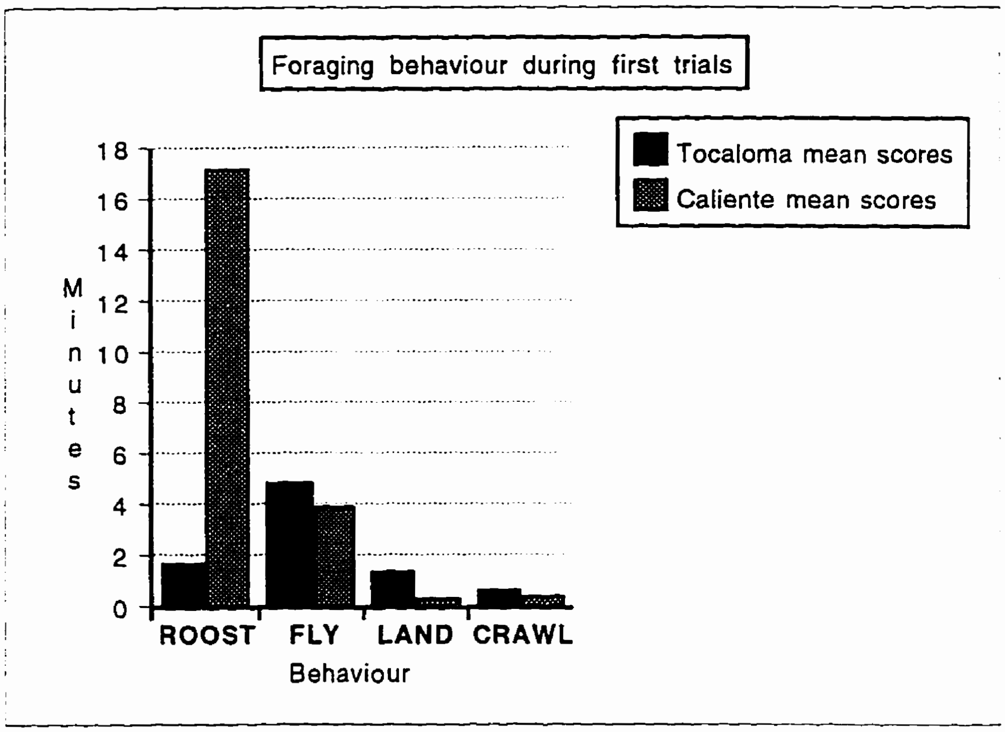

Antrozous and Eptesicus captives
Bat # 601
Bat # 601
Bat # 701
Bat # 702
60
50
40
30
20
10
0
Minutes
Day 1
Day 2
Day 3
Day 4
Day 5
Trial

by Gaudet (1982) and Grant (1988) before landing.

There was no significant difference between tasks for each of the behaviours (one-way ANOVA, df = 2, F = 3.11, p = 0.108). For searching behaviour in both populations, flying time was significantly greater than "land-listening" (one-way ANOVA, df = 1, F = 10.99, p = 0.002). Roosting was significantly greater in the Caliente population (one-way ANOVA df = 10, F = 5.58, p = .028), and land-listening was significantly greater in the Tocaloma population (one-way ANOVA, df = 10, F = 8.78, p = .007) (**Fig. 23**). Roosting time for the Caliente bats could have been biased if these bats were less motivated to forage (see discussion). The Tocaloma bats spent significantly more time on the ground for the land-listening activity (**Fig. 23**) (mean = 1.52, std. = 1.25) than the Caliente bats (mean = 0.22, std. = 0.09) (one-way ANOVA df = 1, F = 8.78, p = 0.007). There was no significant difference in crawling or flying times between the two populations.

There was no significant difference between the individual bats' scores for roosting time, flying time, or "land-listening" time in the Tocaloma population, but there was a significant difference in crawling time among bats. Bat # 19 and Bat #12 spent significantly more time crawling than the other bats (**Fig. 24**) (one-way ANOVA, df = 5, F = 11.64, p < 0.008). For purposes of the discussion and further analysis of the data, I refer to bats that engaged in more than 30 seconds of crawling in a first trial as "crawlers" and all others, with mean crawling times less than 10 seconds, as "non-crawlers". I

Fig. 23. Searching and roosting behaviour organized into mean times for bats from Tocaloma and Caliente.


Foraging behaviour during first trials
Tocaloma mean scores
Caliente mean scores
Minutes
18
16
14
12
10
8
6
4
2
0
ROOST
FLY
LAND
CRAWL
Behaviour

never observed "non-crawlers" crawl for the purpose of investigation or searching for prey. Rather, I found that they only crawled short distances after already appearing to have detected prey (e.g., a non-crawler land-listened on the sand near prey, then crawled for 1 to 4 seconds to capture prey).

Correlation between diet and foraging style

In summer 1995 I found that Bat # 48, Bat # 10, and Bat # 19 only ate wingless, ground dwelling arthropods while Bat # 28 took not only moths but also flies. I had already observed that some bats crawl much more than others, so I hypothesized that there was a relationship between a bat's diet and its foraging style (i.e., how much time it spent flying vs. crawling and which prey it ate). I found a correlation between the number of flightless arthropods in a bat's diet and the amount of time it spent crawling in the first trial of a task (Pearson correlation = 0.991) (**Fig. 25**). I also tested two additional bats, # 23 and #53, and correctly predicted that they were "crawlers" as measured by the amount of time crawling for the first tube task.

Naive juveniles' affinity toward low frequency sounds

Naive juveniles have no apparent affinity to low frequency sounds when they are hungry. There was no significant difference in the naive bat's choice between the speaker with the sound of an

Fig. 24. Mean crawling times for Tocaloma bats.

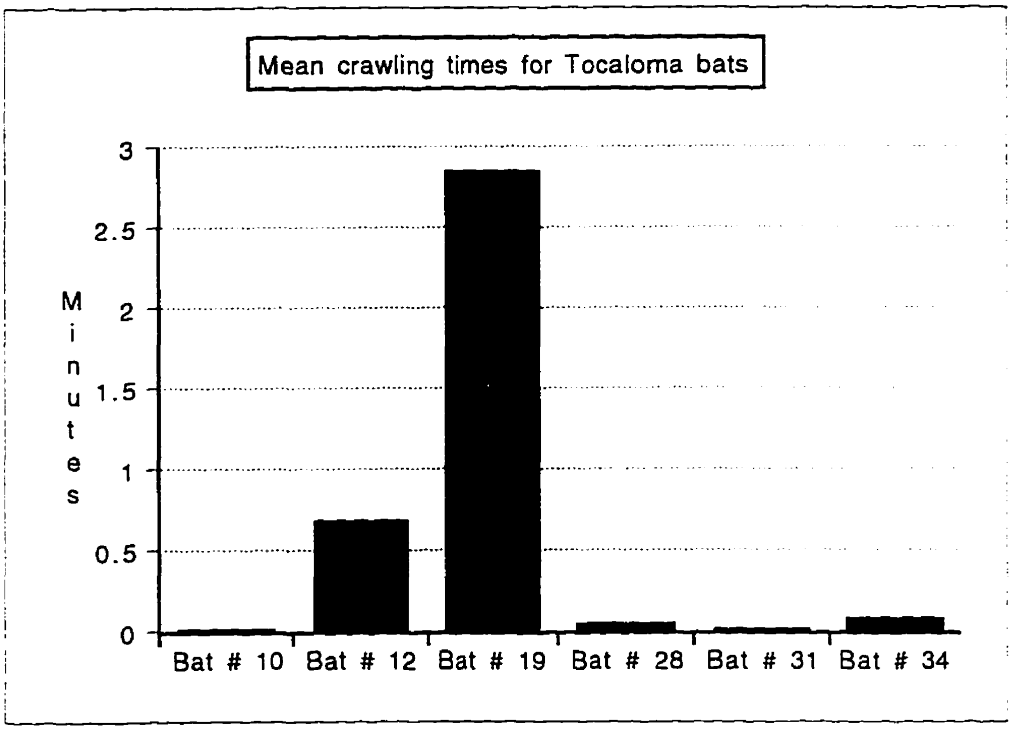
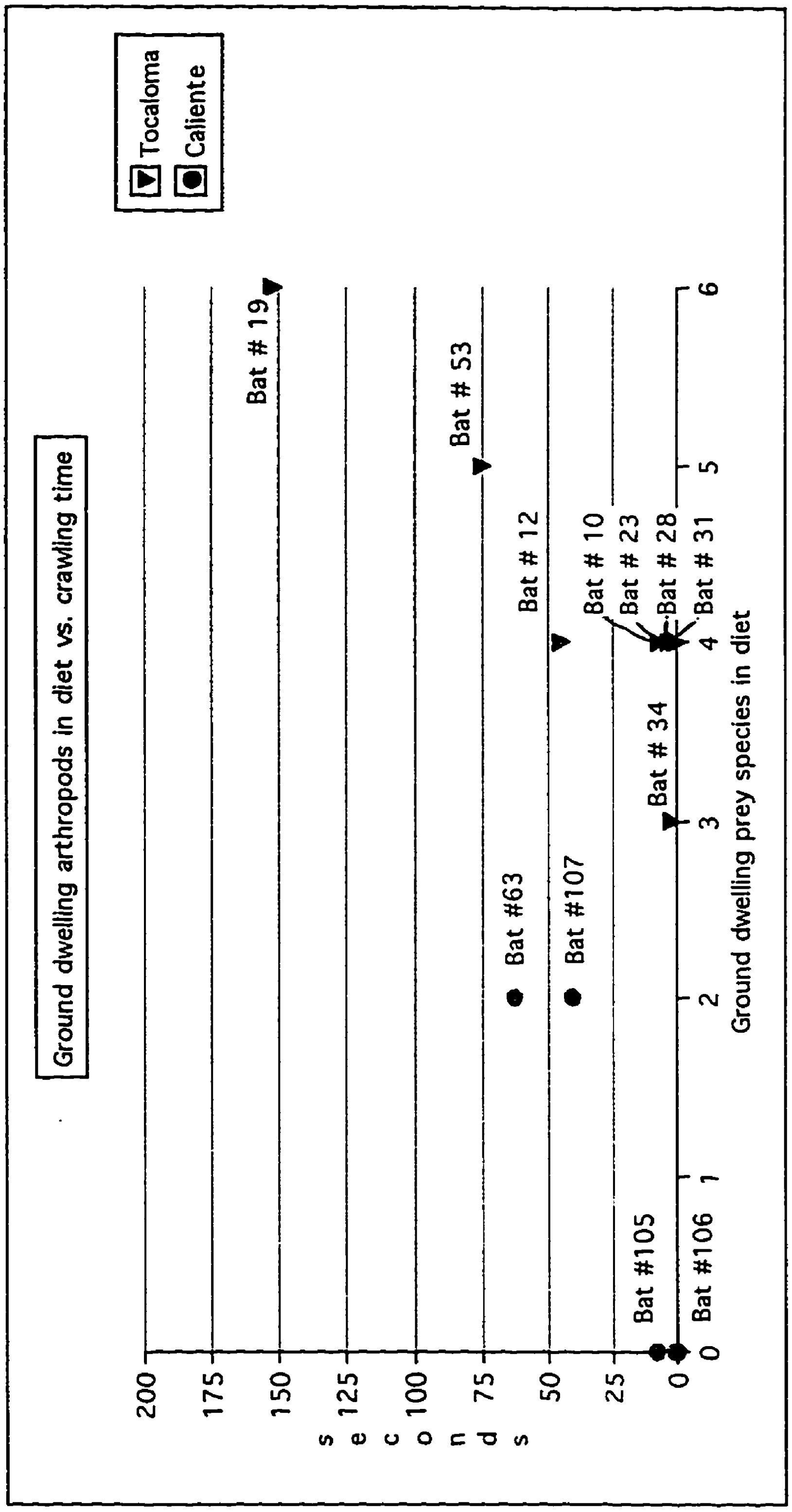

Mean crawling times for Tocaloma bats
Minutes
3
2.5
2
1.5
1
0.5
0
Bat # 10
Bat # 12
Bat # 19
Bat # 28
Bat # 31
Bat # 34

Fig. 25. Number of seconds spent crawling in first tube trial vs. the number of flightless groups of arthropods observed in the diet of 12 bats from Tocaloma and Caliente.


