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Resource use and foraging activity of Mexican free-tailed bats, Tadarida brasiliensis mexicana (Molossidae)

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To the Graduate Council:

I am submitting herewith a dissertation written by Ya-Fu Lee entitled "Resource use and foraging activity of Mexican free-tailed bats, Tadarida brasiliensis mexicana (Molossidae)." I have examined the final electronic copy of this dissertation for form and content and recommend that it be accepted in partial fulfillment of the requirements for the degree of Doctor of Philosophy, with a major in Ecology and Evolutionary Biology.

Gery F. McCracken, Thomas G. Hallam, Major Professor

We have read this dissertation and recommend its acceptance:

Arthur C. Echternacht, Charles D. Pless, Susan E. Riechert

Accepted for the Council:

Carolyn R. Hodges

Vice Provost and Dean of the Graduate School

(Original signatures are on file with official student records.)

To the Graduate Council:

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Associate Vice Chancellor and
Dean of The Graduate School

RESOURCE USE AND FORAGING ACTIVITY
OF MEXICAN FREE-TAILED BATS
TADARIDA BRASILIENSIS MEXICANA
(MOLOSSIDAE)

A Dissertation
Presented for the
Doctor of Philosophy
Degree
The University of Tennessee, Knoxville

Ya-Fu Lee

December, 1999

Dedicate to my parents, Mr. Hsi-Ming Lee and Ms. Lai-Jenn Suen

and my wife, Yem-Min Kuo

for all they have done to support me;

In memory of my grandparents,

Mr. Keh-Huey Suen and Ms. Guey-Sen Jang

with whom I share my most beautiful childhood in Tsoying

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ABSTRACT

Foraging patterns and the food habits of insectivorous bats may evolve in response to a variety of intrinsic (e.g., energetic demands, nutrient requirements, and morphological or physiological constraints in acquiring and consuming food) and extrinsic factors (e.g., the distribution and abundance of insect prey, and interactions with other organisms). This study investigates the foraging behavior and ecology of Mexican free-tailed bats, _Tadarida brasiliensis mexicana_ (Saussure, 1860) (Molossidae) residing in large colonies, with emphases on their dietary breadth and variation, their foraging activity, and their resource use patterns.

Food habits and dietary variation of insectivorous Mexican free-tailed bats were investigated at three large maternity colonies located in south central Texas. Food habits of bats were determined by analyzing fecal samples collected from individuals. Diets of bats from the two nightly feeding bouts, across seasonal phases, and from bats of different sex, age, and reproductive status were compared. Mexican free-tailed bats fed on a variety of insects, including at least 12 orders and 38 families. The size of coleopterans eaten were mostly from ca. 4 to 9 mm in length. Overall, lepidopterans, coleopterans, and hemipterans were the three most abundant prey in the diet. Homopterans, hymenopterans, and dipterans were less abundant, and other insects, including ephemeropterans, neuropterans, odonatans, orthopterans, plecopterans, and trichopterans were present in small amounts.

The diet of bats varied in the relative importance of insect orders in samples collected at midnight versus at dawn, and along seasonal phases. In late May-mid July, coleopterans and hemipterans were in higher proportions in the midnight, but lepidopterans were more abundant at dawn. In mid June-mid July, lepidopterans increased and hemipterans decreased in samples collected at midnight. In late July-August, the proportions of lepidopterans in diets decreased both at midnight and at dawn. The diet also varied among bats of different age, sex, and reproductive status. Pregnant females ate less lepidopterans, but more coleopterans and hemipterans than other adults. Juveniles ate less lepidopterans and neuropterans but higher proportions of coleopterans and homopterans than adults. In addition, reproductive females showed a more diverse diet than males, and juveniles had a more diverse diet than adults.

The foraging activity and resource use of Mexican free-tailed bats was investigated in a large maternity colony in Uvalde County, Texas. Foraging activity of bats was studied by recording their echolocation calls at sites along a sampling transect, which represented three different habitats; towns, cropland, and ranches. The proportion of time in which signals were received and the number of feeding buzzes per unit time were quantified. Insect availability and the relative abundance of different insect orders in the three habitats were assessed using light traps. The food habits of the bats were determined from fecal samples, and were compared to the relative abundance in mass of insect orders.

Mexican free-tailed bats had a higher foraging activity in town habitats than in cropland and ranches. In cropland and ranch habitats, feeding buzzes per unit time were less frequent in the pre-dawn collecting session than in the evening session, corresponding to the pattern of insect abundance in these habitats. In town habitats, however, insect abundance was similar in morning and evening sessions, and the foraging activity of bats did not differ between these two sessions. The relative importance of the common prey orders both in relative frequency of occurrence and relative volume in the diet of the bats were compatible with the relative importance of these respective insect orders in relative frequency of occurrence and in relative mass in trap collections. Graphic comparisons showed a shift of proportions of different prey in the diet between midnight and dawn, in response to the change of abundance of these insects in light traps. In addition, there was a positive correlation between the diet of bats and the light trap collections at the ordinal level, in 9 of 12 comparisons when Orthoptera was included, and in all 12 comparisons if

Orthoptera were removed.

The diverse diet and patterns of foraging activity and resource use of Mexican free-tailed bats have implications for insect pest management and conservation. The temporal and seasonal variation of moth consumption in the diet of the bats showed a clear correlation with the availability of large migratory populations of agriculturally injurious moths. The evaluation at the ordinal and family levels, considering the diversity of insect prey of the bats, also suggests that the insect-eating by the bats might be agriculturally beneficial. Together with other lines of evidence, the data suggest that Mexican free-tailed bats have a potentially significant contribution in regulating agricultural insect pests. The decline of Mexican free-tailed bat populations, and their seasonal and patchy distribution, warrant conservation concerns and efforts.

TABLE OF CONTENTS

PAGE

LIST OF FIGURES

LIST OF TABLES

I. INTRODUCTION

STATEMENT OF THE PROBLEM

Foraging patterns and the food habits of animals evolve in response to a variety of extrinsic and intrinsic factors. Mobile foragers that use food resources that are patchy or unpredictable in distribution must spend substantial time and energy searching. Thus, a general diet and flexible foraging mode may be selected. Species that live in large aggregations may face intensive competition for food resources, which also may lead to a broad pattern of resource use. For mammals, the extremely high energetic demands of females during pregnancy and lactation may cause them to use food differently from other individuals of the same population. Nutrients other than energy also may play an important role in the food resource use of an animal. The presence of predators or a potential risk of predation may prevent animals from foraging, or restrict their foraging to a certain time or at a certain place, and in turn affect their diet.

Many of these factors come together in the foraging behavior and ecology of Mexican free-tailed bats, Tadarida brasiliensis mexicana (Molossidae). These bats migrate annually between Mexico and the southwestern United States. They form large colonies during spring, summer, and fall in the southwestern United States. The energetic demands of these large colonies, particularly during the time these females are nursing their young, is tremendous and extremely large insect resource bases are required to support these colonies.

This study investigates the foraging behavior and ecology of Mexican free-tailed bats residing in large colonies. The emphases are on the dietary breadth and variation of these bats, their foraging activity in different habitats, and their resource use patterns. It is hoped that these data will add to our understanding of foraging strategies of insectivorous bats under the influence of different intrinsic and extrinsic factors. In addition, the information obtained should provide insight into the significance of insectivorous bats in insect pest management and have implications for the conservation of this migratory species.

BACKGROUND

Different species that occupy the same trophic level can show very different resource use patterns, as is illustrated by the diets of different species of finches on the Galapagos islands (Grant, 1986). However, the diets and resource use patterns of conspecific individuals also may differ due to factors such as variation in the food supply over time and space, and the foraging pattern and foraging efficiency of individuals (Morse, 1980). Individual conditions, such as sex, age, reproductive status, degree of hunger, health, and individual variability in feeding, also may affect foraging patterns and foraging efficiencies (Hughes, 1993; Krebs and Davies, 1993). In addition, interactions with other organisms, such as competition, predation, parasitism, and prey behavior are also important (Endler, 1991; Milinski and Parker, 1991; Sih, 1993). Multiple factors are often correlated and affect foraging and dietary patterns in complex ways (Stephens and Krebs, 1986; Hughes, 1993). Below, I focus on some of the factors that are associated with the foraging behavior and ecology of Mexican free-tailed bats.

Aggregations, Intraspecific Competition, and Resource Use

Animals may actively aggregate due to kinship. Examples include termites, many hymenopterans, the Florida Scrub Jay, prairie dogs, and some primates (Wilson, 1980; Slobodchikoff, 1988; Hoogland, 1995). Aggregations of animals may form in response to limited resources, such as water, food, and nesting and roosting sites (Willis and Oniki, 1978; Slobodchikoff, 1988; Brown and Brown, 1996; Alcock, 1998). Animals also may be brought together simply by physical factors, such as tidal movements (e.g., zooplankton, Morse, 1980) and wind (e.g., insects that are blown to high altitudes, Drake and Farrow, 1988). Aggregations of animals may serve different functions, including thermoregulation, cooperative breeding, cooperative hunting, information transfer, resource defense, and defense from predators. There also are costs associated with group living, such as ectoparasitism, the spread of disease, brood parasitism, and attraction to predators (Slobodchikoff, 1988; Brown and Brown, 1996). Another potentially important cost associated with group living is intraspecific competition, which may directly affect the use of food resources and feeding habitats. It has been suggested that the intensified competition for resources is an unavoidable consequence of group living. As group size increases, this cost will increase accordingly (Alexander, 1974).

The idea that species are potentially competing for a variety of resources is one of the basic tenets of ecology. For species living in large aggregations, however, intraspecific competition may be equally or more intense than competition with other species, because the competing individuals have very similar needs (Griffith and Poulson, 1993). Interspecific competition may cause the divergence of diets in competing species, and narrow the breadth of food resource use by each competing species. In contrast, constant and intensified intraspecific competition may increase the variety of resources used by conspecific individuals within a population (Pianka, 1988). Due to intraspecific competition for food resources, direct costs associated with the foraging behavior could cause gregarious foragers to travel a longer distance, cover a larger area, or spend a longer time searching for food (e.g., cliff swallows, Brown and Brown, 1996). Animals that travel and forage far from their roosts or nests will have a higher energetic expense, and also have a potentially higher risk of predation .

Foraging Patterns and Food Habits

Depending on the number of different types of food resources used, a forager may be labeled as a generalist or a specialist. Also, depending on the variability of resource use over time and space, both generalists or specialists may have fixed or flexible resource use patterns (Morse, 1980). This traditional categorical view of foraging patterns, although simplistic, is useful if used with caution and discussed in a relative and comparative basis. In nature, most animals probably fall between the extremes of these two categories, and the spatiotemporal variation of resource use is presumably high in many animals (Morse, 1980; Pianka, 1988).

Feeding efficiency can be defined as the net energy intake per unit of feeding time (Pyke et al., 1977). Key factors determining feeding efficiency are the distribution and the density of available food and the foraging mode of animals. Provided that food resources are stable or predictable, a less mobile forager, such as a sit-and-wait predator, may employ selective feeding and obtain sufficient food with a relatively low energy expenditure. Under the assumption of optimal foraging, high fitness can be achieved by a high net rate of energy intake where prey are abundant, accessible, and predictable (Stephens and Krebs, 1986). Thus, a specialized diet may be selected. However, if food resources are patchy in distribution, or the abundance and availability of food is unpredictable, a mobile forager must actively search for food. In this situation, more time and energy must be spent in searching, and higher predation risk may be involved. Therefore, an opportunistic foraging mode with a diet containing a wide variety of prey may be favored (MacArthur and Pianka, 1966).

Energetics and Feeding in Lactating Mammals

Lactation is the most energetically costly stage in mammalian reproduction (Loudon and Racey, 1987; Bronson, 1989). Energy use in females lactating at peak levels may reach 2.5 to 5 times those of non-reproductive females (Gittleman and Thompson, 1988). In some marine mammals, the production of energy-rich milk with high fat content can result in the loss of approximately 42% of a female's body mass during the lactation period. In these species, females may minimize their activity to achieve metabolic savings (e.g., elephant seals, Costa et al., 1986).

In other mammals, females adjust to this expenditure by increasing caloric intake. This may be achieved by increasing the length of time spent feeding (e.g., pipistrelle bats, Racey and Swift, 1985; gelada baboons, Dunbar and Dunbar, 1988), or by altering the foraging strategy employed and the types of prey pursued (e.g., sea otters, Riedman and Estes, 1987). In other species, such as cheetahs, lactating females employ both strategies to fulfill their energetic demands (Caro, 1994). All these behavioral adaptations during the lactation period can result in females having dietary patterns that are different from those of other individuals or different from what the same females exhibit at other times in their life cycles.

Nutrient Requirements

The foraging activity and diet of a forager should also reflect its needs for nutrients (Robbins, 1994; Schmidt-Nielsen, 1997). In addition to energy, animals need sufficient and balanced amounts of nutrients, such as proteins, minerals, and vitamins, to remain healthy and to reproduce (Robbins, 1994). Proteins are major constituents of an animal's body. Proteins also serve many important functions, such as fat transport, as antibodies and clotting factors in blood, and as carriers in active transport systems (Schmidt-Nielsen, 1997). Minerals include macro-elements (i.e., calcium, phosphorus, sodium, potassium, magnesium, chlorine, and sulfur) and other trace elements, such as iron, zinc, manganese, iodine, copper, molybdenum, selenium, cobalt, fluoride, and chromium.