Ground dwelling arthropods in diet vs. crawling time
▼ Tocaloma
● Caliente
s e c o n d s
200
175
150
125
100
75
50
25
0
0
1
2
3
4
5
6
Ground dwelling prey species in diet
Bat # 19
Bat # 53
Bat # 12
Bat # 10
Bat # 23
Bat # 28
Bat # 31
Bat # 34
Bat #63
Bat #107
Bat #105
Bat #106

active beetle and the silent speaker (one-way ANOVA, df = 2, F = 1.05, p = 0.325). The acclimated wild adult bats chose the "beetle" speaker over the silent speaker every time; they also only landed on or near the bag with a moth and only flying passes were made over the empty bag.

Discussion

Although Kieffer and Colgan (1991) used latency rate of learning scores to measure aspects of individual foraging flexibility, the intercapture rate in a laboratory situation may be a better indicator of spatial memory where flexibility is enhanced in the lab through increased hunger. Werner and Hall (1981), Kislalioglu and Gibson (1995), Ehlinger (1989), and Kamil and Yoerg (1982), have all reported on aspects of foraging flexibility, but did not specifically investigate individual animals' exploring aspects of foraging behaviour. Heinrich (1996) presented various objects to ravens to specifically measure the individuals' investigative response to new objects. This exploratory function in foraging flexibility is an important variable that I believe is underrepresented when measuring foraging flexibility by latency rates of learning, even with new prey types.

The first time of capture may be an indicator of exploring behaviour, but its importance is diluted with the intercapture rate scores which may be better indicators of working and spatial memory in my tests. The Tocaloma bats performed with faster latency rates of learning, but this may be a better indicator of their spatial memory than their ability to forage flexibly in a changing environment. If part of the Tocaloma bats' dietary specialization is due to individual foraging areas within the colony's home range, then I would expect bats from this colony to have better spatial memory than bats from colonies without spatial separations. Clearly more work is needed to determine if bats from any colonies have separated foraging areas. Both learning and exploring behaviour may be important components of foraging flexibility, and I suggest that my latency rate of learning scores are biased for the learning component.

My data suggested that the Tocaloma bats have faster latency rates of learning than the Death Valley bats. Furthermore, there was a significant difference in the learning abilities between individuals in the Caliente population, but not among individuals in the Tocaloma population. Since prey was more uniform at Tocaloma, and those bats specialize individually in dietary preferences, they should improve their fitness by learning faster as individuals (i.e., there is natural selection for individuals who learn to detect, capture, and handle prey faster). In contrast, in a population where individuals are all eating the same ephemeral prey, individual learning may not be as important as exploring behaviour or social learning. Although I did not test for these two behavioural qualities, I would predict that social learning as measured by Gaudet (1982) is faster and exploring behaviour as measured by Heinrich (1995) is more developed in the

Death Valley population than in the Tocaloma population.

Levins (1968) and Stephens (1991) suggested that learning is a mechanism that enables an individual to adapt to changes in its environment. The authors state that in a fixed environment, a genetically fixed pattern of behaviour should evolve assuming some cost is associated with learning. Stephens (1991) suggested the pattern of predictability in relation to an individual's life history could determine the evolutionary advantage of learning. Stephens (1991) further stated that the evolutionary advantage of learning is in dealing with environmental events that change between generations and are predictable within a generation. Anderson (1995) investigated the effects of learning on evolution using genotype and phenotype modeling and pointed out that learning allows an individual with a sub optimal genotype to adapt its phenotype in response to environmental stimuli. Anderson (1995) suggested that learning can then be thought of a generalized form of phenotypic plasticity. Thus, learning can be a mechanism that weakens selection and phenotypic variability is a function of the of the mechanism of learning and of each individual's experience. Gerard et al. (1993) suggested that phenotypic plasticity, and therefore learning, serves as a "buffer" sheltering genetic polymorphism from selective pressures. Bergman and Feldman (1995) argued that in a completely unpredictable environment, where there is absolutely no means of knowing the future state, there should be nothing gained (i.e., fitness is not increased) and therefore, learning should not evolve. Learning is therefore defined as "the ability to construct a representation of the environment and, by proper use of the representation, to predict future states of the environment" (Bergman and Feldman 1995). Thus, for this model, there must be some regularity to the environment to ensure the "learner" can ultimately increase fitness and off set costs of learning. Bergman and Feldman (1995) constructed two genetic models with different genotypes with different capabilities to form representations of a randomly changing environment. The authors found mathematically, the best situation for learning to evolve is for intermediate values of environmental predictability. Stephens (1991) and Bergman and Feldman (1995) showed mathematical models demonstrating that an individual should always track its environment when the environment is highly predictable. This departs from early foraging theory on phenotypic plasticity which assumes that individuals can choose between not tracking and using experience to determine behaviour.

Learning has no selective advantage in fixed environments since, once the optimal genotype is achieved, exploration away from this optimum should reach fitness (Stephens 1993). Hinton and Nowlan (1987) and Fontanari and Meir (1990) used models to demonstrate that as individuals with allelic combinations approached some optimum, the plastic alleles, representing the ability to learn, were selected out of the gene pool. Thus individual learning can only be maintained in a population subject to a changing environment.

I found that there was a greater variance in the latency scores for Caliente bats than Tocaloma bats, and this suggests there is stronger selection for genotypes in the Caliente population. The environment at Caliente may vary to the point that bats may rely more heavily on genotypic selection if their environment changes more than their ability to capitalize on learning from previous experience. The Caliente bats clearly had slower latency scores than the Tocaloma bats suggesting, again, that the environment at Caliente is less optimal than at Tocaloma to favor learning ability. Thus the cost of learning at Caliente may be greater especially if more genotypic variation within the population provides a better evolutionary strategy. The Tocoloma bats may exist in a more optimal situation for learning as a plastic phenotype with a patchy enough environment for learning to pay off, but also an environment not so uniform that learning gives way to "hard-wiring" through mutations over time as suggested by Anderson (1995). Stevens (1991) and Bergman and Feldman (1995) suggested that individuals should always track their environment when the environment is highly predictable. More empirical work on the latency rate of learning of pallid bats from areas more uniform than at Tocaloma may reveal some threshold where learning is a less optimal state than in Tocaloma bats.

Perhaps the greater variation in individual learning ability among Death Valley bats is a result of less selective pressure for learning or plastic alleles than in the Tocaloma bats where prey is more uniform. I would also expect that there is greater variation in physical characters in the Death Valley bats if genotypic selection is stronger than in the Tocaloma bats.

Caliente bats spent more time roosting than Tocaloma bats. Pallid bats can easily detect low frequency sounds from a nearby roost (Fuzussery et al. 1993), and I observed bats many times moving their head and ears towards the floor appearing to listen for sounds. Caliente bats also spent less time land-listening than the Tocaloma bats. Caliente bats may have therefore listened more from their roost while Tocaloma bats may have spent a similar amount of time listening while flying and land-listening. Perhaps the Caliente bats' response to spend more time roosting is due to predator aversion.

My dietary and searching behaviour data for each bat suggested that there is a difference in foraging style among Tocaloma bats that could account for differences in dietary preferences. Although I cannot rule out the possibility that individual bat's diets varied as a result of individuals' different foraging areas, Hughes (1979) predicted that individual behaviour and dietary preferences may develop as a result of individuals learning to forage on very different kinds of prey. After I received some positive criticism for my correlation using 6 Tocaloma bats, I correctly predicted two more "crawlers" by choosing bats with dietary histories of eating flightless arthropods, as shown in my results. An investigation of foraging techniques for prey species by each specialized bat may also determine more individual foraging styles.

O'Shea and Vaughan (1977) and Brown et al. (1978) suggested that young learn from their mothers since adult females have been caught and observed with nearby juveniles. Although there is no evidence that young pallid bats learn to forage by observing their mother, foraging styles could conceivably be learned by offspring in the same way young learn from parent oystercatchers as described by Goss-Custard (1984) or in roof rats as described by Terkel (1996). Perhaps the two foraging styles exhibited by Tocaloma bats are learned from their mothers and this style helps determine prey type. While behavioural transmission may be responsible for learned feeding behaviour as suggested by Sherry and Galef (1984, 1990), and Galef (1976, 1988, 1991), my investigation suggested that there may be ecological constraints placed on populations which become factors shaping the degree of individual specialization. Whitehead (1986) suggested that a socially dependent mechanism may account for the maintenance of individual feeding selectivity, but a socially independent mechanism may account for the underlying origin of individual specializations.

One of my predictions was that pallid bats have a genetically-based affinity towards low frequency sounds which are later articulated through the learning of specific prey by experience. This could have explained how different populations of pallid bats forage on different prey for different geographic areas in the same way white-crowned sparrows maintain different dialects described by

Marler and Peters (1982). Part of the knowledge is inherent, and part is learned within a finite period of time when the organism is young. My data suggested that young, naive, and hungry pallid bats do not have any affinity for low frequency insect sounds. This suggested that pallid bats learn that an association exists between their prey and the sounds prey produce. If learning is the primary means for pallid bats to detect prey, then the lack of an inherent template supports the possibility that learning is an important mechanism in individual bats' dietary specialization. However, they are not necessarily mutually exclusive. There still may be other aspects of foraging behaviour not yet investigated that could provide a foraging template, especially through another sense such as sight or smell.

Chapter IV

General Discussion

In my investigation, I have demonstrated foraging flexibility in pallid bats which can lead to different strategies for adapting to a variety of environmental constraints. I did not address such constraints made by risk of predation or the specific business of intraspecific and interspecific competition. Rather, I concentrated on the evenness of the quality of prey availability and individual bats' dietary response in a single bat species found in two remarkably different climatic regimes, the California coast and Death Valley. Several investigators have reported on bat populations' flexible foraging behaviour in response to varying prey availability (e.g. Bell 1982, Fenton and Morris 1976, Fenton and Thomas 1980 and Grant 1988). What is surprising is the coastal population individuals' specialized response to the evenness in prey availability, while individuals from the desert population temporally follow their population's generalized diet according to the changing availability of prey. Individuals from the coast also specialized in foraging style in addition to dietary preference, as predicted by Hughs (1979) for situations where learning is an important component of capturing very different prey and where availability of prey is not a constraint. Such differences in the two populations may be explained through Optimal Foraging Theory if risks and rewards for foraging flexibility (i.e., exploring and learning) are modeled.

The information presented on the dietary intake of rare items such as slugs or 3 mm flies suggests that pallid bats forage on some specific items that may not fit optimal foraging theory in a short term model equation of energetics. Pallid bats may take unpalatable or "uneconomical" prey to gain knowledge. This foraging behaviour may fit a model designed to test the long-term strategy of foraging flexibility. OFT also supports specialization if roosts are a limiting factor and preferred prey occurs temporally evenly and in low densities. In that situation, a colony of individuals that specialize could reduce the cost of flying distances, especially if intraspecific competition is minimized.

My investigation suggests the coastal population has shorter latency scores (i.e., learn faster) than the desert population. This supports recent theoretical work by Stephens (1991), Anderson (1995) and Bergman and Feldman (1995) who hypothesized through mathematical models that more uniform environments select for "plastic" alleles allowing individuals to take advantage of experience and memory. These models assumed that learning was already evolved since a completely uniform environment should select for genotypic variation, not phenotypic plasticity with learning real costs. In a population where individuals specialize, fitness may be increased by learning faster individually, but not necessarily socially. I did not test for social learning ability, but individuals in a colony that temporally forage on the same locally abundant prey species may be better at learning socially than individuals that specialize.

Although I looked for a foraging template, my results suggested that juveniles must learn that prey can give detection cues through low frequency sounds. This information supports the possibility that learning is an important mechanism for flexibility and therefore phenotypic plasticity in pallid bats.

Several animal groups show behavioural flexibility (e.g., some vespertilionid bats, corvids, primates, and cetaceans), but too little is known about flexibility to predict how animal species can survive in the wild with the continued hoarding of resources by human populations. Like many animal groups, bats were more abundant and widespread only fifty years ago, barely a flash in time when compared to bats' 60 plus million years of presence. Over the past 20 years I have noticed some species integrating into suburban sprawl that were once eliminated by this impending doomsday machine covering the earth. In some cases such as the California brown pelican (Pelicanus occidentalis) causes for probable population declines were known (i.e., thinning of eggshells by pesticides), and when mitigated, populations returned. In many cases however, we attribute population declines to habitat loss perhaps without really understanding specific underlying problems. Red shouldered hawks (Buteo lineatus) declined during the latter part of the twentieth century in California, presumably from "habitat loss" but recent studies suggested that this species is now using urban and suburban habitat (Unpubl. data, Rottenborn) where it was thought to be eliminated. Rottenborn suggested (pers. comm.) that several species that previously were not tolerant of human activity are now coexisting in developed areas. I have found 3 situations in central coastal California where pallid bats have taken residence or night roosted in newly developed areas. Rather than the bats "moving into the area" as suggested by disgruntled home owners, I suspect that the home builders built their home within pallid bats' habitat and the bats simply made use of the new features. In many cases the bats' natural roosts were removed (e.g., oaks were cut and rocky outcroppings scraped flat) for development. As is most situations. humans seem more intolerant of the animals that have enough phenotypic plasticity to attempt adapting to human environments. My hope is that studies, such as this one on foraging flexibility, will ultimately contribute to our ability to understand and implement ways that animal populations can learn to coexist with the encroachment of human development.

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APPENDICES

Appendix 1. Social and Behavioural Well-being of Captive Bats

Over the past 10 to 15 years bats have increasingly been studied more. In order to conduct behavioural studies without bias, animals need to be physically as well as psychologically healthy to prevent biased results (Olfert et al. 1993), but little or no information has been written about the well-being of bats in captivity.

There are over 900 species of bats, and our knowledge about them is limited compared to most other vertebrate species. Most information regarding bat husbandry is directed towards providing a proper diet, containing them hygienically, and providing proper caging with temperature controls.

Blood and Stodart (1988) define animal welfare as "maintaining appropriate standards of accommodation, feeding and general care for the prevention and treatment of disease..." The American Veterinary Medical Association (Anon. 1990) defines it as "all aspects of animal well-being, including proper housing, management, nutrition, disease prevention and treatment, responsible care, humane handling, and, when necessary, humane euthanasia." Some authors recognize the specific importance of psychological factors as part of the health and well-being of captive animals. Fraser (1989) defines an animal's well-being with both physical and psychological components, and states that these normally coexist. He defines psychological well-being, as evident in the presence of normal behavior and the absence of substantial abnormal behaviour. Hurnik (1988) defines animal well-being as "a state or condition of physical and psychological harmony between the organism and its surroundings." Most common species of bats have been studied enough to allow researchers access to literature on "normal" behaviour in the wild, although a state of well-being maybe difficult to assess in lesser-known species. Nonetheless, it is evident that the psychological well-being of an animal may affect its physical well-being and vice versa (Olfert et al. 1993). Therefore, captive bats should be maintained in a state of physical and behavioural well-being in order to conduct research with a minimum of aberrant results.

Environmental enrichment

Environmental enrichment is defined by Beaver (1989) as "additions to an animal's environment with which it can interact." Beaver (1989) suggests five different ways in which non-human primates' social and behavioural well-being may be promoted thorough improving the animals' environment: Behavioural enrichment created by an environment similar to the wild habitat, social peers, artificial appliances, food gathering activities and control of non-food items.

The amount of space should be appropriate to the species , but simply increasing the amount of space in a given cage does not necessarily promote better space utilization (Line 1987, Fajzi et al. 1989) nor does it necessarily improve the well-being of an animal in captivity (Novak and Suomi 1988). Some bats have narrow wings or high wing ratios creating a need for a larger area for flying, such as big brown bats (*Eptesicus fuscus*) (Kunz 1988). I suggest that the size of any cage or flight room take this into consideration. Certainly big brown bats need wider areas to fly than a bat with a low wing ratio such as little brown bats (*Myotis lucifugus*).

Crockett (1990) suggested that innovative ways of providing food to monkeys are effective in enhancing well-being, especially of animals individually caged with no opportunities for social interactions. Foraging tasks provide the animal with challenges to help prevent boredom, and also provide exercise (Kaman et al. 1987). MacDonald (pers. comm.) suggests that gorillas given foraging tasks, are less bored and exhibit behaviour closer to that found in the wild.

In a flight room 10 feet by 12 feet by 8 feet high, I gave pallid bats (*Antrozous pallidus*) simple foraging tasks designed to mimic situations in the wild. By providing these tasks, captive bats got regular exercise. In 1993, I released 6 pallid bats that were in captivity for about 10 weeks. The following year, I recaptured two of these and in 1995, I recaptured a third bat making a 50% recapture rate. Fenton (pers. comm.) suggests that it's unusual to observe wild bats that were once acclimated to captivity. Barnard (1991) suggests that flying exercise is not important to the good health of bats. I suggest that if captive bats are to be released back into the wild, they should get regular flying exercise to improve survivorship.

Social needs

The social needs of research, teaching, or testing animals should be given equal consideration with environmental factors such as lighting, heating, ventilation and caging (Olfert et al. 1993). Many bats are solitary during most of an annual cycle (e.g. hoary bat, *Lasiurus cinereus*, red bat *L. boreas)*, while other species are colonial and form groups (e.g. pallid bat, Mexican free-tail bat *Tadarida braziliensis*, and the little brown bat); (for review see Bradbury 1974). Although social behaviour is not addressed in the literature for social bats in captivity, much work has been done to establish the need for other social mammals to continue social contact to remain healthy and behaviourally normal.

Olfert et al. (1993) suggested there are four ways in which social animals' well-being may be threatened while a group of animals is being established: first "space is insufficient for maintaining behavioural adequate distance; feeding or resting space for all individuals is insufficient; or when feeding and resting cannot be accomplished concurrently; regrouping is performed so frequently that animals must repeatedly undergo the stabilization process; and, group sizes are inappropriate for the species".

Wilson (1988) states that individual bats are often ostracized when introduced into an already established colony. I found this to be true for captive pallid bats. Social bats should not be housed singly unless required by a medical condition or aggression. Without specific controls, I have observed that pallid bats changed their behaviour when housed separately after being housed with individuals from the some colony. A pallid bat housed in the Bat Lab at York University appeared more irritable (more likely to bite during handling after it had been separated for a few days). Another pallid bat housed in the lab usually appeared more lethargic and inactive after it was housed singly. Although these observations were not part of a formal study, they are consistent with observations made in many studies on dogs (review by Beaver 1981) and on non-human primates (Reinhardt 1990).

Crockett (1990) states that the best psychological enrichment is social enrichment for non-human primates. Thus, by providing opportunities for social interactions, these animals can better cope with the two main problems associated with captivity: boredom and fear. The author suggests that social interactions appear to provide the best source of stimulation and the best source of emotional security. Segal (1989) concludes in a review that several authors independently reached the conclusion that "the single most important thing one can do to enrich the life of a captive primate is to provide it with a companion animal".

Although no studies have been made regarding the well-being of bats in captivity and their requirements for psychological balance, one might predict that the behaviour of bats will be altered if individuals are under "emotional" stress; social bats will need companions in captivity to help provide stimulation and emotional security; and solitary bats should have a minimum of contact with the researcher or other bats. Many environmental factors may contribute to captive bats' psychological well-being. It seems clear that we need more information on the social and behavioural needs of bats in captivity, especially for behavioural studies, if we expect to provide unbiased results. We also need to provide them with the best possible chance of being reintroduced into the wild after any captive situation, through rehabilitation, research, or education.