Minerals and vitamins, although required in low or trace amounts compared to proteins, carbohydrates, and lipids, are essential and often the limiting components to growth and the maintenance of health (Robbins, 1994). For instance, calcium and phosphorus are the two major mineral constituents associated with skeletal formation of vertebrates. About 99% of the calcium and 80% of the phosphorus of the body of a mature vertebrate animal are contained in bone (Comar and Bronner, 1964). For both birds and bats, it has been suggested that calcium, rather than energy, is the major constraint on reproductive success, growth of the young, and other life history characteristics, such as the litter size (Barclay, 1994, 1995). Thus, the diets of animals may also reflect the nutritional requirements during different stages of their life cycle (e.g., hispid cotton rats, Randolph et al., 1995). Animals that achieve a balance between maximizing the net rate of energy intake and essential nutrients may be able to maintain a better health, a higher reproductive success, and higher fitness (Stephens and Krebs, 1986; Hughes, 1993).

Predation Risk and Resource Use

A forager, whether a carnivore, insectivore, or herbivore, may encounter a higher risk of predation while feeding because of increased exposure, conspicuous movement, or reduced vigilance (Endler, 1991; Alcock, 1998). In the absence of predators or under a low risk of predation, a forager may choose food or food patches primarily based on quality (e.g., energy content and nutrient content) or the abundance of the food. However, in the presence of such risk, safety may become a major concern (Metcalfe et al., 1987; Orr, 1992).

Predation risk may alter the habitat use or foraging behavior of foragers, or reduce their foraging activity (Werner et al., 1983; Hughes et al., 1994; Jones and Rydell, 1994; Romey, 1995). For instance, foragers may choose a safer place to feed, feed only at a safer time, or they may tend to move often instead of staying at a single place. All these considerations may in turn affect the food resource encountered by a forager and affect its diet. In addition, depending on the risk associated with different foraging stages (i.e., searching, pursuing, handling, and ingestion), foragers may become more or less selective in food choice (Lima and Dill, 1990). If handling exposes a forager to a higher risk than searching, a forager should be more selective. Many of these predictions have been tested for a variety of species and confirmed in both field and laboratory experiments (see Lima and Dill, 1990; Krebs and Kacelnik, 1991; Sih, 1993).

Foraging Patterns of Temperate Insectivorous Bats

Although some bat species have a wing-span of nearly two meters, and can reach a body weight of 1,500 g (e.g., the Lyle's flying fox, Pteropus lylei, in Thailand and Vietnam), most insectivorous bats are small (Nowak, 1999). Due to a large surface/volume ratio, bats have high basal metabolic rates to maintain their body temperature (McNab, 1982). Most insectivorous bats search for and prey on insects by using echolocation during continuous flight, both of which are energetically expensive (Speakman and Racey, 1991; Norberg, 1998).

In temperate areas, bats also face the pressure of compressing crucial stages of their life history (i.e., gestation, lactation, growth and development of young, and physiological preparations for hibernation, migration, or both) into a period of several months between late spring to early fall. In the summer, particularly, nights are shorter and bats have less time to forage. In addition, insects are typically patchy in distribution, and their species composition and abundance often change seasonally (Wolda, 1988) and with daily weather patterns (Price, 1984). From the point of view of energetic demands and food acquisition, insectivorous bats in the temperate zone are excellent organisms to study dietary variation and resource use patterns.

Using echolocation calls, nocturnal aerial-hunting insectivorous bats not only can detect the presence of their potential prey, but also are able to localize the position of the target, and classify the target on properties such as size, form, and texture (Schnitzler and

Kalko, 1998). This suggests that echolocating bats need not feed at random. Furthermore, the morphological characteristics of bats may restrict the foraging mode employed, and thus the prey they can catch and consume (Norberg and Rayner, 1987; Fenton, 1990). For instance, wing shape and size (i.e., wing loading and aspect ratio) can affect the flight characteristics of bats, such as their speed, agility, and maneuverability (Norberg and Rayner, 1987; Norberg, 1990). The relative lengths of pinna to forearm are correlated with the echolocation call frequency used to detect and pursue prey (Fenton, 1972). The auditory capability and types and structures of echolocation signals used by different bat species are adaptations specifically towards the acoustic constraints associated with different foraging patterns and habitats (Neuweiler, 1989, 1990). Finally, body size, cranial morphology, and tooth morphology of bats are correlated with the size range of insects that bats can consume (Findley, 1972; Freeman, 1981). Insects that are above a certain size range may be beyond the ability of small-sized bats to catch and handle. Insects below a certain size range may be too small to be detected by the echolocation calls, or being detected, bats may not be fast and maneuverable enough to catch them (Fenton, 1995a).

Specialized diets of one or two dominant prey types (e.g., beetles or moths) and narrow diets (here defined as containing less than five orders of insect prey) have been reported in several species of temperate insectivorous bats. Most bat species with specialized diets are in the Family Vespertilionidae, and from their wing morphology and the size of pinna are known or predicted to glean insects from the ground or foliage (Norberg and Rayner, 1987). Examples include *Antrozous pallidus* (Bell, 1982), *Corynorhinus rafinesquii* (Hurst and Lacki, 1997), *Idionycteris phyllotis* (Warner, 1985), *Myotis blythii* and *M. myotis* (Arlettaz, 1996), *M. daubentoni* (Swift and Racey, 1983), *M. evotis* (Barclay, 1991), *M. thysanodes* (Whitaker et al., 1981), *Otonycteris hemprichi* (Arlettaz et al., 1995). A few others are aerial-hunting bats, such as *Eptesicus serotinus*

(Catto et al., 1994), Lasiurus borealis (Whitaker et al., 1997), Nyctalus leisleri (Waters et al., 1995), Pipistrellus pipistrellus (Hoare, 1991), Rhinolophus ferrumequinum (Jones, 1990; Jones et al., 1995), and Vespertilio murinus (Rydell, 1992b).

More generalized diets (containing more than five orders of insect prey) have been found in many other studies of insectivorous bats. Examples of typical aerial-hunting species with diverse diets are Barbastella barbastella (Rydell et al., 1996b), Eptesicus fuscus (Whitaker, 1995), E. serotinus (Robinson and Stebbings, 1993), Lasionycteris noctivagans and Lasiurus cinereus (Barclay, 1985), L. borealis (Whitaker, 1972), Nyctalus leisleri (Shiel et al., 1998), Nycticeius humeralis (Whitaker and Clem, 1992), Pipistrellus mimus (Whitaker et al., 1999), P. pipistrellus (Sullivan et al., 1993), P. subflavus (Griffith and Gates, 1985), Hipposideros armiger and Rhinolophus monoceros (Chen, 1995), R. hipposideros (McAney and Fairley, 1989), Tadarida brasiliensis (Whitaker et al., 1996), and Vespertilio murinus (Bauerova and Ruprecht, 1989). Species such as Plecotus auritus and P. austriacus that are thought of as gleaners, which in general have slower and more maneuverable flight and smaller foraging ranges (Audet, 1990), can also have diverse diets (Bauerova, 1982; Shiel et al., 1991). A diverse diet is typically reported for species within the largest genus of bats (i.e., Myotis), which includes species capable of both aerial-hunting or gleaning. Examples include M. californicus, M. evotis, and M. yumanensis (Whitaker et al., 1981), M. daubentoni (Sullivan et al., 1993), M. emarginatus (Bauerova, 1986), M. grisescens (Best et al., 1997), M. lucifugus and M. septentrionlis (Griffith and Gates, 1985), M. nattereri (Shiel et al., 1991), M. sodalis (Kurta and Whitaker, 1998), M. velifer (Kunz, 1974), and M. volan (Saunders and Barclay, 1992).

Occasionally, some studies identify a given species as specialist; whereas, other studies identify the same species as a generalist. A conclusion to be drawn from these many dietary studies is that bats with morphological and echolocation features suitable for certain prey types may not be restricted to feeding only on those types, and species that are predicted to be dietary generalists or specialists may not be in all circumstances. In addition, even for conspecific insectivorous bats that are known as generalists, diets may show spatiotemporal and intra-population variations, presumably due to the factors of prey availability, habitats, and individual differences. This has been reported in some of the more commonly studied species, such as E. fuscus (Hamilton and Barclay, 1998), M. lucifugus (Belwood and Fenton, 1976; Griffith and Gates, 1985; Adams, 1997), M. sodalis (Brack and LaVal, 1985; Kurta and Whitaker, 1998), M. grisescens (Lacki et al., 1995; Best et al., 1997), and P. pipistrellus (Barlow, 1997).

Due to the different emergence times of many insects (Rydell et al., 1996a), their short life spans, and local fluctuations of insect populations, insectivorous bats may not encounter large numbers of insects of the same taxa or the same type night after night within their foraging range. In addition, the high energy demands of bats due to their small body sizes, high metabolic rates, and continuous flights while searching for food, may force aerial-hunting insectivorous bats to minimize search times by feeding opportunistically on those insects that are available (Fenton, 1982a). These factors may restrict the ability of insectivorous bats to specialize on certain insects.

Furthermore, many insects that are potential prey of insectivorous bats have evolved defensive mechanisms or elusive behavior patterns to escape from being caught and eaten. For example, some moths (e.g., arctiids) emit clicks in response to echolocation calls of bats, which presumably serve to startle foraging bats (Bates and Fenton, 1990) or provide acoustic aposematism associated with their distasteful odor (Dunning et al., 1992). Many moths, including the largest families Noctuidae, Geometridae, and Pyralidae, have auditory organs that are tuned to frequencies of the echolocation calls of certain bats (Fullard, 1987). Tympanic ears also occur in insects of at least six other orders, including Coleoptera (e.g., tiger beetles, Spangler, 1988), Diptera (e.g., tachinids, Robert et al., 1992; Stumpner and Lakes-Harlan, 1996), Homoptera (e.g., cicadas, Michelson and Larson, 1985), Mantodea (praying mantises, Yager et al., 1990), Neuroptera (e.g., green lacewings, Miller, 1975), and Orthoptera (e.g., crickets, locusts, katydids, Michelson and Larson, 1985; Robert, 1989). Their functional ears, have probably evolved primarily for intraspecific communication; however, the ability to hear may also allow defensive mechanisms (Fullard and Yack, 1993).

Using simulated bat calls, Roeder (1962) has demonstrated that eared moths (e.g., noctuids and geometrids) turn away from ultrasound calls of low intensity. In the presence of high intensity calls, however, moths may show complex evasive behaviors, involving looping, zigzag flying, passive falling, diving, or a combination of these patterns (Roeder, 1962). These elusive behaviors may reduce the chance of being caught by 40% (Roeder and Treat, 1961; Acharya, 1992). Evasive aerial maneuvers in response to the ultrasonic bat calls also have been experimentally demonstrated in tiger beetles, praying mantises, green lacewings, and various orthopterans (Miller, 1975; Spangler, 1988; Robert, 1989; Yager et al., 1990; May, 1991).

It is possible that many, if not all, insectivorous bats in temperate areas employ a foraging strategy combining both selective and flexible modes (Fenton, 1995b). They may be selective at a certain level, for example, foraging in certain habitats (e.g., cluttered, or open space) due to intrinsic constraints, such as the wing morphology and the design of echolocation structures. Within their foraging habitats, however, most insectivorous bats appear to be flexible and opportunistic foragers, pursuing the most abundant insects that are available and feeding on a variety of prey, particularly when food resources are scarce (Fenton and Morris, 1976; Fenton, 1985).

The Mexican Free-tailed Bat

Mexican free-tailed bats, Tadarida brasiliensis mexicana (Saussure, 1860), migrate each year between the southwestern United States and Mexico, with some individuals traveling over 1,200 km (Cockrum, 1969). Long distance migration is costly energetically, and support of these movements requires specific patterns of energy allocation. Migrants may travel through areas with scarce food resources, different types of food resources, and the abundance of food resources may be unpredictable (Dingle, 1996). In addition, migrants are often subject to daily changes in habitats, local weather, and food conditions (Morse, 1980; Alcock, 1998). These pressures may favor a general and flexible pattern of food resource use.

The summer maternity colonies of T. b. mexicana in south central Texas are among the largest known aggregations of vertebrates in the world (Cockrum, 1969). These bats give birth and nurse pups in early-mid June. Pups grow fast and, on average, become volant and able to feed on their own in five to six weeks after birth (McCracken and Gustin, 1991; Kunz and Robson, 1995). From early to mid-lactation, the dry matter and energy concentration in milk increase significantly, largely because of a rise in fat concentration (Kunz et al., 1995a). Lactation is a great energetic cost to these females. The enormous energetic demands in females doubles or even triples the average nightly feeding rate from pregnancy to mid-lactation (Kunz et al., 1995b).

The flight of T. b. mexicana is fast and agile. Davis et al. (1962) found that some individuals travel at an average speed of 40 km/h, and fly over 50 km from the cave roost in one night. The foraging dispersal of a large Mexican free-tailed bat colony may cover an area at least 400 km^2 (Williams et al., 1973). During the evening emergence, these bats may ascend up to 3,000 m after leaving the cave roost (Williams et al., 1973). Their feeding also has been documented at altitudes up to 1,200 m through the use of ultrasonic detecting radio microphones (Griffin and Thompson, 1982; McCracken et al., 1996, 1997). However, many individuals also feed locally close to roosts, and at considerably lower elevations (Caire et al., 1984; Lee, pers. obs.).

Different predators prey on T. b. mexicana at or near the roost. Possums, raccoons, roadrunners, and snakes often attack bats from or near the ground (Gillette and Kimbrough, 1970; McCracken et al., 1986; Lee and Kuo, 1999). However, the major threat of predation probably comes from aerial raptors. The nocturnal habits of bats make them unavailable to most raptors, and it has been suggested that nocturnal behavior is in itself an adaptation to avoid aerial predators (Speakman, 1995). Even so, there are reports of at least eight diurnal raptor species from five genera (i.e., Accipiter, Buteo, Circus, and Ictinia [Accipitridae], and Falco [Falconidae]) and three nocturnal raptors (i.e., Athene cunicularia and Bubo virginianus [Strigidae], and Tyto alba [Tytonidae]) preying on Mexican free-tailed bats at their colony sites (Stager, 1941; Sprung, 1950; Twente, 1954; Eads et al., 1957; Baker, 1962; Taylor, 1964; Black, 1976; Caire and Ports, 1981; Botelho and Arrowood, 1996). Observations suggest that during the crepuscular emergence and return, the high concentration of bats at caves are a great attraction to raptors. This threat of predation may in turn affect the patterns of emergence and return to the cave, and affect the bats' foraging activity patterns.