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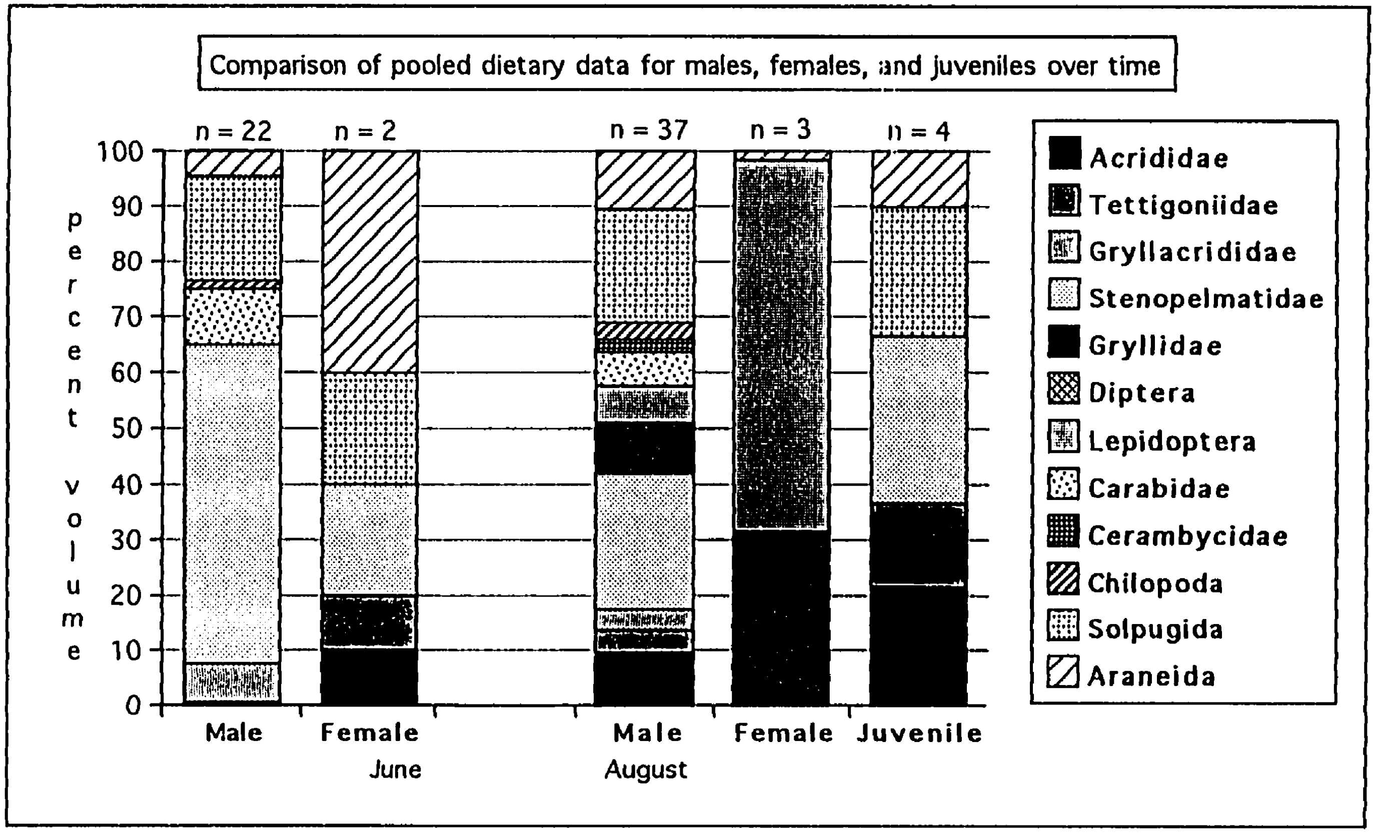
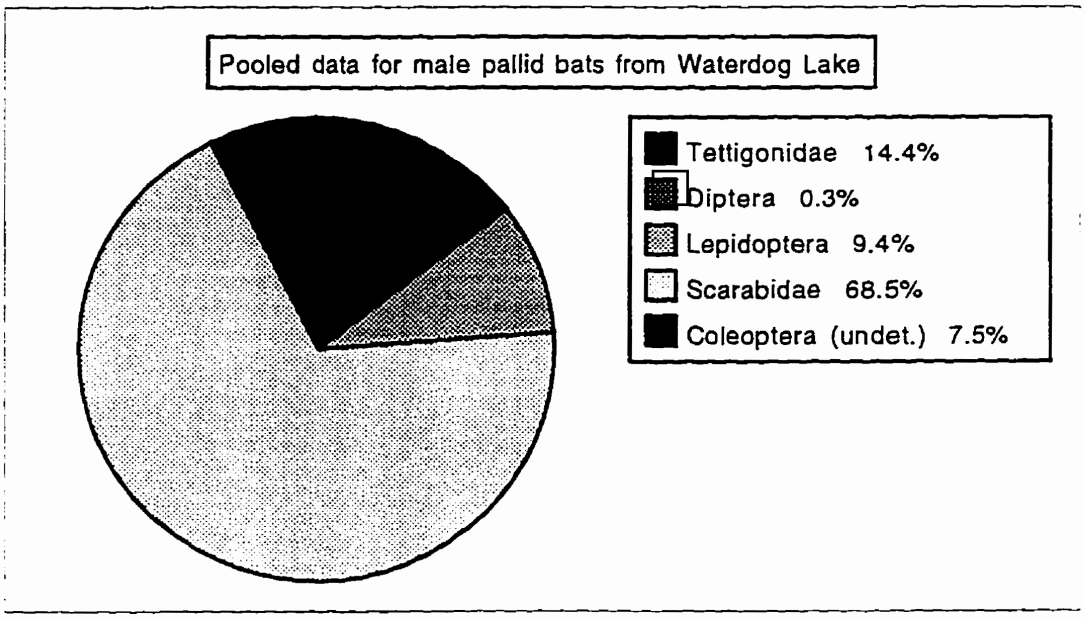
Appendix 2. Pooled dietary data for males, females, and juveniles bats from Tocaloma over time.



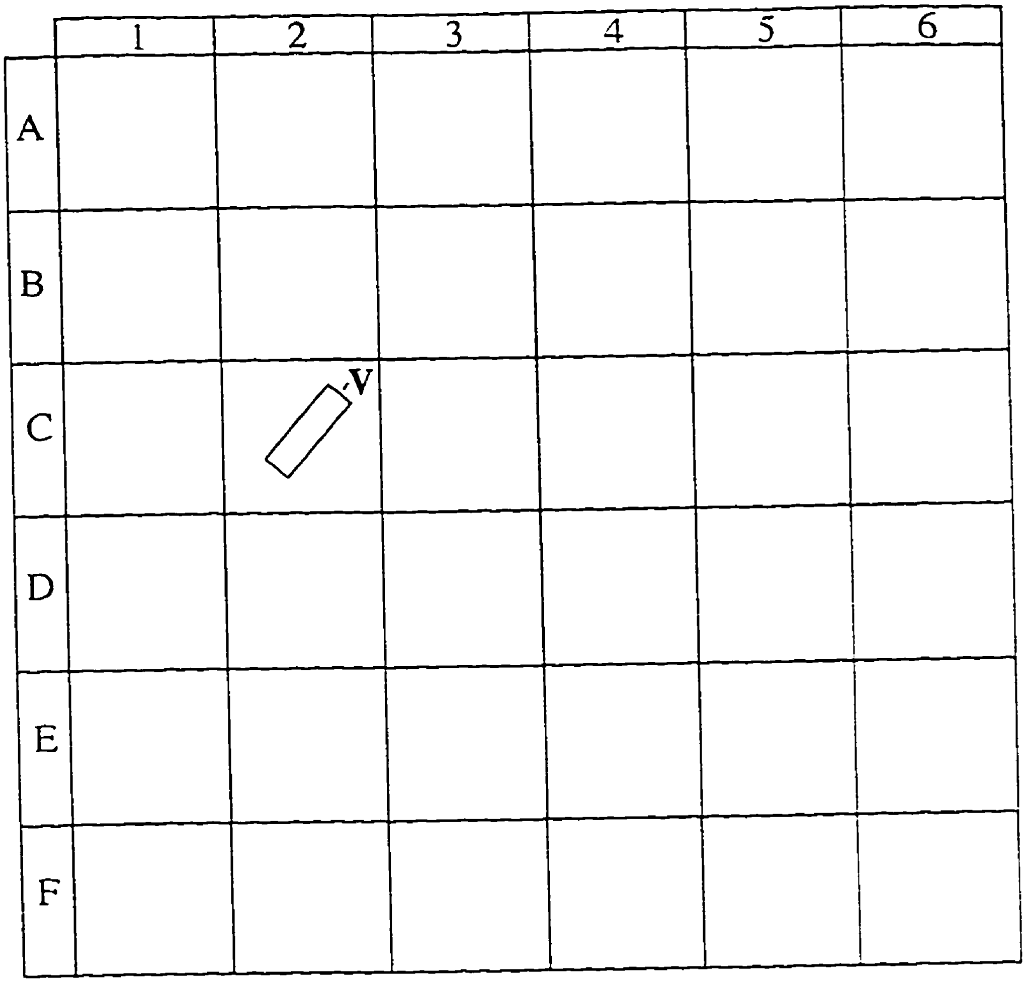
Appendix 3. Pooled dietary data for male pallid bats from Waterdog Lake, British Columbia, n = 7.



Appendix 4a-m. Foraging grids for 13 bats recording landing and crawling behaviour from the first trial of each bat for the tube foraging task.

Appendix 4a. Foraging grid for Bat #10
Appendix 4b. Foraging grid for Bat #12
Appendix 4c. Foraging grid for Bat #19
Appendix 4d. Foraging grid for Bat #28
Appendix 4e. Foraging grid for Bat #31
Appendix 4f. Foraging grid for Bat #34
Appendix 4g. Foraging grid for Bat #63
Appendix 4h. Foraging grid for Bat #101
Appendix 4i. Foraging grid for Bat #102
Appendix 4j. Foraging grid for Bat #103
Appendix 4k. Foraging grid for Bat #104
Appendix 4l. Foraging grid for Bat #601
Appendix 4m. Foraging grid for Bat #602

Appendix 4a. Foraging grid for Bat #10

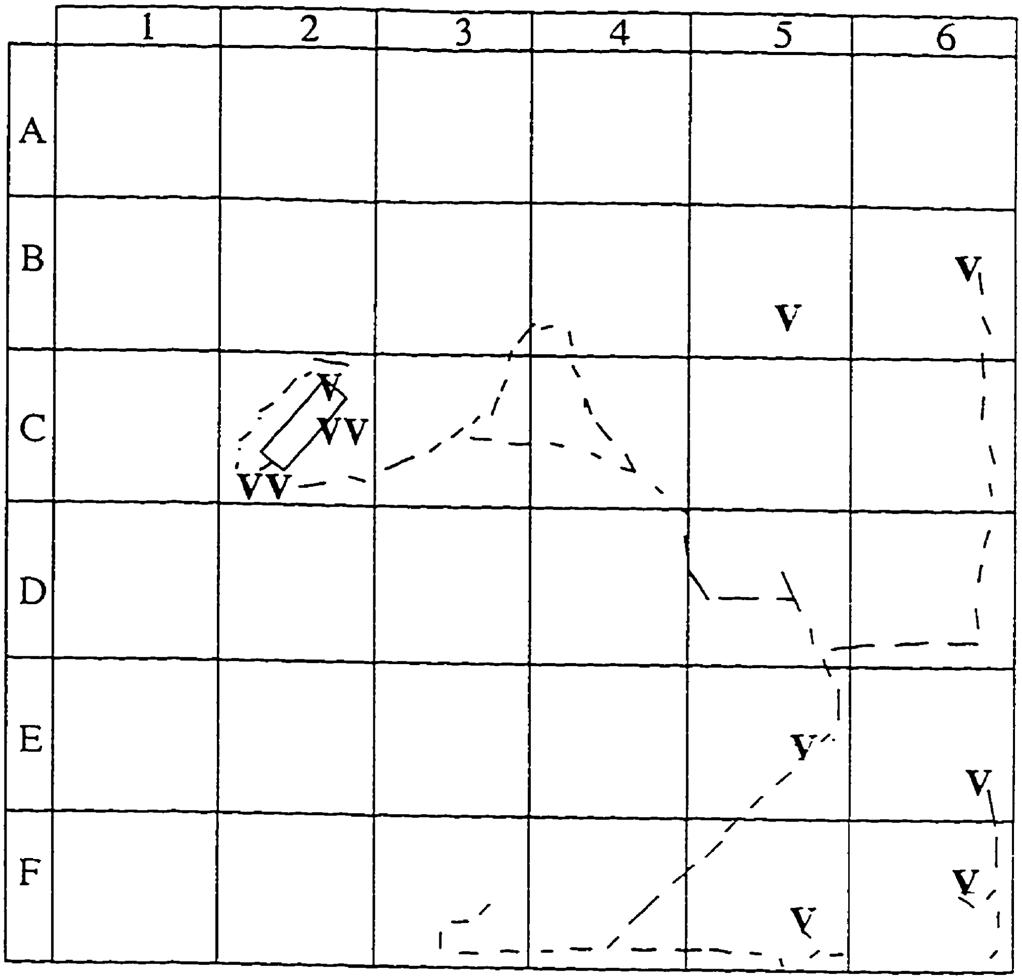


V = landing

,′ = crawling

▱ = placement of tube

Appendix 4b. Foraging grid for Bat #12

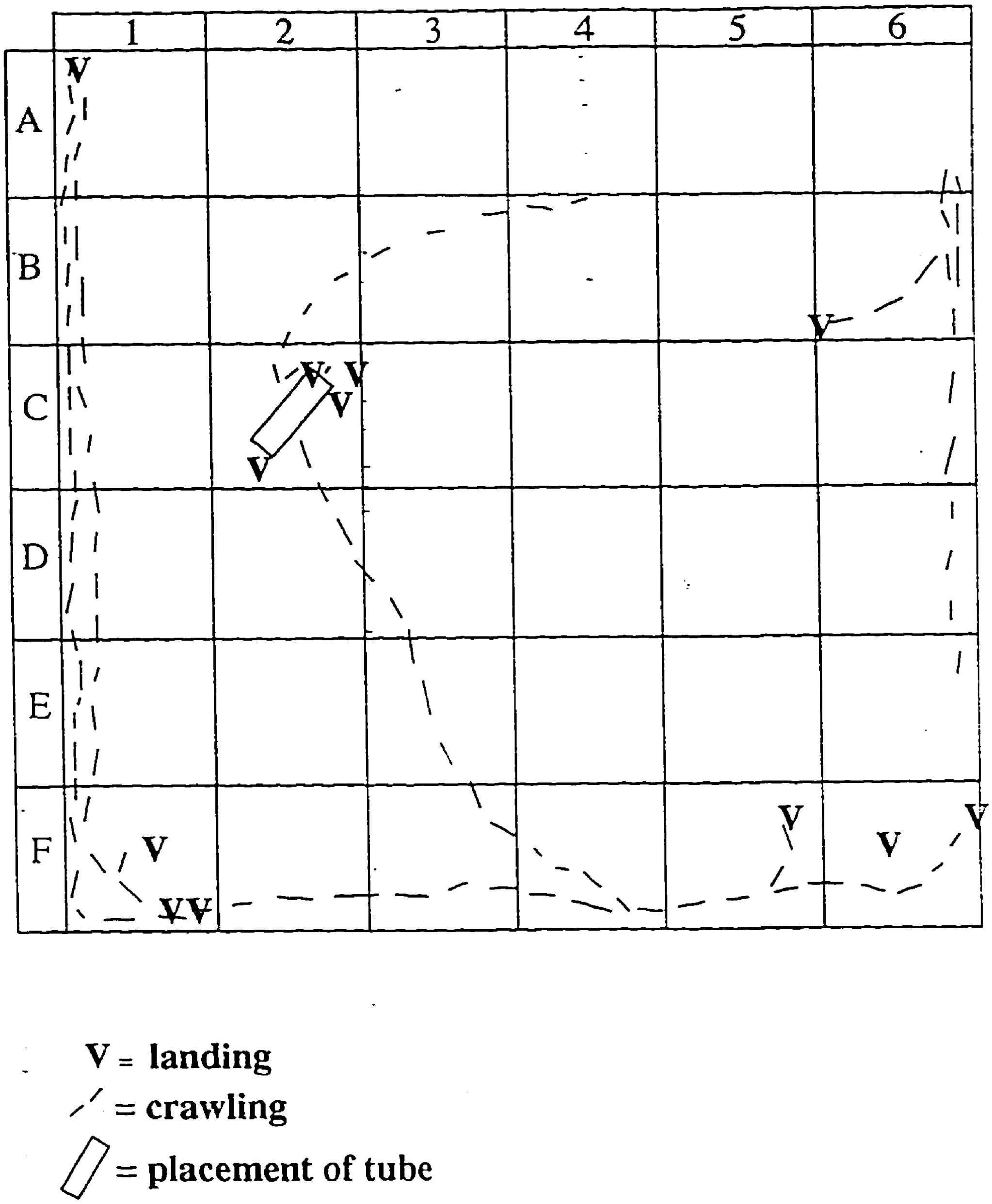


V = landing

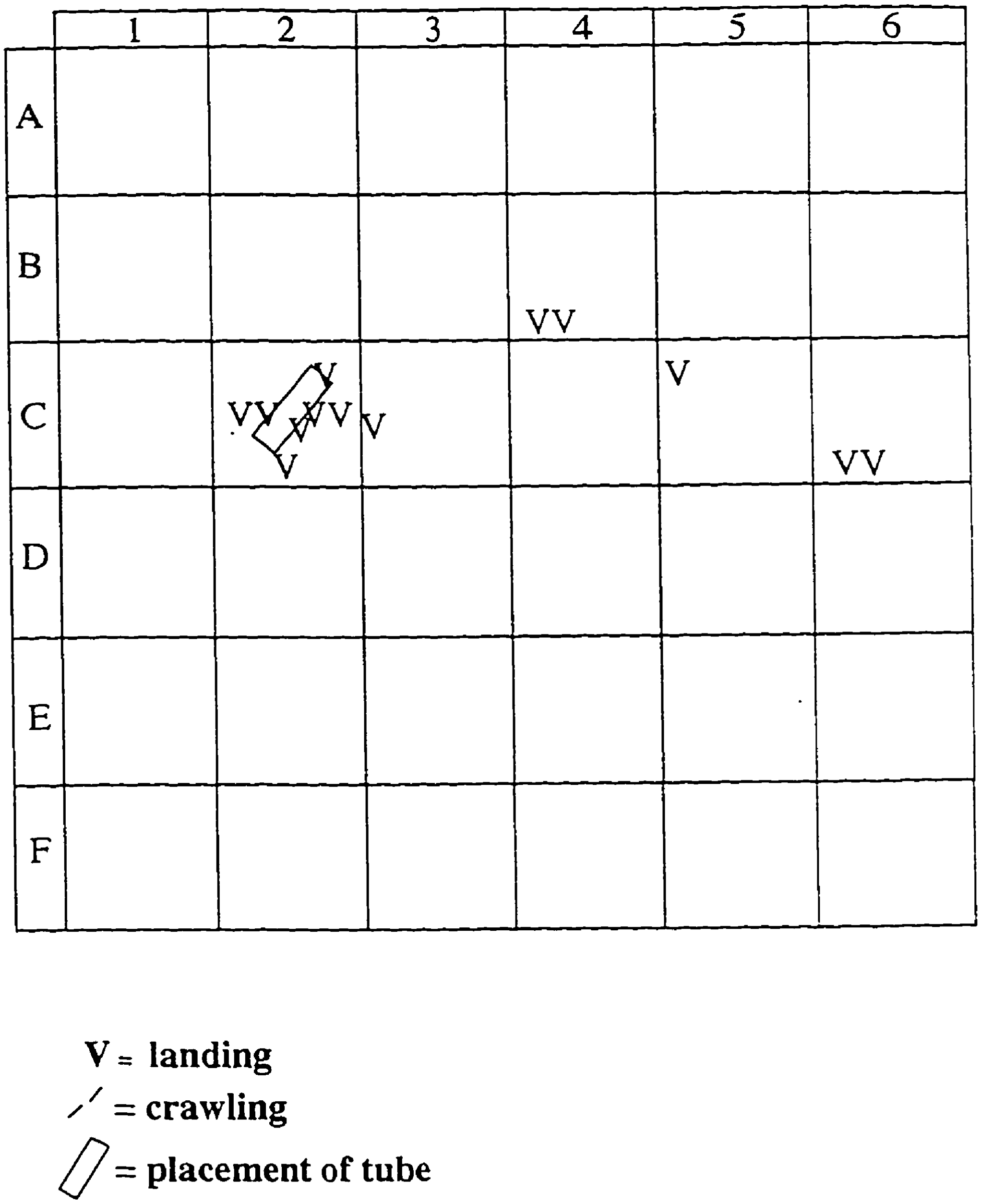
/ / = crawling

▱ = placement of tube

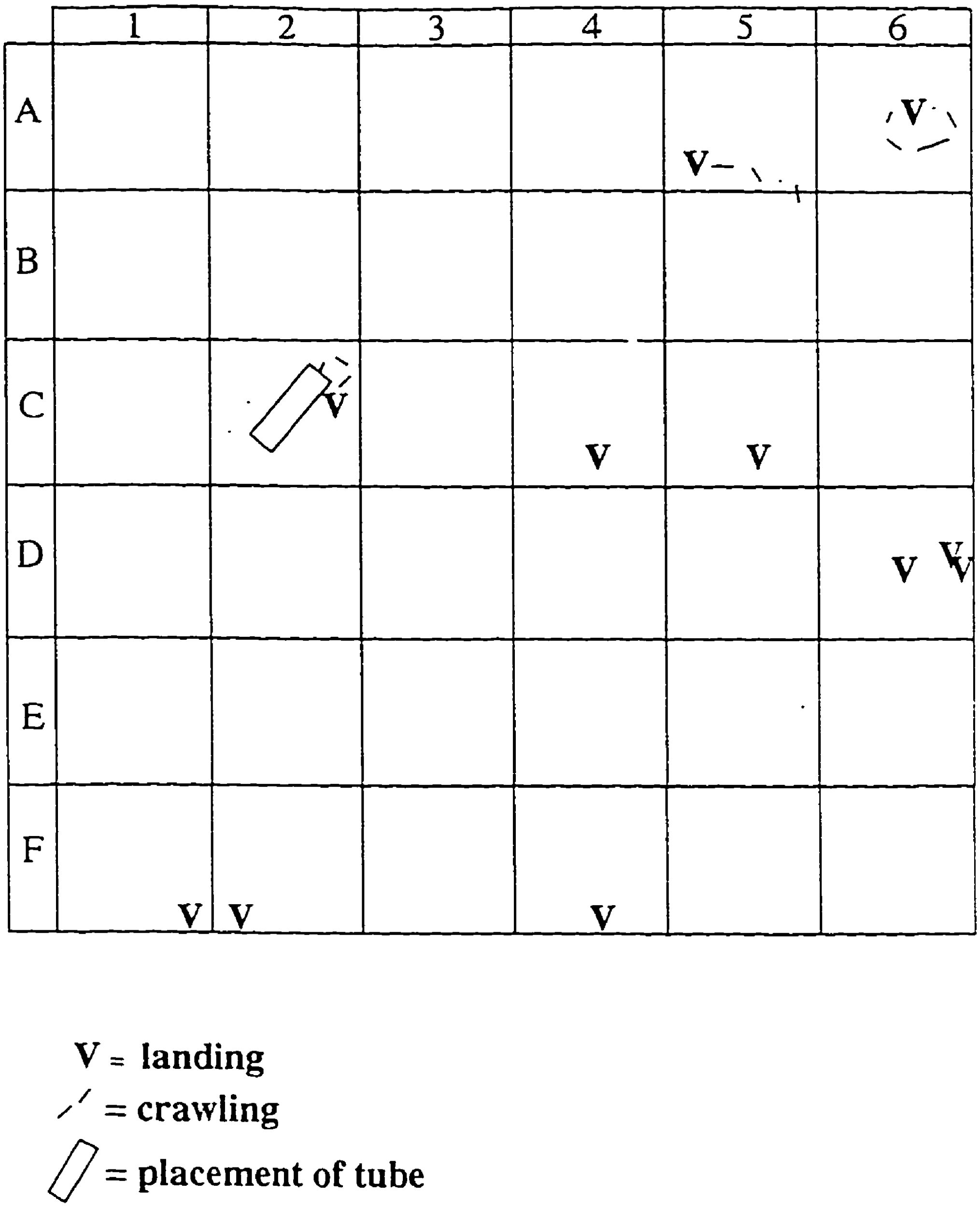
Appendix 4c. Foraging grid for Bat #19



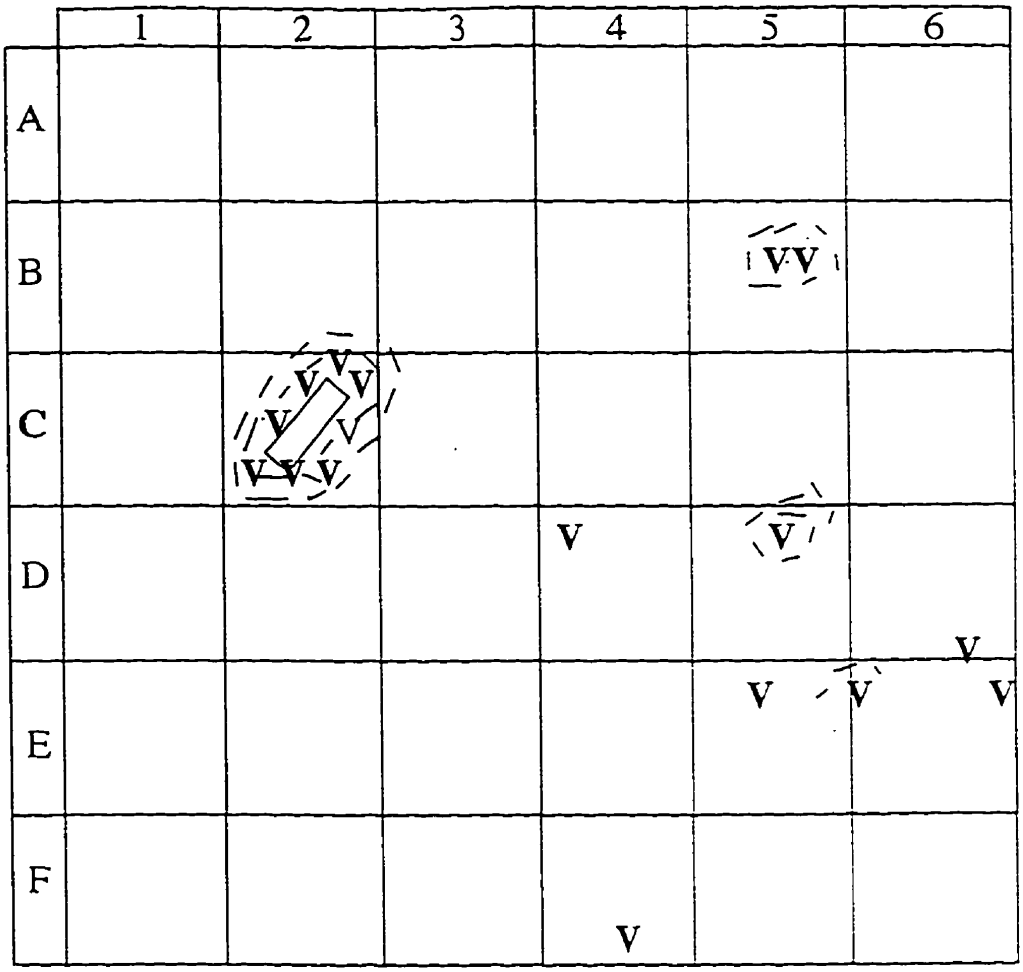
Appendix 4d. Foraging grid for Bat #28



Appendix 4e. Foraging grid for Bat #31

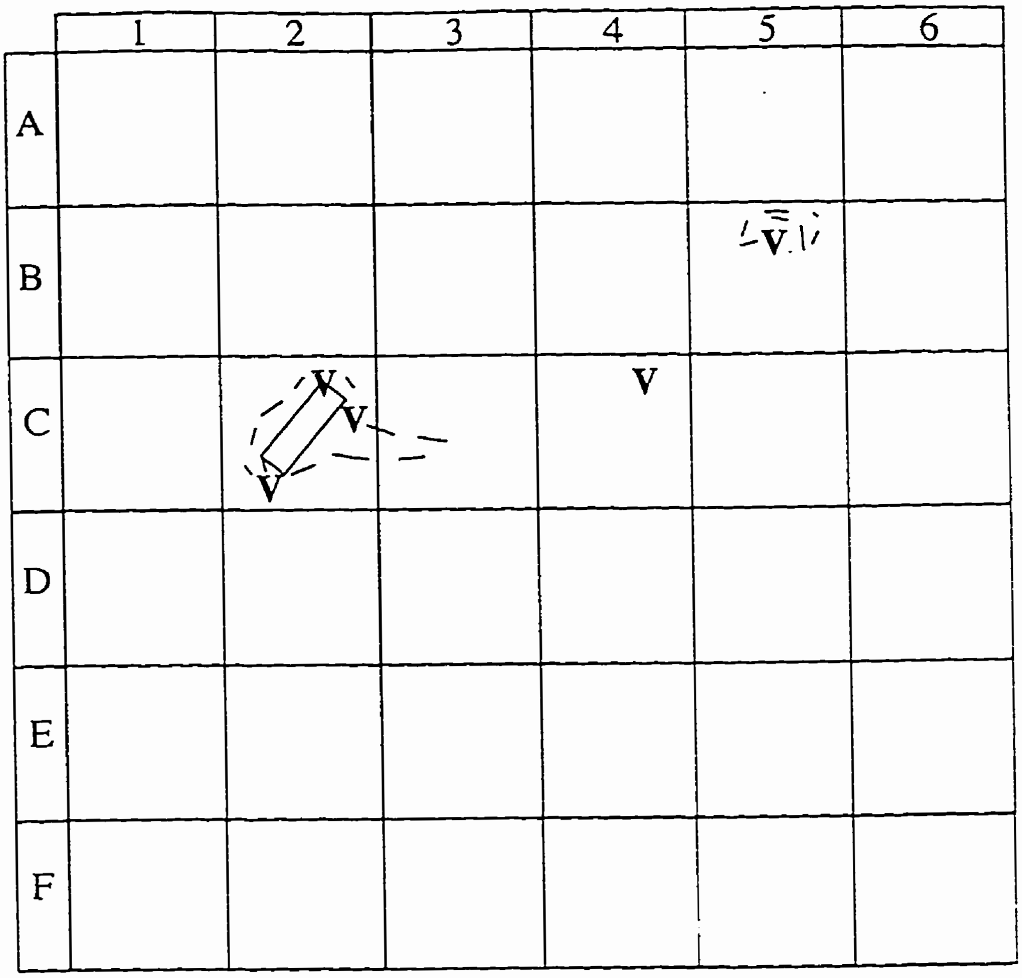


Appendix 4f. Foraging grid for Bat #34



V = landing
/ = crawling
▱ = placement of tube

Appendix 4g. Foraging grid for Bat #63

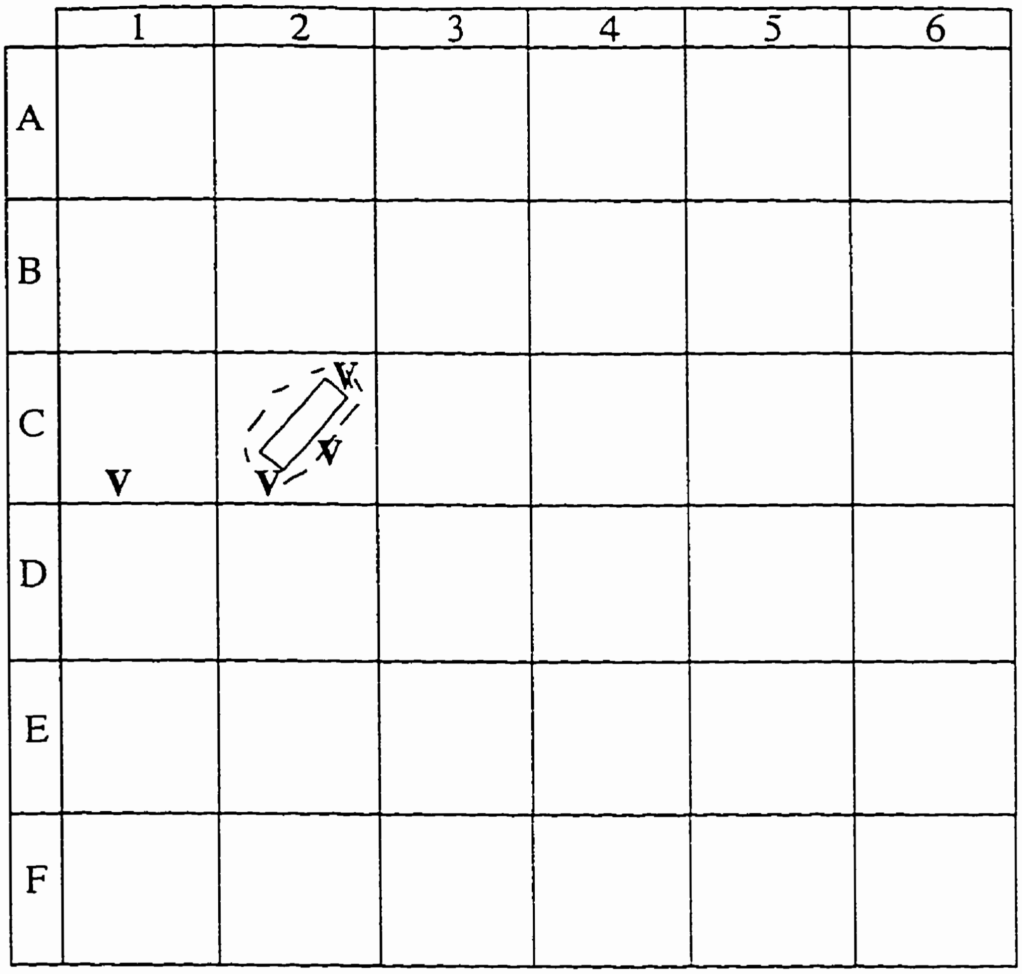


V = landing