Due to their very large aggregations and high energetic demands, intraspecific competition for food must be intense within large colonies of T. b. mexicana. This is supported by the long distances that they disperse for foraging. Factors such as the sizes of these colonies, their massive density in the emergence and returns, and enormous energetic demands of females during their lactating period, make this mobile, nocturnal, insectivorous forager an excellent example to investigate the effects of large aggregations, lactation energetics, and predation risk, on activity patterns, diet breadth, and resource use patterns among individuals, and the variation in these factors, over time. Furthermore, the energetic demands of these large colonies suggest that their insectivory is significant.

Since the 1950s, severe declines in many colonies have been documented in both Mexico and the US, due to disturbance and destruction of cave roosts and possibly pesticide poisoning (McCracken, 1986). These declines provide important concerns for the conservation of these bats.

OBJECTIVES

The objectives of this study are to determine (1) the dietary breadth and variation of T. b. mexicana; (2) if individuals of different age, sex, and reproductive status display different dietary breadth and resource use patterns over the season, as a consequence of their different energetic or nutrient demands; (3) if T. b. mexicana in large colonies tend to be opportunistic in foraging. In addition, this study (4) provides information on the significance of foraging by these large colonies for insect pest management. A brief summary of each subsequent chapter is as follows:

Chapter II.—I describe the food habits, establish the dietary patterns, and examine the dietary variation of T. b. mexicana in space (among replicate colonies), time (temporal and seasonal), and among individuals (bats of different age, sex, and reproductive classes).

Chapter III.—I measure the foraging activities of T. b. mexicana, and the composition and abundance of potential insect prey in different habitats. I compare and correlate the dietary data with the data on insect composition and abundance to determine the dietary breadth of T. b. mexicana and to assess whether these bats are opportunistic in foraging.

Chapter IV.—I synthesize the results of activity patterns, dietary variation, and the resource use pattern of T. b. mexicana, and discuss the significance and the implications for insect pest management and for conservation concerns for this species.

II. FOOD HABITS AND DIETARY VARIATION OF MEXICAN FREE-TAILED BATS IN SOUTH CENTRAL TEXAS

Abstract. Food habits and dietary variation of insectivorous Mexican free-tailed bats, Tadarida brasiliensis mexicana, were investigated at three large maternity colonies located in south central Texas. Food habits of bats were determined by analyzing fecal samples collected from individuals. Diets of bats from the two nightly feeding bouts, across seasonal phases, and from bats of different sex, age, and reproductive status were compared. Mexican free-tailed bats fed on a variety of insects, including at least 12 orders and 38 families. The size of coleopterans eaten were mostly from ca. 4 to 9 mm in length. Overall, lepidopterans, coleopterans, and hemipterans were the three most abundant prey in the diet. Homopterans, hymenopterans, and dipterans were less abundant, and other insects, including ephemeropterans, neuropterans, odonates, orthopterans, plecopterans, and trichopterans were present in small amounts.

The diet of bats varied in the relative importance of insect orders in samples collected at midnight versus at dawn, and along seasonal phases. In late May-mid July, coleopterans and hemipterans were in higher proportions in the midnight than at dawn, but lepidopterans were more abundant at dawn than in the midnight. In mid June-mid July, lepidopterans increased and hemipterans decreased in samples collected at midnight. In late July-August, the proportions of lepidopterans in diets decreased both at midnight and at dawn. The diet also varied among bats of different age, sex, and reproductive status. Pregnant females ate less lepidopterans, but more coleopterans and hemipterans than other adults. Juveniles ate less lepidopterans and neuropterans but higher proportions of coleopterans and homopterans than adults. In addition, reproductive females showed a more diverse diet than males, and juveniles had a more diverse diet than adults.

INTRODUCTION

Food habits and dietary variation provide the most fundamental information to understand patterns of resource use by animals. Diets of insectivorous bats have shown variation when assessed at different times of year (Fenton and Thomas, 1980; Whitaker et al., 1999), or at different places and years (e.g., Indiana bats, Brack and LaVal, 1985 vs. Kurta and Whitaker, 1998; grey bats, Lacki et al., 1995 vs. Best et al., 1997), probably reflecting spatiotemporal variability in the composition and relative abundance of prey. Bats of different sex, age, and reproductive status from the same population can also show dietary variation. Bats under different body conditions (e.g., body mass and wing loading), energetic demands, and nutrient requirements may employ different foraging strategies (Anthony and Kunz, 1977), forage in different habitats (Kalcounis and Brigham, 1995; Adams, 1996), spend different lengths of time foraging (Anthony et al., 1981; Barclay, 1989; Brigham, 1991; Grinevitch et al., 1995), and exploit different food resources.

Migratory Mexican free-tailed bats, Tadarida brasiliensis mexicana (Saussure, 1860) (Molossidae), are among the most widely distributed insectivorous bats in the southwestern United States (Davis et al., 1962). Tadarida b. mexicana is also among the most locally abundant bat species in their range during the summer. Most known populations concentrate at only a few caves, mostly in Texas, New Mexico, and Oklahoma. The estimated 20 million bats in Bracken Cave, Texas, form the largest known mammalian aggregation in the world (Davis et al., 1962). In one night, the foraging dispersal of a Mexican free-tailed bat colony may cover an area of over 400 km^2 (Williams et al., 1973), with these bats feeding from a few meters above the ground to altitudes of over 1,200 meters (Griffin and Thompson, 1982; Caire et al., 1984; McCracken et al., 1996).

Earlier dietary studies, based on small numbers of stomach or guano samples that were collected over brief periods from one or two localities, indicate that T. b. mexicana feed almost exclusively on small moths (see reviews in Freeman, 1979). Rose (1967) reported six insect orders from examining 88 stomachs, and also concluded that Lepidoptera is the most important prey. Most of these studies did not include quantitative analyses or only reported the percentage occurrence of each prey item identified. Kunz et al. (1995b) found no difference in the diet of pregnant and lactating females, based on 38 stomach contents collected from one site. Whitaker et al. (1996) presented by far the most detailed information on diet of this species, based on 77 fecal samples collected from one site and over an eight-day period in late June. Whitaker et al. (1996) also compared diets of bats between their evening and pre-dawn feeding periods, and suggested that temporal variation in the consumption of moths by T. b. mexicana is correlated with the timing and migration patterns of large moth populations (e.g., corn earworms, Helicoverpa zea (Boddie)) from the lower Rio Grande Valley in Texas and Mexico (Wolf et al., 1994; Westbrook et al., 1995).

The results of Whitaker et al. (1996) suggested the necessity of further studies at a larger spatiotemporal scale. If migratory moth populations serve as an important food resource of T. b. mexicana, the pattern of moth consumption should reveal not only variation between the two nightly feeding bouts, but also variation along the seasonal phases in accordance to the timing of emergence, local establishment, and senescence of moth populations. In addition, as the summer progresses, the composition of the bat colonies also changes. Reproductive females dominate the colony from late spring to mid July, but many juveniles start to forage since mid-late July.

A major objective of this study was to describe the diet of three large maternity colonies of T. b. mexicana during the late spring-summer period. I predicted that (1) moth consumption will be higher in mornings than in evenings during the migration period of corn earworms from Mexico; (2) moth consumption will increase in evenings as corn earworm populations become resident in south central Texas; and (3) moth consumption in both evenings and mornings will decrease in mid-late summer with the harvesting of corn and movement of corn earworms to cotton. A second objective was to examine the variation among the diets of bats of different age, sex, and reproductive classes. In this regard, I predicted that (4) reproductive females will show a different and a more diverse diet than bats of other classes present during the same time period, because of their apparently higher energetic demands and requirements of some critical nutrients (e.g., calcium) during pregnancy to lactation; and that (5) juveniles will have a different diet than adults present during the same time period, because of their less skilled hunting due to gradually developed flying and echolocation abilities.

MATERIALS AND METHODS

Study Sites

I conducted field work at Bracken Cave (Comal County), James River Bat Cave (hereafter as JRBC; Mason County), and Frio Cave (Uvalde County) in south central Texas. All three are limestone caves, located at the south-eastern, north-eastern, and southern edges of the Edwards Plateau, respectively, and each cave is about 150 km from the others (Fig. 2.1). All three caves contain large maternity colonies of T. b. mexicana. Their most recently estimated population sizes are about 6 million bats in JRBC, 10 million bats in Frio Cave, and about 20 million bats in Bracken Cave (Davis et al., 1962; Wahl, 1989).

Bat and Fecal Sampling

Bats were sampled weekly, from late May to mid-August, at Bracken, JRBC, and Frio in the summer of 1995, and also at Frio in the summers of 1996 and 1997. I used a hoop net (ca. 46.5 cm in diameter, with a 3 m long aluminum pole) to sample bats

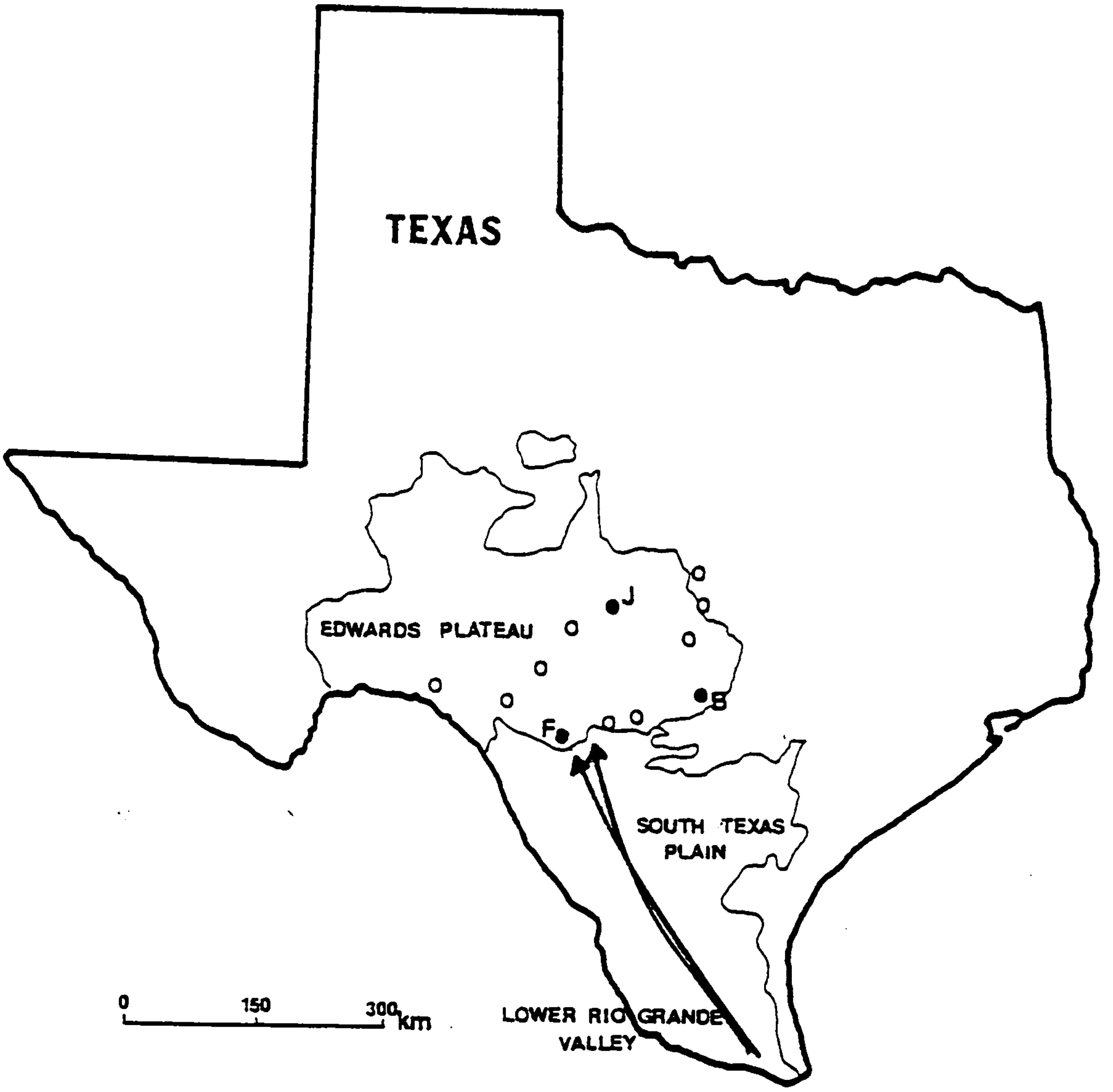

Figure 2.1. The locations of Bracken (B), JRBC (J), and Frio (F) Caves, and other major cave roosts (open circles) of Mexican free-tailed bats in the Edwards Plateau region in south central Texas. Arrows in the South Texas Plain region where major agricultural areas are distributed indicate the flying direction of corn earworm moths from source areas in northeastern Mexico and southern Texas based on tetroon trojectories (after Westbrook et al., 1995).

returning to the cave entrance following each of their two nightly foraging bouts. The first sampling session started at 2330 h to 2400 h, and the second sampling session at about 0600 h. During each sampling session, I randomly collected three or four bats every 15 minutes, and repeated this process several times until a minimum of 25 bats was caught. The total sampling in each session took about two hours. I placed each bat in a separate cloth bag for about four hours. Bats collected at midnight were released at about 0400 h, and bats collected at dawn were released at about 1000 h. I examined the age, sex, and reproductive status of each bat and collected fecal pellets. Juveniles were distinguished from adults by the presence of cartilaginous epiphyseal plates in finger bones (Anthony, 1988). Pregnant females were distinguished by the presence of a palpable embryo, and lactating females were distinguished by the presence of enlarged, cornified nipples, and by the presence of milk expressed from mammary glands (Racey, 1988). Each fecal sample (i.e., the collective fecal pellets from one bat) was placed in a labeled envelope, and air dried in sunlight, and all envelopes were then sealed in a plastic container for later analysis.