⁄ ⁄ = crawling

▱ = placement of tube

Appendix 4h. Foraging grid for Bat #101

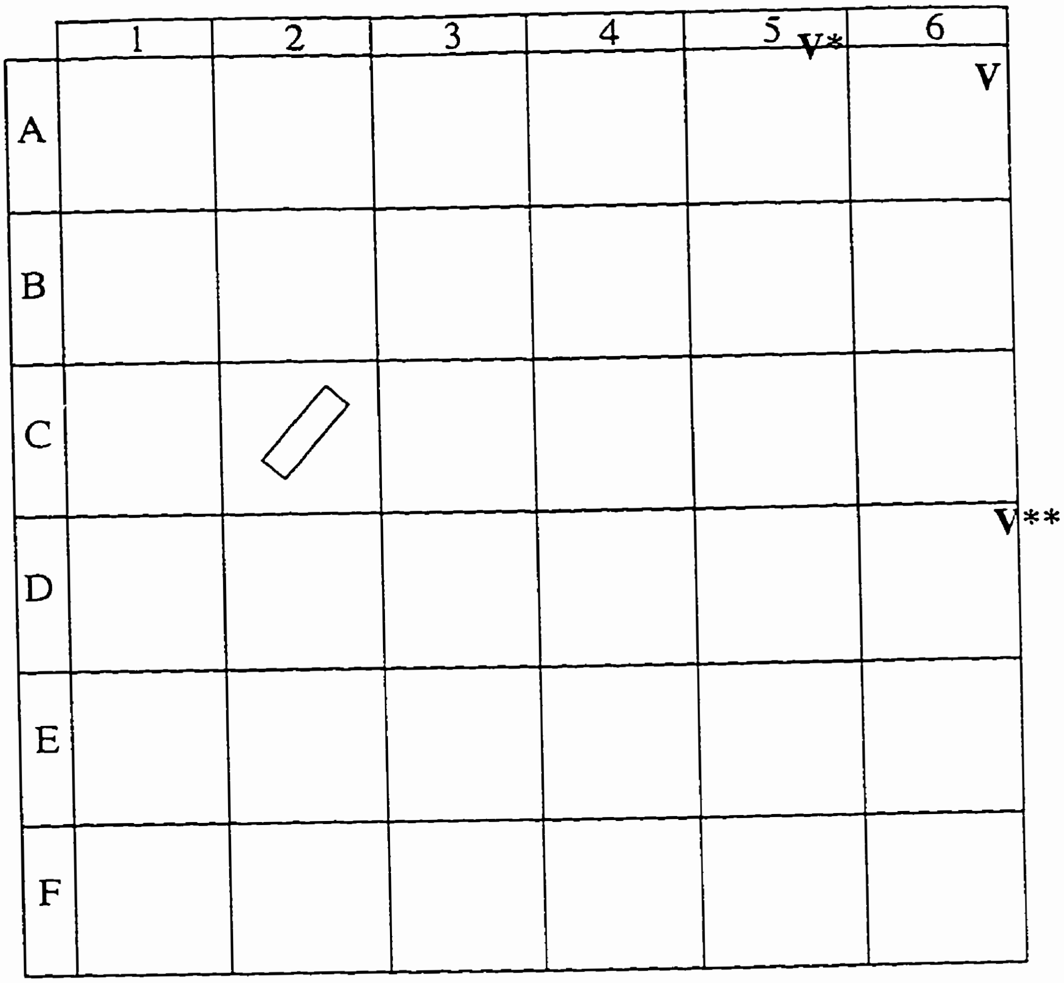


V = **landing**

⁄ ⁄ = crawling

▱ = placement of tube

Appendix 4i. Foraging grid for Bat #102

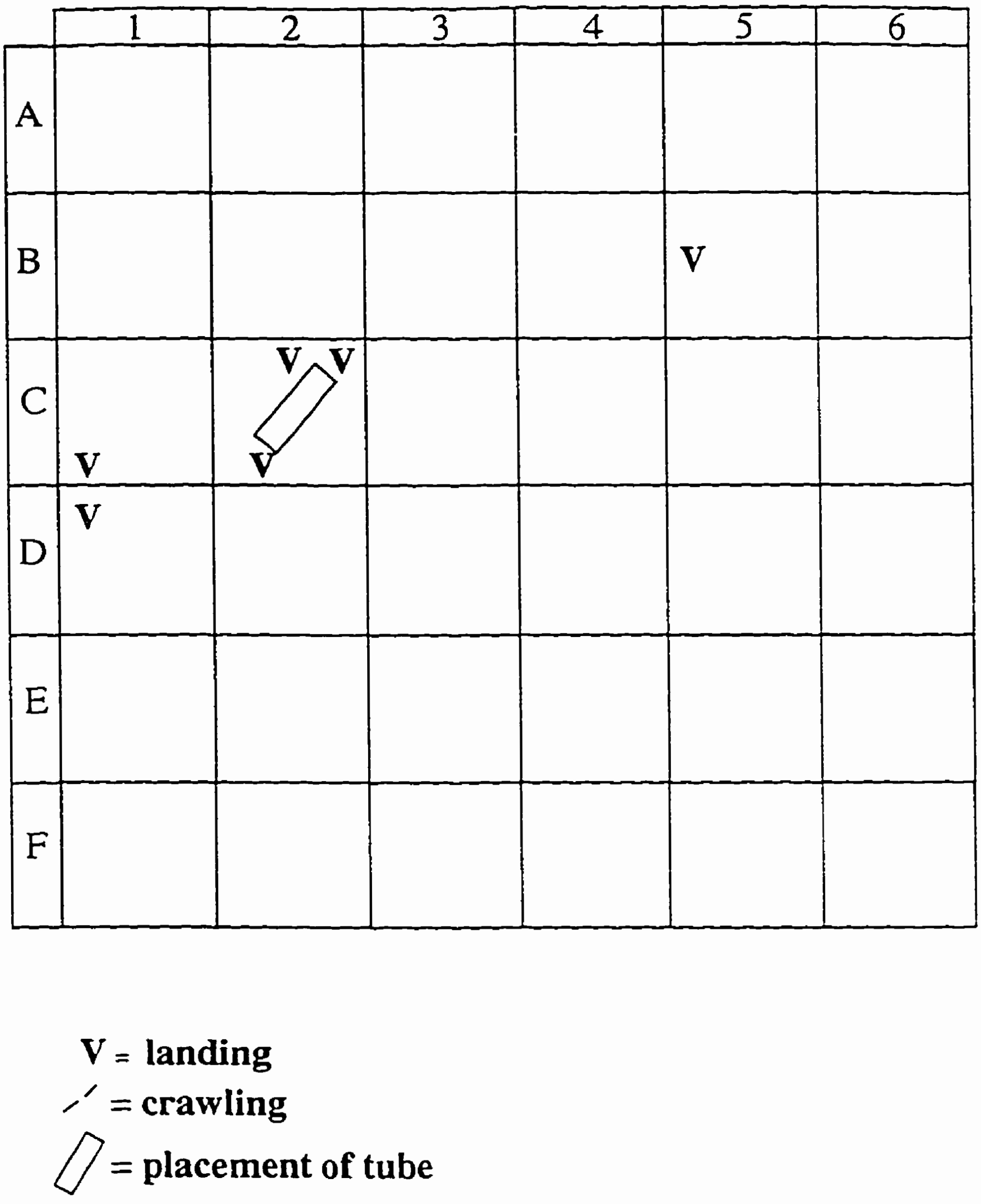


V = landing

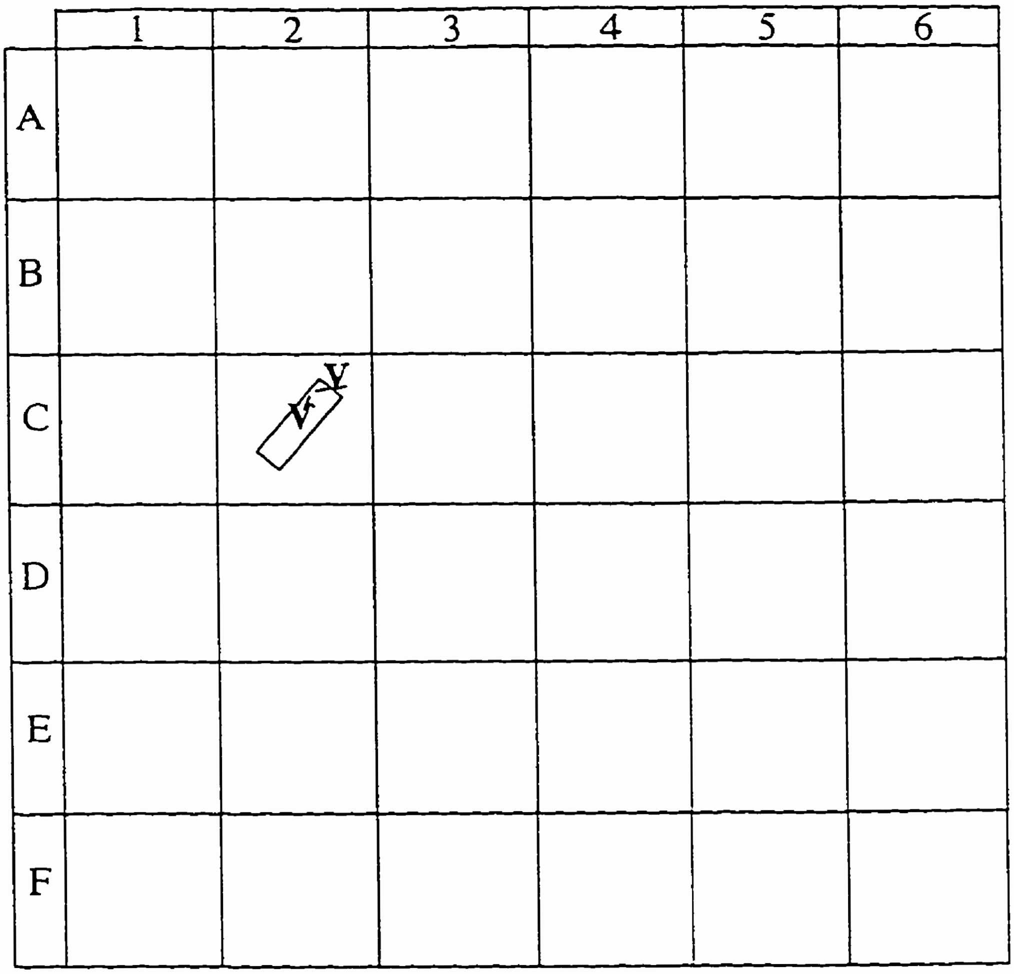
⁄ ⁄ = crawling

▱ = placement of tube

Appendix 4j. Foraging grid for Bat #103



Appendix 4k. Foraging grid for Bat #104

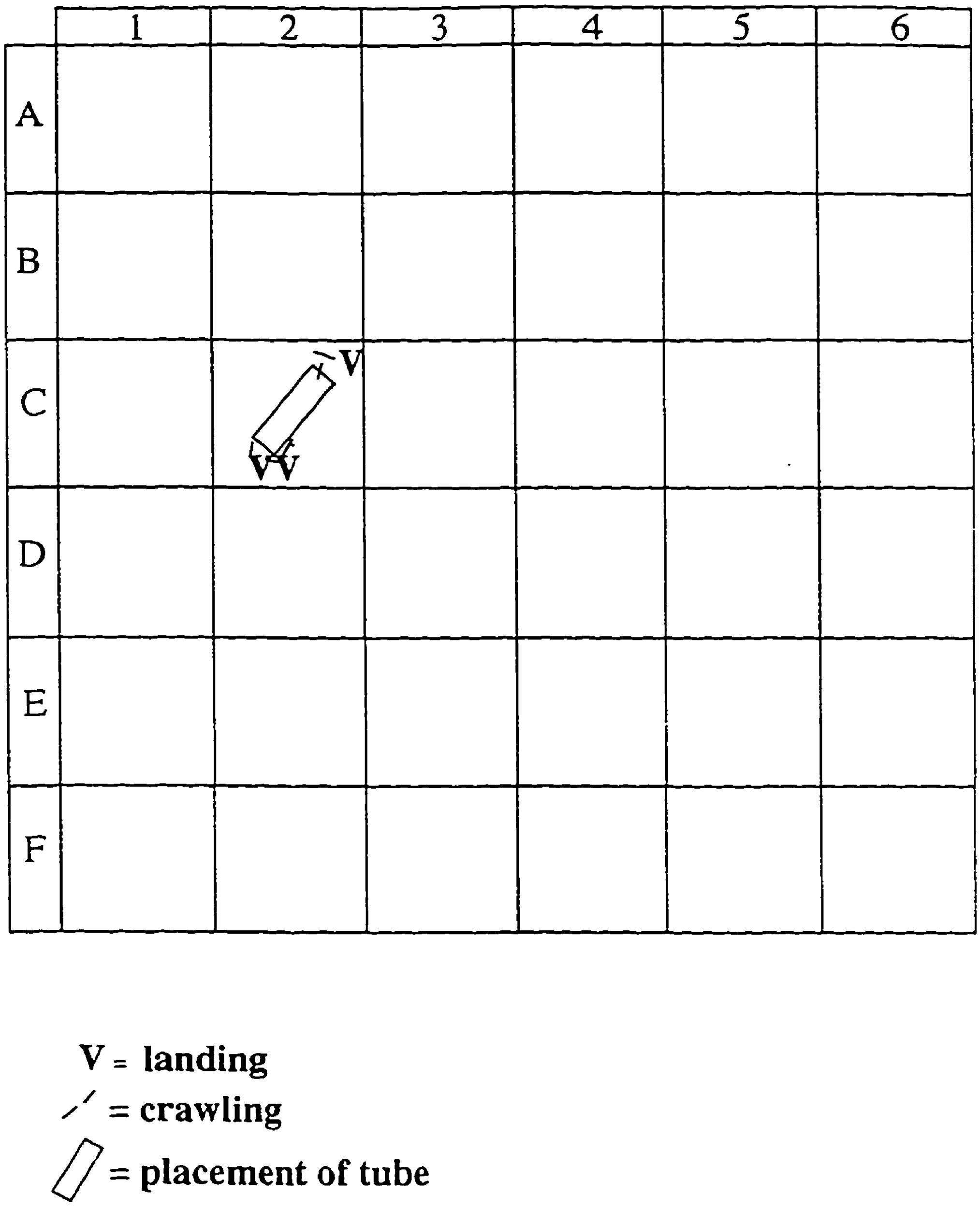


V = landing

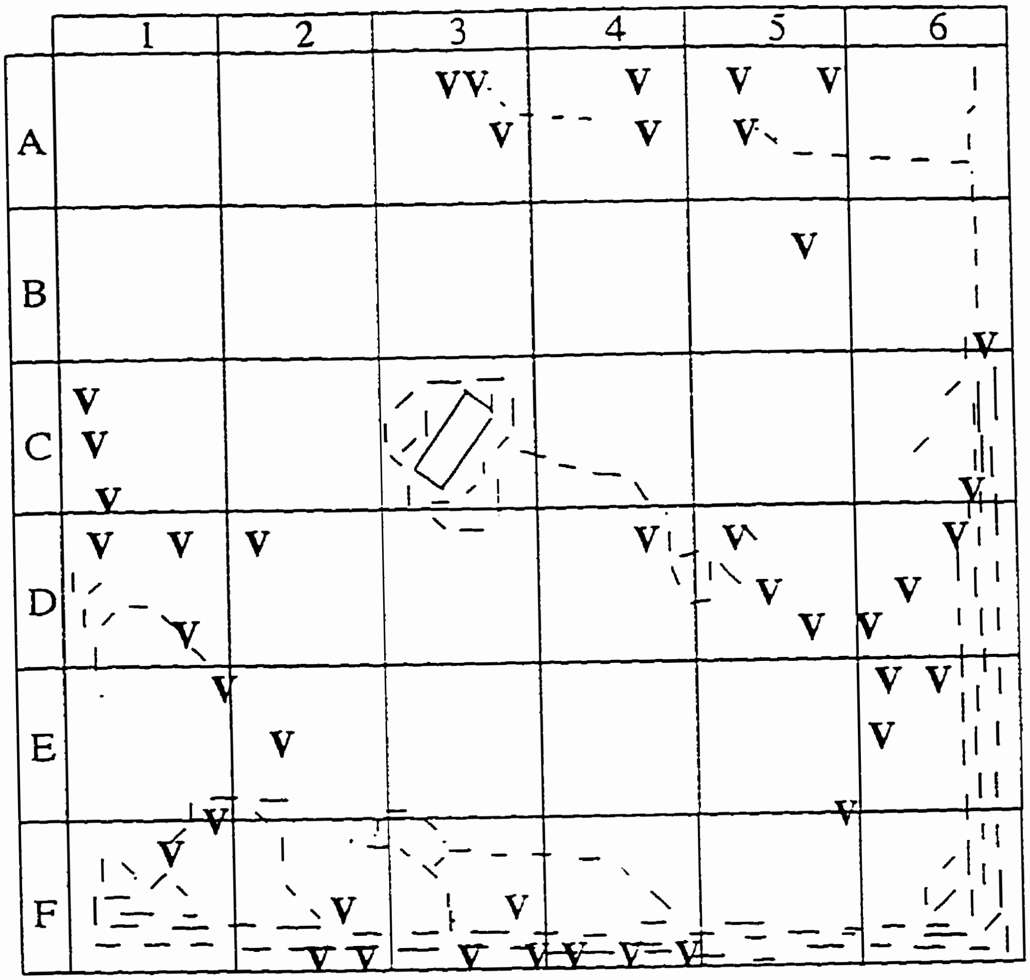
/ = crawling

▱ = placement of tube

Appendix 41. Foraging grid for Bat #601



Appendix 4m. Foraging grid for Bat #602



V = landing

⁄ ⁄ = crawling

▱ = placement of tube

Appendix 5a - e. Mean times and standard deviations for foraging tasks.

a). Pooled data for latency scores for 6 Tocaloma bats. Mean times for the combined 18 tasks performed for each of five consecutive days.

Day 1	8.70 min	std.	19.25
Day 2	2.50 min	std.	7.99
Day 3	0.90 min	std.	2.07
Day 4	0.70 min	std.	1.58
Day 5	0.50 min	std.	0.39

b). Latency scores for 3 tasks for 6 individual bats from Tocaloma over the course of 5 trials. Mean scores and standard deviations for each bat.

Bat # 10	1.06 min.	std.	0.78
Bat # 12	3.32 min.	std.	9.12
Bat # 19	4.10 min.	std.	7.77
Bat # 28	1.32 min.	std.	1.25
Bat # 31	4.47 min.	std.	6.99
Bat # 34	1.58 min.	std.	2.23

c). Pooled data for combined latency scores for 5 Caliente bats performing three tasks. Mean times for each of five consecutive days from the combined 15 tasks:

Day 1	30.44 min.	std. 25.25
Day 2	19.56 min.	std. 25.57
Day 3	11.73 min.	std. 20.18
Day 4	5.87 min.	std. 15.20
Day 5	5.03 min.	std. 15.23

d). Latency scores for 3 tasks for 5 individual bats from Caliente over the course of 5 trials. Mean scores and standard deviations for each bat.

Bat # 063	8.90 min.	std 19.01
Bat # 101	3.82 min.	std 4.01
Bat # 102	23.90 min.	std 27.85
Bat # 103	31.76 min.	std 27.65
Bat # 104	4.28 min.	std 6.82

e). Latency scores for tube task trials for 2 captive pallid bats and 2 captive big brown bats. Mean scores and standard deviations for each bat:

Bat # 601	2.30 min.	std. 2.49;
Bat # 602	22.46 min.	std. 10.78;
Bat # 601	1.09 min.	std. 1.03;
Bat # 602	2.36 min.	std. 3.12.