Dietary Analysis

I used conventional methods of fecal analysis, following the procedures described by Whitaker (1988). For each midnight or dawn sampling session, I analyzed at least 8 samples (about one third of the total samples collected in a session) representing all of the age, sex, and reproductive classes present, so the total numbers of samples analyzed in all bat classes were similar. Within each bat class, samples were selected arbitrarily (odd code numbers for midnight samples, and even code numbers for dawn samples). If a bat class contained only three or less samples in a sampling session, I analyzed all of these samples.

In each sample, I chose and examined five of the largest (ca. 5 to 8 mm long) fecal pellets, because smaller pellets tended to become fragmented. Whitaker et al. (1996) have previously demonstrated that this number is sufficient to determine the diet of a single T. b. mexicana, and that the sizes of pellets do not bias particular prey items. I soaked and softened each pellet in a petri dish with 70% ethyl alcohol, and dissected the pellet with fine forceps and a dissecting needle. Fragments were examined and sorted to different prey items under a 10 x 20 magnification dissecting microscope. I estimated the proportion of each prey item visually with the aid of grid paper (10 x 10 units) attached to the bottom of the petri dish. Available insect keys and drawings of insects and insect structures (e.g., Whitaker, 1988; Borror et al., 1989; McAney et al., 1991; Arnett, 1993; Merritt and Cummins, 1996) and voucher specimens were consulted for identification.

Insect fragments in fecal pellets were identified to the lowest possible taxonomic level, mostly the family, but most soft-bodied insects (e.g., moths, caddisflies, mayflies) were only identified to orders. Identification of insect prey in the diet of bats relied on body parts and appendages with noticeable characteristics (e.g., antennae, mouth parts, elytra, wings and venation, legs, tarsi, cerci, halteres, scales, and hairs). In rare occasions, items such as vegetative materials, rock and soil particles, string fibers, and fur occurred in feces. Presumably, they were taken by bats accidentally when bats picked up insects from foliage or the ground, from chewing cloth bags, or during grooming. These items were disregarded.

The relative frequency of occurrence and the relative volume in the feces were determined for each taxon eaten. The relative frequency of occurrence of a particular item (i.e., a prey taxon) is the number of occurrences of this item in fecal samples divided by the total occurrences for all prey items. The relative frequencies provide an idea of the relative importance of each prey item in commonness (McAney et al., 1991). The relative volume of a particular prey item in a sample is the sum of the proportions of this item in each fecal pellet divided by the total number of fecal pellets examined for each sample

(Whitaker, 1988). The relative volumes of all prey items provide an estimate of the relative importance of each item in abundance. I also measured the length of all coleopteran femora found in feces. I estimated the size of coleopterans eaten by bats by applying an equation which describes the relationship of femoral length to body size of coleopterans, where $y = 0.71 + 3.87x$ (x is the femoral length in mm, and y is the body length excluding the head in mm; Csada et al., 1992).

Data Analysis

All means were presented as (± 1 SE) unless otherwise noted. I used R x C tests of independence to determine if the distribution of relative frequencies was random among prey items. I used ANOVA to examine the effects of different spatiotemporal factors (i.e., site, year, and collecting session) on the variance of relative volume of each item, the differences in diets among seasonal phases (late May-mid June, late June-mid July, and late July-August), and among bats of different age, sex, and reproductive classes. If a significant difference was detected, additional multiple range comparisons (Fisher's PLSD) were conducted to find the location of differences. Volume data were arcsine transformed before a test to meet the normality requirement (Sokal and Rohlf, 1981). I also employed the reciprocal Simpson index, $1/D = 1/\sum (P_i^2)$, as to assess for the heterogeneity of diet (Krebs, 1989), where P_i is the relative volume (%) of a particular prey item i (i = 1 to n, n is the total number of prey items). A higher index value indicates a more diverse diet with a more even volume distribution. All statistical tests were determined at the significance level of 0.05.

RESULTS

Food Habits

In total, I analyzed 1,550 fecal samples (from 248 juveniles, 290 adult males, 287 pregnant females, 483 lactating females, and 242 post-lactating or non-reproductive females) that were collected over the three summers. The number of different prey items found in each fecal sample varied from 1 to 11 (mean 5.4 ± 0.05), but about 72.7% of samples contained 4 to 7 prey items (Fig. 2.2). The overall diet of Tadarida brasiliensis mexicana contained members of 12 orders, 35 families, and 3 groups of insects for which family could not be confidently determined (i.e., Nematocera, Schizophora, and Zygoptera) (Table 2.1). Lepidopterans, coleopterans, and hemipterans were most frequently found and were in the highest proportions in the diet. Together, they accounted for nearly 60% of the total occurrence, and over 76% of the total volume. These three orders and less common homopterans, hymenopterans, and dipterans collectively accounted for over 90% of the total occurrence and over 95% of the total volume. Neuropterans appeared in diet in less than 4% of the total occurrence, and other minor orders appeared in less than 1.5% each. Collectively, six minor orders accounted for only about 3% of the total volume. A small proportion (ca. 1.6% of volume) of unidentifiable items also occurred, which comprised unknown arthropod fragments, egg-like materials, and unidentifiable white or light green tissue-like materials (Table 2.1). I found 545 coleopteran femora that could be used for prey size estimation. The estimated sizes of coleopterans ranged from 4.5 to 16 mm, but most ranged from 4.5 to 8.5 mm (91.4%), followed by the range of 8.5 to 12.3 mm (7.7%). I found an almost complete homopteran (Cercopidae) of 5 mm long in one sample, and in another sample a partially fragmented body of about 10 mm of an unknown moth without wings.

Among the 12 prey orders, lepidopterans and coleopterans appeared as the predominant prey items (here defined as contributing over half of the volume in a sample) in the diets of the first and second highest proportions of bats (Fig. 2.3). Hymenopterans ranked third in this regard, and exceeded hemipterans, although the latter contributed a higher overall relative volume. In 14 samples, numerous large pieces of same

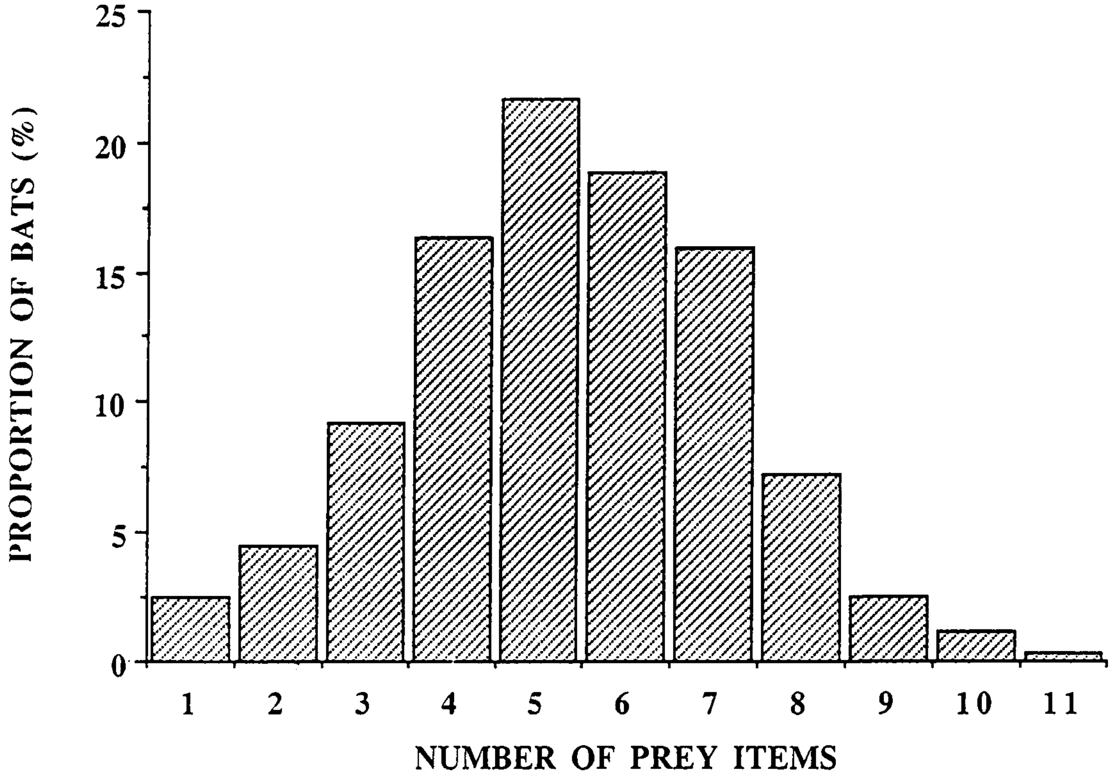

Figure 2.2. The proportion of bats in which different numbers of prey items were found in the diet (n = 1,550). Mean: 5.4 ± 0.05 (95% confident intervals: 5.31, 5.49), median: 5, mode: 5.

Table 2.1. Relative frequency (%) of occurrence of each prey item and relative volume (%) of each prey order revealed in the diet of *T. b. mexicana* (n = 1,550).

Prey Item	Relative Frequency		Relative Volume
	Order	Family[†]	Order
COLEOPTERA	19.8		29.04 ± 0.70
Brentidae (straight-snouted beetles)[‡]		0.1	
Carabidae (ground beetles)		22.3	
Chrysomelidae (leaf beetles)		16.4	
Curculionidae (weevils)		5.1	
Dytiscidae (predaceous diving beetles)[*]		1.0	
Scarabaeidae (scarab beetles)[‡]		19.7	
Scolytidae (bark beetles)[‡]		0.1	
Unidentified beetles		35.3	
DIPTERA	8.7		2.24 ± 0.15
Dolichopodidae (long-legged flies)		1.3	
Drosophilidae (vinegar flies)[‡]		1.1	
Nematocera (long-horned flies)		6.3	
Schizophora (muscoid flies)		4.5	
Sciaridae (dark-winged fungus flies)		0.3	
Syrphidae (syrphid flies)		1.8	
Tephritidae (fruit flies)[‡]		17.0	
Unidentified dipterans		67.7	
EPHEMEROPTERA (mayflies)[*]	0.9		0.32 ± 0.08
HEMIPTERA	18.3		14.78 ± 0.49
Coreidae (coreid bugs)[‡]		1.0	
Corixidae (water boatmen)[*]		3.7	

Table 2.1 (continued).

Prey Item	Relative Frequency		Relative Volume
	Order	Family[†]	Order
Cydnidae (burrower bugs)[‡]		12.1	
Lygaeidae (seed bugs)[‡]		25.0	
Miridae (plant bugs)[‡]		7.8	
Nabidae (damsel bugs)[‡]		5.3	
Pentatomidae (stink bugs)[‡]		26.8	
Reduviidae (assassin bugs)[‡]		1.2	
Saldidae (shore bugs)[*]		0.1	
Tingidae (lace bugs)[‡]		0.3	
Unidentified hemipterans		16.7	
HOMOPTERA[‡]	14.9		7.73 ± 0.34
Cercopidae (Spittlebugs)		29.4	
Cicadellidae (leafhoppers)		37.3	
Cixiidae (cixiid planthoppers)		15.8	
Delphacidae (delphacid planthoppers)		8.0	
Flatidae (flatid planthoppers)		0.4	
Unidentified homopterans		9.1	
HYMENOPTERA	7.9		9.51 ± 0.58
Braconidae (braconids)		8.7	
Formicidae (winged ants)[‡]		38.9	
Tiphiidae (tiphiids)[‡]		9.6	
Unidentified hymenopterans		42.8	
LEPIDOPTERA (moths)	20.5		32.41 ± 0.78
NEUROPTERA	3.7		1.13 ± 0.10

Table 2.1 (continued).

Prey Item	Relative Frequency		Relative Volume
	Order	Family†	Order
Chrysopidae (green lacewings)‡		45.8	
Hemerobiidae (brown lacewings)‡		51.9	
Myrmeleontidae (antlions)‡		2.3	
ODONATA (Zygoptera)*	0.3		0.04 ± 0.02
Coenagrionidae (narrow-winged damselflies)			
ORTHOPTERA	1.3		0.83 ± 0.15
Acrididae (short-horned grasshoppers)		4.5	
Gryllidae (crickets)		95.5	
PLECOPTERA (stoneflies)*	0.2		0.03 ± 0.01
TRICHOPTERA (caddisflies)*	1.0		0.75 ± 0.12
Unidentified fragments	2.5		1.59 ± 0.29
Total	100.0		100.0

† The relative frequency (%) of occurrence of each prey family is measured within the prey order to which the family belongs.

‡ Insect taxa that are known as exclusively terrestrial.

* Insect taxa that are considered as aquatic, with almost all species having one or more aquatic stages, and adult forms are common around aquatic or semi-aquatic environments (based on Borror et al., 1989; Arnett, 1993; Merritt and Cummins, 1996).

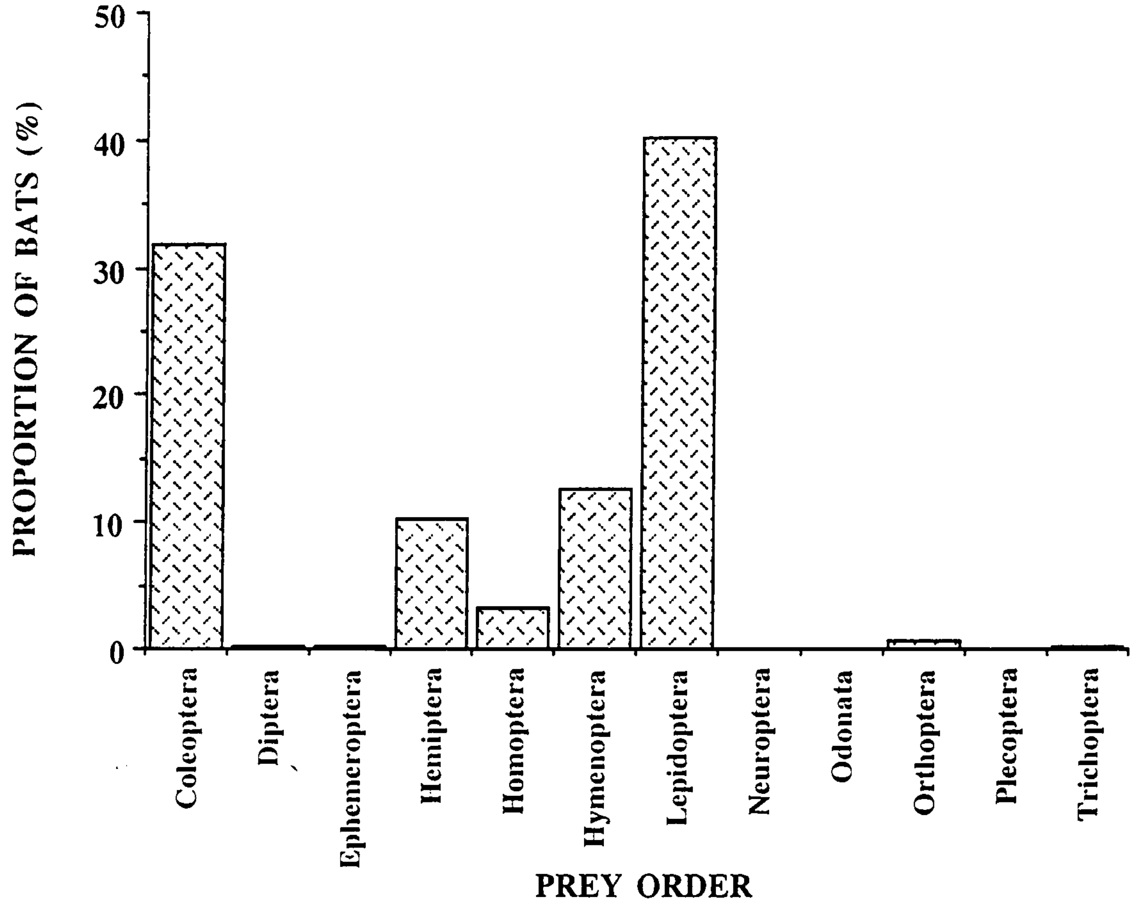

Figure 2.3. The frequency distribution of bats containing different prey orders as predominant prey (contributing over half of the relative volume in a sample) in diets (n = 959).

hymenopterous wings or legs allowed me to estimate that a minimum of 2 to 7 (mean = 4) of these hymenopterans were taken by each bat. Among the six major prey orders, lepidopterans had the lowest frequency of absence in the diets of individual bats, and were followed by coleopterans, hemipterans, and homopterans. Hymenopterans and dipterans had high frequencies of absence in individual diets. Minor orders all had high frequencies of absence in individual diets (each over 83%), and rarely were predominant prey items in the diets (Fig. 2.3).

Based on the availability of fragments with recognizable characteristics in fecal samples, I was able to identify different numbers of prey families for the common insect orders and some minor orders (Table 2.1). Carabids, scarabaeids, and chrysomelids (coleopterans); tephretids (dipterans); lygaeids, pentatomids, and cydnids (hemipterans); cicadellids, cercopids, and cixiids (homopterans); and formicids (hymenopterans) are families which appeared most frequently (each above 10% of the total occurrence within an order). Within the minor orders, brown lacewings and green lacewings (neuropterans) and crickets (orthopterans) were the most common prey families. Families of other insect orders, such as ephemeropterans, lepidopterans, plecopterans, and trichopterans could not be determined due to the lack of diagnostic fragments in fecal pellets. On occasion, I was able to identify prey items to a level lower than family, because of the presence of unusually large pieces of fragments. These included Diabrotica undecimpunctata howardi Barber (spotted cucumber beetles), Copris spp. (dung beetles), and Pangaeus bilineatus (Say) (burrower bugs). Because not all the fragments in each prey order could be identified to the family level, and the relative volumes of prey families could not be estimated reliably, I restricted further analyses of diet variation to the ordinal level.

Variation in Diet

Spatial and Temporal Variation.—There was a non-random distribution in relative frequency of occurrence among prey orders at the three caves in 1995 ($G = 62.4$, d.f. $= 24$, $P < 0.001$) and over the three summers at Frio Cave ($G = 103.15$, d.f. $= 24$, $P < 0.001$). Variance in the relative volume of each prey order could be attributed to different factors (i.e., site, year, collecting session, and added effects of paired factors; Table 2.2 and 2.3). Bats at JRBC fed on higher proportions of dipterans ($F_{(2, 837)} = 9.12$, $P < 0.001$; JRBC – Bracken = 1.83, PLSD = 1.11, JRBC – Frio = 2.22, PLSD = 1.08, $P < 0.05$) and trichopterans ($F_{(2, 837)} = 5.1$, $P < 0.01$; JRBC – Bracken = 1.04, PLSD = 1.01, JRBC – Frio = 1.59, PLSD = 0.99, $P < 0.05$), but on a lower proportion of hemipterans ($F_{(2, 837)} = 3.85$, $P < 0.05$; Bracken – JRBC = 4.65, PLSD = 3.43, $P < 0.05$) than the bats of the other caves. Bats at Frio Cave also showed year to year dietary variation. The diet of 1995 contained a lower proportion of neuropterans ($F_{(2, 1007)} = 8.24$, $P < 0.001$; Y96 – Y95 = 1.18, PLSD = 0.67, Y97 – Y95 = 1.26, PLSD = 0.67, $P < 0.05$) than their diet in 1996 and 1997. The diet of 1996 contained a lower proportion of hemipterans ($F_{(2, 1007)} = 21.27$, $P < 0.001$; Y95 – Y96 = 6.58, PLSD = 2.93, Y97 – Y96 = 8.8, PLSD = 2.8, $P < 0.05$), and bats in 1997 fed on higher proportions of dipterans ($F_{(2, 1007)} = 5.44$, $P < 0.005$; Y97 – Y95 = 0.94, PLSD = 0.75, Y97 – Y96 = 1.12, PLSD = 0.72, $P < 0.05$) and homopterans ($F_{(2, 1007)} = 3.56$, $P < 0.05$; Y97 – Y96 = 2.41, PLSD = 1.97, $P < 0.05$) compared to their diet in the other years. The variances on relative volume of the other major orders and neuropterans and orthopterans also were affected by the collecting session and/or factor-factor interaction.

At all three caves and over the three summers at Frio Cave, fecal samples from the midnight and dawn collecting sessions showed differences in relative volume of prey items, with higher proportions of lepidopterans in the dawn samples than in the midnight samples, and coleopterans and hemipterans in higher proportions in the midnight samples than in the dawn samples (Fig. 2.4 (a)-(e)). With less consistency, homopterans and hymenopterans also showed a general pattern of a higher proportion in the dawn samples

Table 2.2. Diet of Mexican free-tailed bats in relative frequency (%) of occurrence and relative volume (mean ± 1SE) of each prey order over the summer, 1995. Significant effects of site (1), collecting session (2), and site x session interaction (3), as determined by a 2-factor ANOVA analysis of the percent volume for each prey order, are indicated. Sample size n = bats.

	Bracken (n=270)		JRBC (n=270)		Frio (n=300)	
Prey	Frequency	Volume	Frequency	Volume	Frequency	Volume
Coleoptera^{123}	19.6	26.33 ± 1.44	20.0	30.62 ± 1.67	20.6	33.23 ± 1.81
Diptera^{12}	9.2	2.00 ± 0.28	10.4	3.83 ± 0.56	6.9	1.61 ± 0.30
Ephemeroptera	0.8	0.26 ± 0.12	1.5	0.81 ± 0.37	0.3	0.10 ± 0.08
Hemiptera^{12}	18.6	17.81 ± 1.25	18.6	13.16 ± 1.11	20.6	15.94 ± 1.26
Homoptera^{23}	15.5	8.95 ± 0.83	13.8	7.09 ± 0.79	16.3	7.25 ± 0.84
Hymenoptera^{23}	7.1	11.57 ± 1.53	8.2	11.32 ± 1.43	8.6	15.78 ± 1.81
Lepidoptera^{23}	20.8	28.42 ± 1.73	21.1	28.95 ± 1.70	21.3	24.69 ± 1.63
Neuroptera	3.1	0.90 ± 0.23	1.4	0.43 ± 0.19	2.2	0.52 ± 0.18
Odonata	0.4	0.02 ± 0.01	0.2	0.04 ± 0.03	0.6	0.12 ± 0.08
Orthoptera^{123}	1.9	1.85 ± 0.60	0.7	0.30 ± 0.19	0.9	0.21 ± 0.10
Plecoptera	0.4	0.03 ± 0.01	0.1	0.03 ± 0.02	0.2	0.02 ± 0.01
Trichoptera^{1}	1.2	0.95 ± 0.31	2.0	1.99 ± 0.50	0.4	0.40 ± 0.25
Unidentified	1.5	0.91 ± 0.53	2.1	1.44 ± 0.61	1.2	0.14 ± 0.10
Total	100.1	100.01	100.1	100.01	100.1	100.01

Table 2.3. Diet of Mexican free-tailed bats at Frio Cave in relative frequency (%) of occurrence and relative volume (mean ± 1SE) of each prey order over three summers. Significant effects of year (1), collecting session (2), and year x session interaction (3), as determined by a 2-factor ANOVA analysis of the percent volume for each prey order, are indicated. Sample size n = bats.

	1995 (n=300)		1996 (n=355)		1997 (n=355)	
Prey	Frequency	Volume	Frequency	Volume	Frequency	Volume
Coleoptera^{123}	20.6	33.23 ± 1.81	20.8	26.83 ± 1.49	18.5	28.58 ± 1.38
Diptera^{1}	6.9	1.61 ± 0.30	7.5	1.43 ± 0.21	9.4	2.55 ± 0.29
Ephemeroptera	0.3	0.10 ± 0.08	0.8	0.15 ± 0.07	1.1	0.34 ± 0.12
Hemiptera^{12}	20.6	15.94 ± 1.26	15.1	9.36 ± 0.87	18.9	18.16 ± 1.00
Homoptera^{12}	16.3	7.25 ± 0.84	13.0	5.65 ± 0.70	15.7	8.06 ± 0.67
Hymenoptera^{123}	8.6	15.78 ± 1.81	8.5	5.58 ± 0.81	7.2	5.19 ± 0.82
Lepidoptera^{123}	21.3	24.69 ± 1.63	21.7	42.68 ± 1.88	18.7	34.33 ± 1.53
Neuroptera^{12}	2.2	0.52 ± 0.18	5.0	1.70 ± 0.28	5.4	1.78 ± 0.24
Odonata	0.6	0.12 ± 0.08	0.1	0.01 ± 0.01	0.2	0.004 ± 0.003
Orthoptera^{123}	0.9	0.21 ± 0.10	1.8	1.47 ± 0.38	1.0	0.35 ± 0.13
Plecoptera	0.2	0.02 ± 0.01	0.2	0.01 ± 0.01	0.3	0.04 ± 0.02
Trichoptera	0.4	0.40 ± 0.25	0.8	0.32 ± 0.18	0.8	0.39 ± 0.15
Unidentified	1.2	0.14 ± 0.10	4.6	4.81 ± 1.08	2.9	0.23 ± 0.13
Total	100.1	100.01	100.1	100.01	100.1	100.01

Figure 2.4. Diet of Mexican free-tailed bats at (a) Bracken, (b) JRBC, (c) Frio-95, (d) Frio-96, and (e) Frio-97. Asterisks indicate the prey orders where a significant difference in relative volume occurred between the two nightly collecting sessions by one-factor ANOVA analysis. * $P < 0.05$, ** $P < 0.01$, *** $P < 0.005$. Col: Coleoptera, Dip: Diptera, Eph: Ephemeroptera, Hem: Hemiptera, Hom: Homoptera, Hym: Hymenoptera, Lep: Lepidoptera, Neu: Neuroptera, Odo: Odonata, Ort: Orthoptera, Ple: Plecoptera, Tri: Trichoptera.

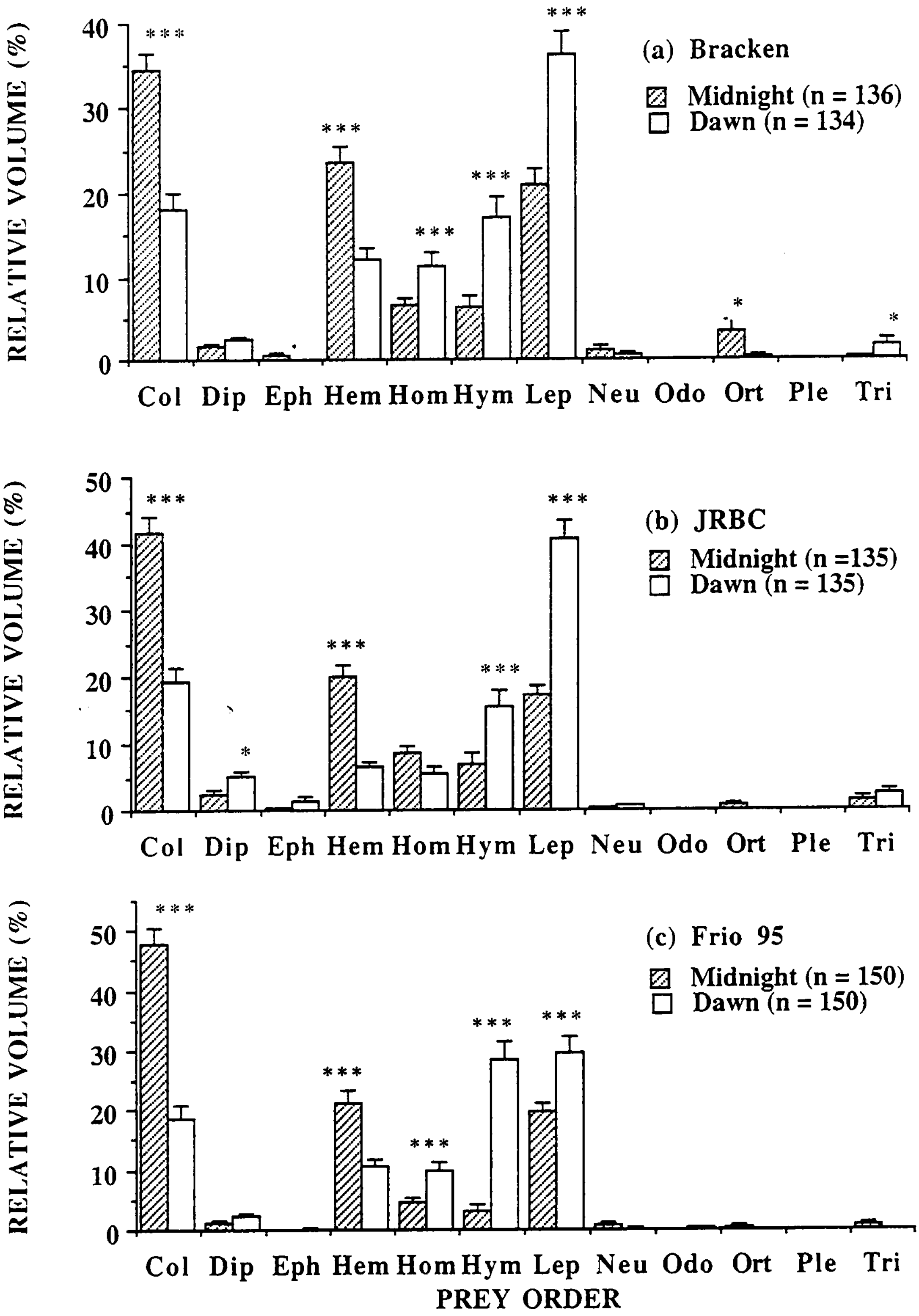

Figure 2.4 (see the previous page for the legend).

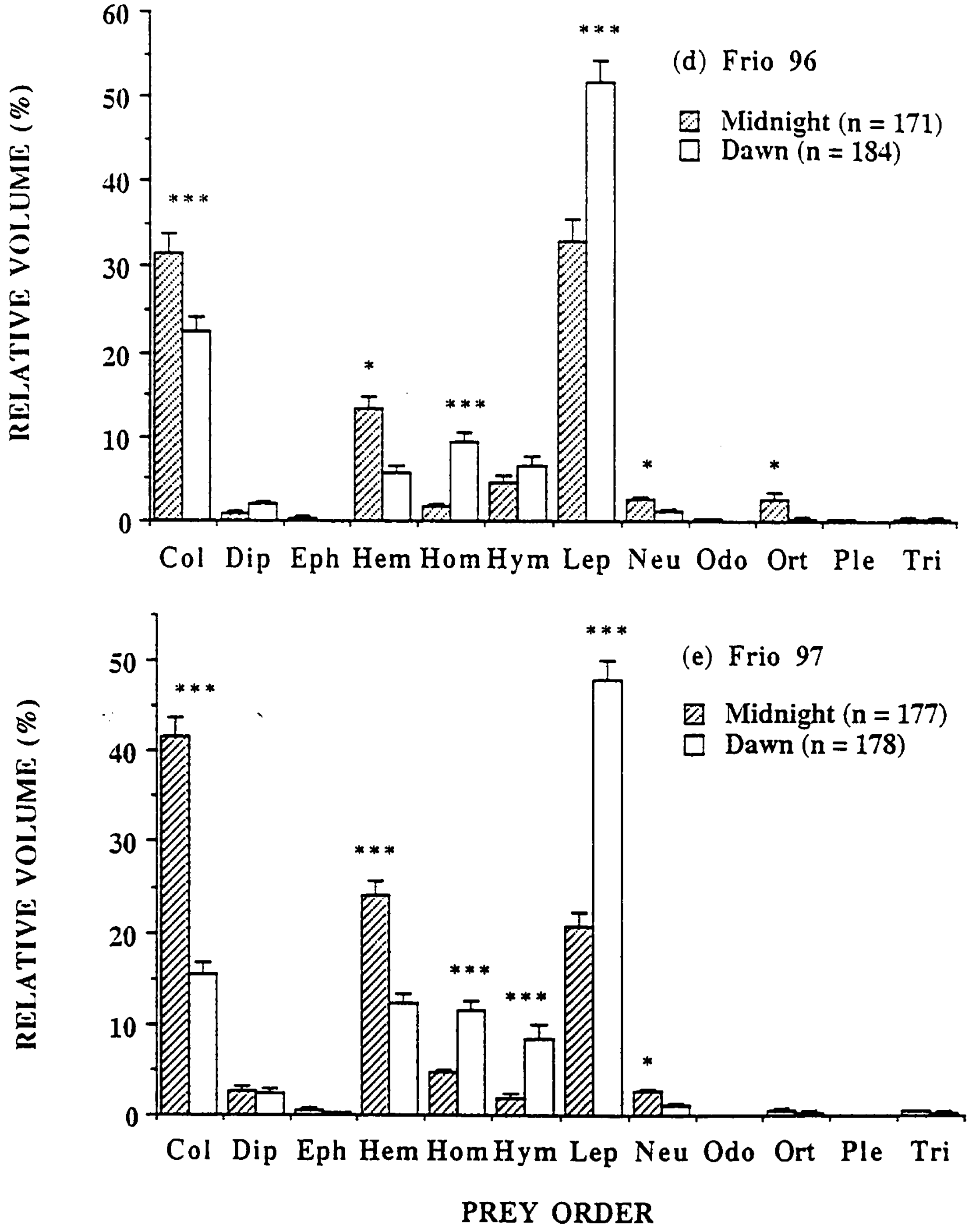

Figure 2.4 (continued).

than in the midnight samples. Dipterans and minor prey orders showed no significant patterns between the two time periods at different sites or at different years. For coleopterans, hemipterans, and lepidopterans, the temporal pattern of dietary variation persisted through the season, except for lepidopterans in mid-late summer (Fig. 2.5).

Cross-seasonal comparisons (i.e., late May-mid June, late June-mid July, and late July-August) showed fluctuations in the relative volumes of the three major prey orders (Fig. 2.5). During the first and the second seasonal phases, the proportion of lepidopterans in the diet was significantly higher in the dawn samples than in the midnight samples. Into the second phase, however, the proportion of lepidopterans in the midnight samples significantly increased ($F_{(2, 418)} = 21.82$, $P < 0.001$; II – I = 15.17, PLSD = 4.7, $P < 0.05$) but that of hemipterans decreased ($F_{(2, 418)} = 10.5$, $P < 0.001$; I – II = 11.63, PLSD = 5.45, $P < 0.05$). In the third phase, lepidopterans in both midnight (II – III = 9.89, PLSD = 4.32, $P < 0.05$) and dawn samples ($F_{(2, 416)} = 33.65$, $P < 0.001$; II – III = 24.88, PLSD = 6.99, $P < 0.05$) significantly decreased, and showed no difference between each other. On the other hand, the proportions of coleopterans (dawn: $F_{(2, 416)} = 9.18$, $P < 0.001$; III – II = 10.02, PLSD = 5.33, $P < 0.05$) and hemipterans increased (midnight: III – II = 9, PLSD = 5.01, $P < 0.05$; dawn: $F_{(2, 416)} = 4.68$, $P < 0.01$; III – II = 4, PLSD = 3.52, $P < 0.05$).

Among Bat Classes.—On average, adults excreted more fecal pellets (29.1 ± 0.3, n = 1,302) than juveniles (15.5 ± 0.5, n = 248; $t = 17.5$, $P < 0.001$). Forty bats in my total bat collections (n = 3,945) did not excrete any fecal pellet during the confinement, and 33 of these 40 bats were juveniles (82.5%). Adults of different classes also excreted different numbers of pellets (males = 32.6 ± 0.8; reproductive females (pregnant and lactating) = 29.0 ± 0.3; non-reproductive and post-lactating females = 25.4 ± 0.7) ($F_{(2, 3440)} = 23.83$, $P < 0.001$). The overall diets were similar among bats of different age, sex, and reproductive classes with regard to diet composition, and the ranking of the

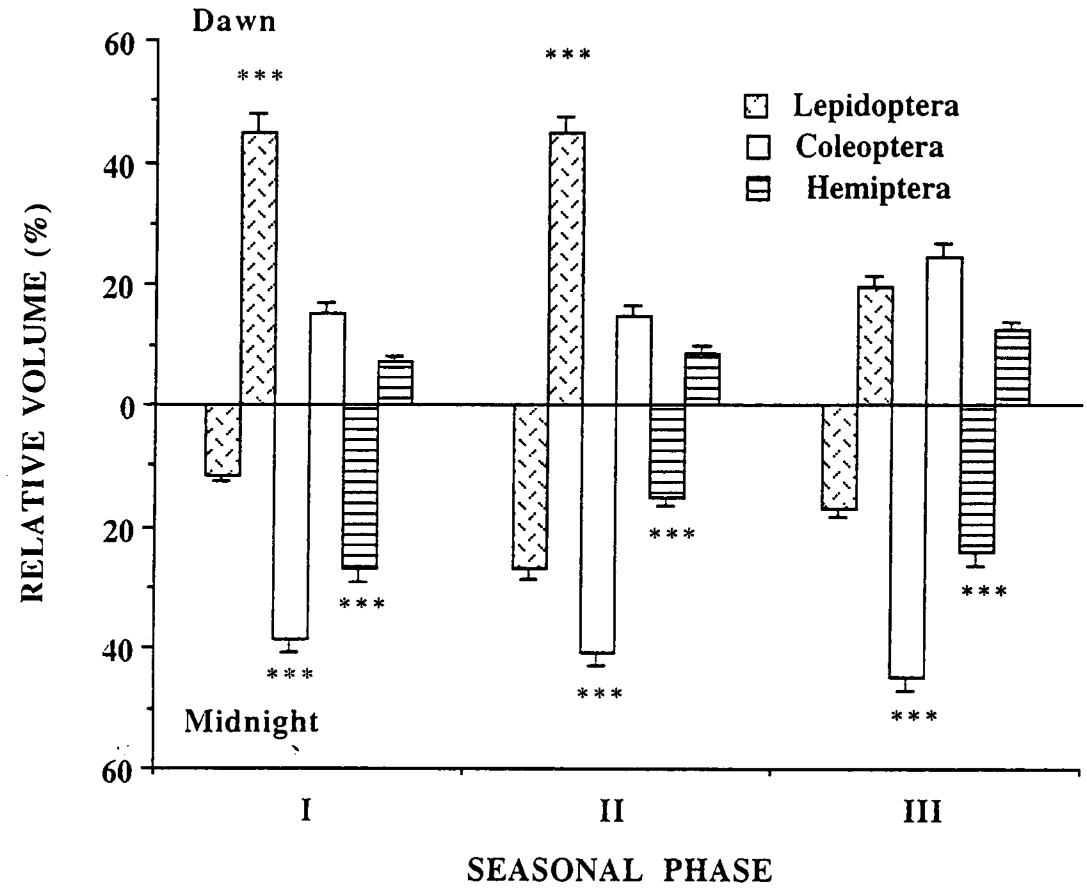

Figure 2.5. Differences of relative volumes of lepidopterans, coleopterans, and hemipterans between the midnight and dawn collecting sessions through the three seasonal phases (I. late May-mid June, II. late June-mid July, and III. late July-August). Asterisks indicate where a significant difference in the relative volume occurred between the two nightly collecting sessions by one-factor ANOVA analysis. *** $P < 0.005$. See text for cross-phase comparisons.

relative frequency and relative volume of each prey order (Fig. 2.6). However, at different periods of their life history cycles, different classes of bats also showed dietary variation.

From late May to mid July, before juveniles were born or before juveniles were capable of independent foraging, pregnant females ate a significantly higher proportion of hemipterans (in midnight samples) and coleopterans (in dawn samples) than adults of other classes (Fig. 2.7). Males ate a higher proportion of lepidopterans than pregnant females in midnight samples, and a higher proportion of lepidopterans than both pregnant and lactating females in dawn samples. Reproductive females had a more diverse diet (pregnant: $1/D = 4.11$, lactating: $1/D = 4.06$) than males ($1/D = 3.559$).

From late July to late August, after juveniles began to forage, the diets of males and lactating and post-lactating females were not significantly different ($P > 0.05$ for all prey orders) and therefore were pooled. Juveniles ate higher proportions of coleopterans and homopterans than adults during the pre-dawn feeding bout, but lesser amounts of lepidopterans and neuropterans in midnight samples and a lower proportion of lepidopterans in dawn samples than adults (Fig. 2.8). The diet of juveniles was more diverse ($1/D = 5.039$) than adults (lactating: $1/D = 4.543$, post-lactating: $1/D = 4.605$, male: $1/D = 4.398$). Given the dietary differences between adults and juveniles within each feeding bout, the diet of juveniles was similar to adults in the pattern of temporal variation between midnight and dawn. Juveniles did not show significant dietary shifts among major orders, during the ca. 35-day period from they started foraging (late July) until August ($P > 0.05$ for all six major prey orders). Only a higher proportion of orthopterans was found in the evening feeding bout of juveniles during mid August ($F_{(2,125)} = 3.15$, $P < 0.05$, mid August – late July = 4.38, PLSD = 3.68, mid August – early August = 4.4, PLSD = 3.79, $P < 0.05$).

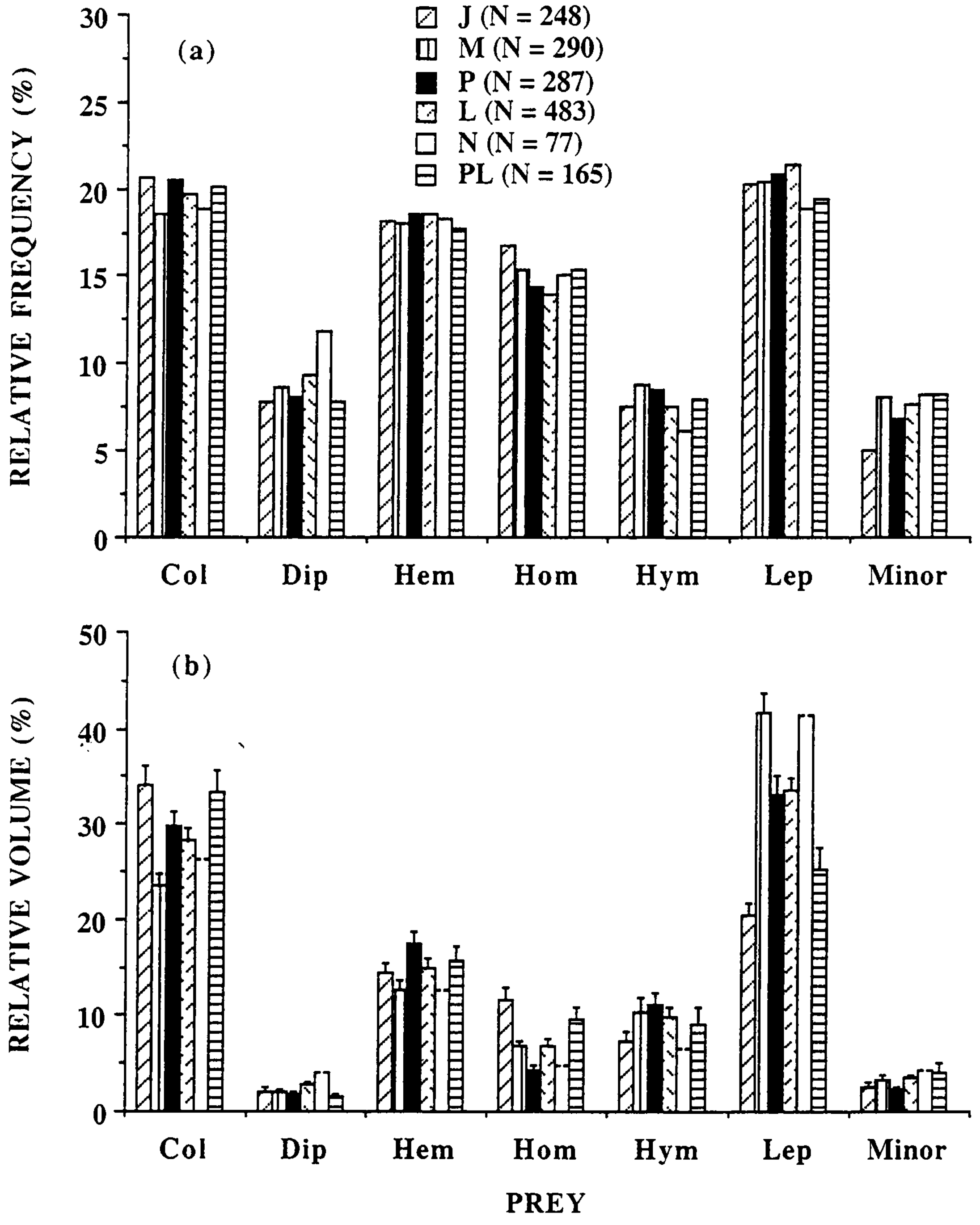

Figure 2.6. The (a) relative frequency of occurrence and (b) relative volume of the six major prey orders and the combined minor prey orders in the diet of different classes of bats. J: juveniles, M: adult males, P: pregnant females, L: lactating females, N: adult non-reproductive females, PL: post-lactating females.

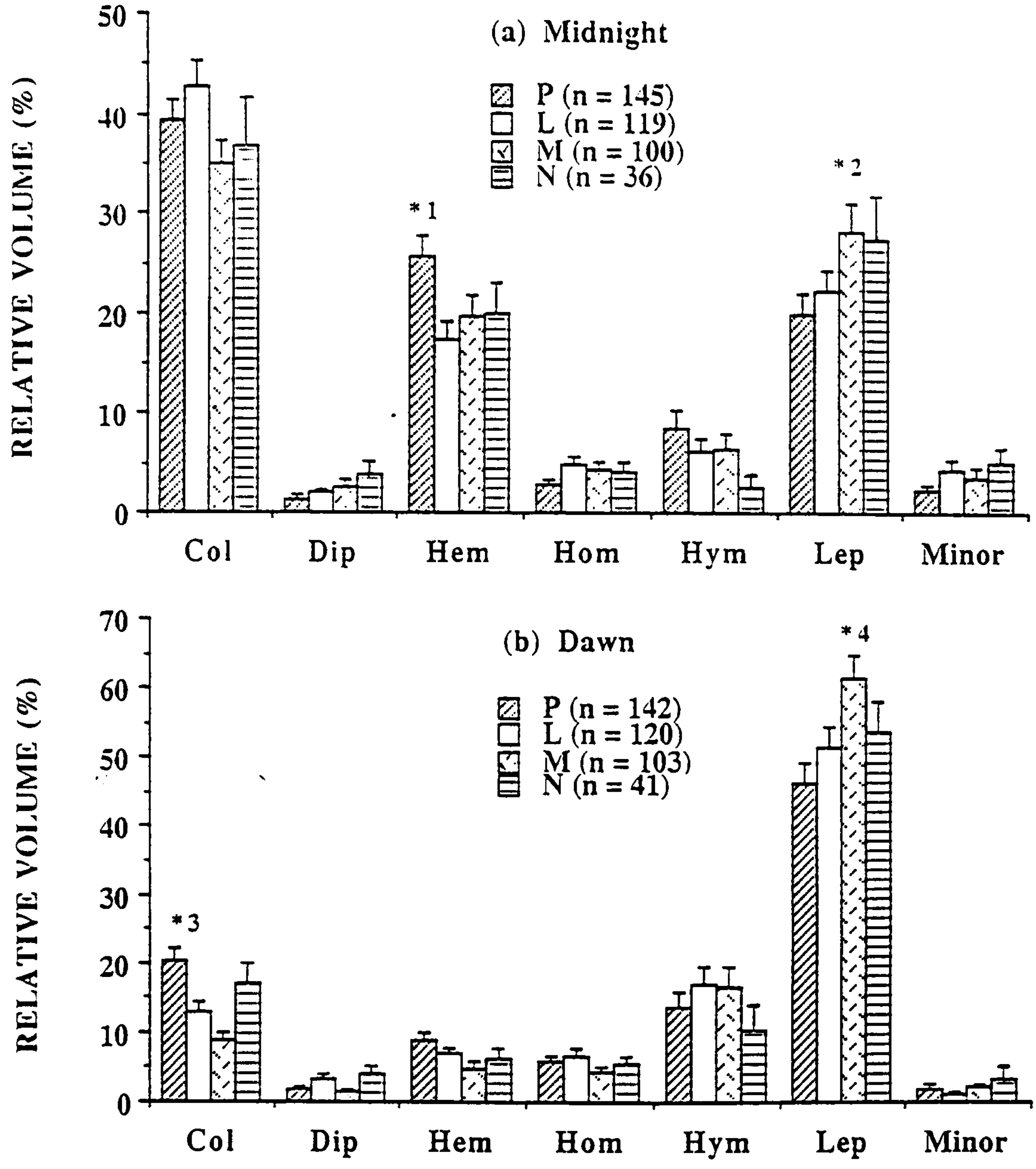

Figure 2.7. Dietary differences between pregnant (P), lactating (L), non-reproductive (N) females, and males (M) in (a) midnight and (b) dawn samples, during late May-mid July. Asterisks indicate prey orders where significant differences occurred. The significance level of all paired comparisons was 0.05. *1: F = 3.59, $P < 0.05$, P - L = 8.3, PLSD = 5.2, P - M = 5.93, PLSD = 5.46; *2: F = 2.58, $P < 0.05$, M - P = 8.4, PLSD = 6.43; *3: F = 8.77, $P < 0.001$, P - L = 7.44, PLSD = 4.38, P - M = 11.34, PLSD = 4.57; *4: F = 3.96, $P < 0.01$, M - P = 14.75, PLSD = 8.47, M - L = 9.71, PLSD = 8.79.

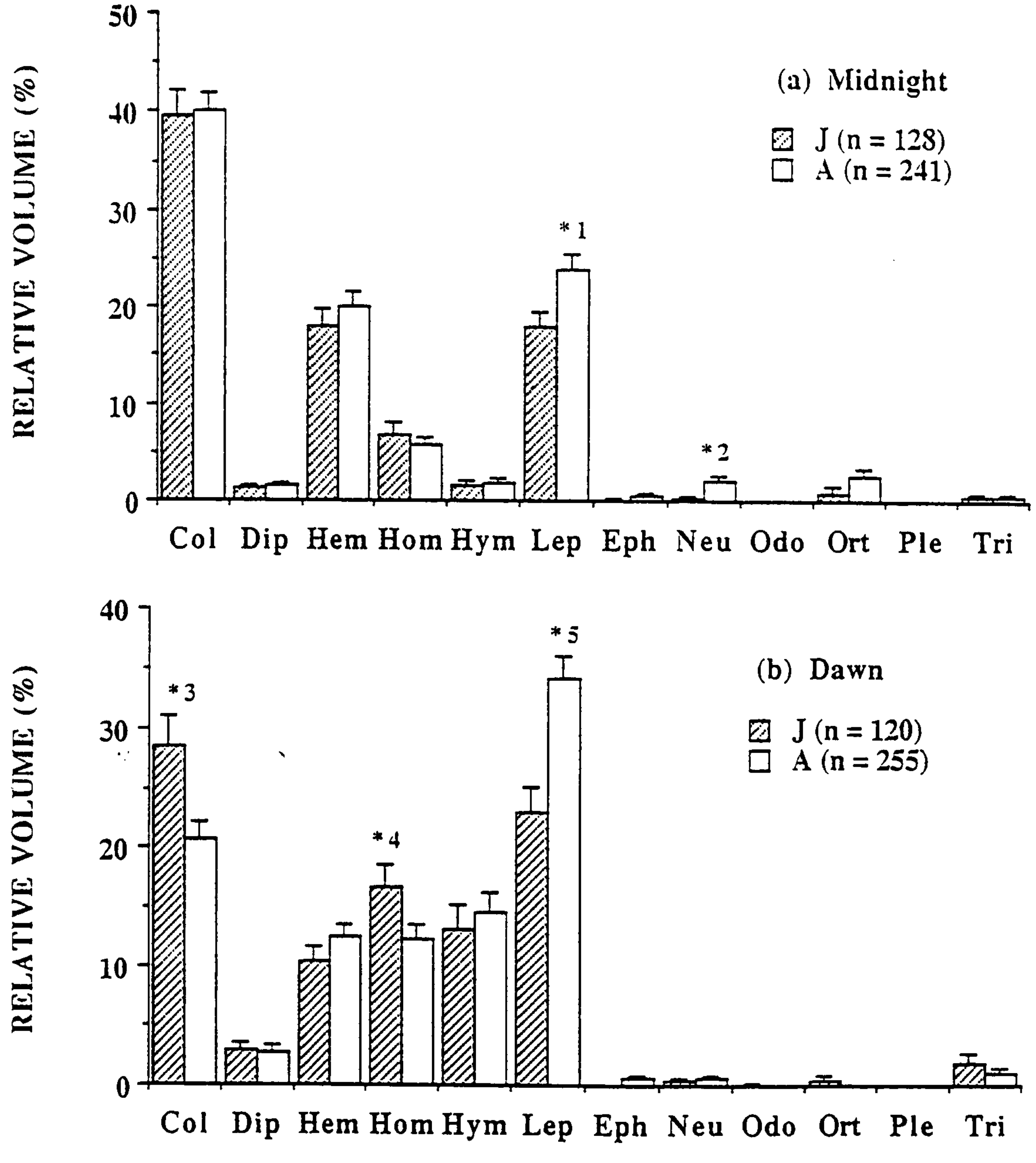

Figure 2.8. Dietary differences between juveniles (J) and pooled adults (A, i.e., males, post lactating and lactating females, see the text) in (a) midnight and (b) dawn samples, during late July to August. Asterisks indicate prey orders where significant differences occurred. *1: F = 6.35, $P < 0.05$; *2: F = 10.99, P = 0.001; *3: F = 7.64, $P < 0.01$; *4: F = 4.09, $P < 0.05$; *5: F = 11.5, $P < 0.001$.

DISCUSSION

Diet Composition

My dietary data reveal that Tadarida brasiliensis mexicana eat a wide variety of prey, comprised mainly of flying insects, but also insects that are mostly ground-dwelling (e.g., carabid beetles) or less active fliers (e.g., homopterans). Many of their insect prey are exclusively non-aquatic, such as scarabaeids, tephritids, most families in Hemiptera (except Corixidae and Saldidae), all families of Homoptera, formicids, and neuropterans; however, adult forms of some aquatic insects (i.e., Ephemeroptera, Plecoptera, Trichoptera, Zygoptera, Dytiscidae, Corixidae, and Saldidae) also are eaten (Table 2.1). Other prey taxa contain both aquatic and non aquatic species (Borror et al., 1989; Arnett, 1993; Merritt and Cummins, 1996). The total number of prey orders and families identified is by far the highest ever documented in the diet of this species, and is among the highest ever for any bat species. Best et al. (1997) found 14 insect orders and Araneae and Acari in the diet of Myotis grisescens, but did not report any families. The diet of Pipistrellus pipistrellus includes 39 families from 10 insect orders (Swift et al., 1985; Hoare, 1991; Sullivan et al., 1993). The diverse diet of T. b. mexicana is not surprising taking into account their wide foraging range on both horizontal and vertical scales, and the large sample sizes involved in this study.

Overall, lepidopterans, coleopterans, and hemipterans are the most commonly found and predominant prey in their diet, and are followed by hymenopterans, homopterans, and dipterans. The composition of common prey and the overall ranking of their relative importance are largely consistent with the previous reports for this species (Kunz et al., 1995b; Whitaker et al., 1996). The prey size estimates also are similar to the range (5 to 9 mm) reported by Rose (1961). Although based solely on coleopteran femora, this size range probably applies to other common prey of T. b. mexicana, such as hemipterans, homopterans, and hymenopterans. However, these bats apparently also feed on smaller insects (e.g., Drosophilidae and many members in Nematocera, mostly 2 to 3 mm long), and are capable of eating larger insects as well (e.g., myrmeleontids and Odonata).

Tadarida b. mexicana has been reported to forage in small groups (Davis et al., 1962), and to feed on insects in dense swarms (Rose, 1967). However, their prey also includes non-swarming insects, such as some hemipterans and homopterans. Localized air convection is an important mechanism that can generate and maintain spatiotemporal patches in insect distribution. The open and arid to semi-arid nature of the areas where Mexican free-tailed bat colonies are located and forage is characterized by frequent thermals, and convection supported thunderstorms during late afternoon and evening (Jordan et al., 1984). Thermals of rising warm air may transport small insects aloft to great heights and concentrate them into localized areas (Drake and Farrow, 1988), and make them available to foraging bats at high altitudes. This in part may explain the presence of some non swarming, more weakly flying, and diurnal insects in the diet of these bats.

Hymenopterans (mostly flying ants) ranked third in overall percent volume and fifth in relative frequency (Table 2.1), however, except for lepidopterans and coleopterans, they were the predominant prey items in the greatest number of bats (Fig. 2.3). This is probably a result of periodical but locally concentrated mating swarms of these insects (Baldridge et al., 1980). Orthopterans have not been reported previously in the diet of T. b. mexicana (reviews in Freeman, 1979; Whitaker et al., 1996). They occurred in small amounts and in small numbers of bats, usually only near or after the end of July. The presence of orthopterans may reflect a change in the relative abundance of different types of insects. In mid to late summer, when volant juvenile bats join adults and more bats are foraging each night, some of their most common prey (e.g., moths) may not be as abundant as earlier in the summer. However, my insect trapping data show that the relative abundance of orthopterans increases in late summer (Chapter III).

The diet of T. b. mexicana also occasionally contained mayflies, stoneflies, caddisflies, and damselflies. Due to their soft body forms, the presence of these insects in the diet was determined largely by highly fragmented pieces of wings, and the percent volumes of these insects may be underestimated. These insects are exclusively aquatic; winged adults of all these insects are common near water or shores, and stoneflies and caddisflies are known to be weak fliers (Borror et al., 1989). Although Mexican free-tailed bats have been caught over and near water (Svoboda and Choate, 1987), whether they feed or drink over water bodies remains unclear (Kunz et al., 1995b). Presumably, these bats take advantage of the localized and ephemeral mass emergencies of some aquatic insects, such as mayflies, of which the swarms may be 15 meters or more above the ground. Adult caddisflies and many stoneflies also are frequently attracted to lights (Borror et al., 1989), where bats may forage on concentrations of insects (Rydell, 1992a; also see Chapter III). Members of Odonata, including damselflies and dragonflies, are diurnal and generally good fliers. However, the activity pattern of T. b. mexicana (Herreid and Davis, 1966; Lee, pers. obs.) suggests that at dusk or during dawn to early morning, bats would likely encounter these insects if foraging near or at a short distance from water. Odonata also have been reported previously in the diet of T. b. mexicana (Storer, 1926; Whitaker et al., 1996) and other fast high flying insectivorous bats (e.g., Lasiurus cinereus, Barclay, 1986).

Variation in Diet

The diet of T. b. mexicana at the three caves in 1995 and their diet at Frio Cave over the three summers show differences among both common and less common prey orders (e.g., hemipterans, dipterans, homopterans, neuropterans, and trichopterans), which may reflect local differences and year to year fluctuations in insect compositions. I did not assess the insect composition and relative abundance at all three sites each year, and am not able to confirm this speculation. However, the significant variation in coleopterans and hemipterans versus lepidopterans between the two nightly feeding bouts is compatible with the findings of Whitaker et al. (1996) conducted at JRBC in late June 1991. My study extended the sampling scale and confirmed that this variation occurs at different caves and in different years. Moths are known to have higher peak activity and abundance later in the night than most other nocturnal insects, such as coleopterans and dipterans, which typically have peak activity shortly after the dusk and then subside (Anthony and Kunz, 1977; Brack and LaVal, 1985). Thus, the temporal dietary variation between nightly sampling sessions may be due at least in part to the differences of nightly activity of the different insect taxa.

The hypothesis of migratory moth populations provides an additional possibility for the temporal dietary variation of T. b. mexicana (McCracken, 1996). Annually, billions of adult corn earworms, Helicoverpa zea (Boddie), and fall armyworms, Spodoptera frugiperda (J. E. Smith), ascend to altitudes up to several thousand meters in the evening during late spring to early summer, from approximately 200,000 ha of corn fields in the Lower Rio Grande Valley of Mexico and migrate into south-central Texas and adjacent states (Wolf et al., 1994; Westbrook et al., 1995). The migration pathways and the agricultural fields where these insects stop for egg-laying are within the flight distance of several major maternity colonies of T. b. mexicana in south-central Texas (Fig. 2.1). The timing of high moth consumption also corresponds with the time when most female bats are either in late pregnancy or lactation, and at peak energy needs.

These moths pass the winter in the pupal stage in areas south of the limit of the spring freeze (Burkhardt, 1985). Before mid June, the adult moth populations emerge in Mexico or the far south of Texas (Wolf et al., 1990). Adult migration begins with huge numbers ascending at dusk, and moths will not arrive within the estimated foraging range of T. b. mexicana until after midnight or early dawn. Thus, bats from the major colonies in south central Texas will not have access to these potential food resources in their evening feeding bout. However, the bats will have access to the moths as they reach the south central Texas region in the early hours of the morning. From late June to mid July, when moth populations have already laid eggs in corn fields in south central Texas (Wolf et al., 1990), and the following generations start to emerge from corn fields, bats will have access to these moths in both the evening and the morning feeding bouts. In late July and August, after the harvest of corn, the moths move to cotton. Cotton alone cannot sustain the moth populations and moth populations decline (Lee and McCracken, 1998; Westbrook, pers. comm.). My dietary data on the consumption of lepidopterans between evening and dawn feeding bouts of bats along the three seasonal phases provide evidence supporting the hypothesis that large free-tailed bat colonies in south central Texas take an advantage of this large food resource and feed on these migratory moth populations when they are available.

Radar observations, and tetroons (tetrahedral weather balloons) and kites used to monitor high altitude foraging of bats, also have documented both the presence of these moth populations and intense feeding activities of T. b. mexicana (McCracken et al., 1996, 1997). Future studies are needed to confirm the consumption of these migratory moth populations by T. b. mexicana, and to quantitatively estimate the potential contribution of this consumption in regulating populations of these and other agricultural insect pests.

Different age, sex, and reproductive classes of T. b. mexicana show differences in their diet. Pregnant females ate higher proportions of coleopterans and hemipterans than other adults, and less lepidopterans than males (Fig. 2.8). Juveniles ate lower proportions of lepidopterans and neuropterans but more coleopterans and homopterans than adults

(Fig. 2.9). In addition, reproductive females and juveniles had more diverse diets than other bats compared in the same period. The energy budgets of female bats in reproductive condition may influence their foraging strategies. For instance, their high energetic demands may require a longer foraging duration (Barclay, 1989), which may result in their encountering and eating different prey (Belwood and Fenton, 1976). In Mexican free-tailed bats, higher proportions of pregnant and lactating females leave the roost for foraging earlier in the evening and return to the roost later at dawn than males, juveniles, and non reproductive females (Lee, unpublished data). However, energetic demand may not be the only or main factor contributing to the differences in diet observed among bat classes. In almost all cases, the diets of lactating females, a group with high energetic demands, were not significantly different from the diets of males, which supposedly have a much lower energetic demands during the summer. The fact that the dietary composition of all classes of bats show a similar ranking of the major prey taxa eaten and a similar temporal changes in dietary composition suggests that all classes of bats largely consume similar types of prey, and their behavioral responses to changes in the relative abundance of different prey are similar.

Calcium has been identified as a crucial nutrient requirement for the reproductive activities of females and the growth of juveniles (Barclay, 1994). Available comparative data show that insects are good sources of nitrogen, potassium, and magnesium, but in most cases provide an inadequate source of calcium to meet the requirements of birds and mammals in reproductive conditions (Studier and Sevick, 1992). Among the common prey of bats, hemipterans and homopterans contain higher calcium contents than lepidopterans and coleopterans. This may in part explain the higher proportion of hemipterans in the diet of pregnant females, and the higher proportion of homopterans in the diet of juveniles than in others. However, my data on the diet of lactating females do not appear to show increased consumption of insects with higher calcium contents.

Many moths, including the most common and abundant groups that are often eaten by bats (e.g., noctuids, geometrids, pyralids, arctiids), have tympanal ears that enable them to detect the echolocation calls of foraging bats (Fenton and Fullard, 1979; Fullard, 1987). The echolocation calls of T. b. mexicana have most energy at about 25-30 kHz (McCracken, pers. comm.; not ca. 40 to 45 kHz, as previously reported by Simmons et al. 1978, 1979). These tympanum moths all are powerful flyers, and the ears of corn earworm moths are known to be tuned to this frequency range (Agee, 1967). High maneuverability, being able to make swift rolls and tight turns, is critical for a bat to catch a moth, and can be achieved by having a lower wing loading (Norberg, 1990). Tadarida b. mexicana have a high wing loading (Norberg and Rayner, 1987). Comparative data on wing loading measurements between different classes of T. b. mexicana are not available. However, the mass of a fetus will increase the body mass, and thus wing loading, of pregnant females by up to 30% in late pregnancy (Lee, unpublished data; McCracken, pers. comm.), which could affect their flying ability (Webb et al., 1992), and hunting efficiency and their success in capturing moths. This may have resulted in the difference in moth consumption between pregnant females and males.

The elusive behavior of moths, and the less skillful flying and echolocation ability of juveniles (Buchler, 1980) also may cause the lower volume of moths in the diets of juveniles versus adults. The fact that juveniles excreted less fecal pellets than adults and that some juveniles did not excrete any at all, also suggests less successful foraging by juveniles. The energy needs of newly volant juveniles are often supplemented by milk from their mothers (Jones et al., 1995; Kunz and Stern, 1995). Unfortunately, because of the extremely large colony sizes, it was not possible to repeatedly catch the same bats to check for ontogenetic changes in their diets. All of the juveniles that I sampled were of unknown age, and it was not possible to test if juveniles show a shift of diet through developmental stages, as has been demonstrated in other insectivorous bats (e.g., Myotis lucifugus, Adams, 1996). Nevertheless, in this study, juvenile T. b. mexicana had similar diets during the about 35-day period in which they foraged.

Parturition of T. b. mexicana is highly synchronous, and over 90% of pregnant females give birth within a ca. 10 to 15-day period (Davis et al., 1962; McCracken and Gustin, 1991). Pups grow very fast, and their forearm length can reach the average adult size in the 6th week after birth (Kunz and Robson, 1995), which is in late July. Juveniles that were sampled during the 15-day period in late July would represent the earliest born pups, and juveniles sampled during August may comprise pups born both earlier and later. However, juveniles from the three periods (late July, and early and mid August) showed similar forearm lengths (42.5 to 42.9 mm, $F_{(2, 199)} = 2.95$, $P > 0.05$), which were about 98.7 to 99.6% of mean forearm length of adults (Lee, unpublished data). Thus, although juveniles are not as efficient as adults in hunting, all the juveniles that were sampled were very similar in size and probably similarly efficient to one another in their ability to locate and catch insects.

III. FORAGING ACTIVITY AND RESOURCE USE

Abstract. The foraging activity and resource use of migratory Mexican free-tailed bats, Tadarida brasiliensis mexicana, was investigated in a large maternity colony in Uvalde County, Texas. Foraging activity of bats was studied by recording their echolocation calls at sites along a sampling transect, which represented three different habitats; towns, cropland, and ranches. The proportion of time in which signals were received and the number of feeding buzzes per unit time were quantified. Insect availability and the relative abundance of different insect orders in the three habitats were assessed using light traps. The food habits of the bats were determined from fecal samples, and were compared to the relative abundance in mass of insect orders.

Tadarida b. mexicana had a higher foraging activity in town habitats than in cropland and ranches. In cropland and ranch habitats, feeding buzzes per unit time were less frequent in the pre-dawn collecting session than in the evening session, corresponding to the pattern of insect abundance in these habitats. In town habitats, however, insect abundance was similar in morning and evening sessions, and the foraging activity of bats did not differ between these two sessions. The relative importance of the common prey orders both in relative frequency of occurrence and relative volume in the diet of the bats were compatible with the relative importance of these respective insect orders in relative frequency of occurrence and in relative mass in trap collections. Graphic comparisons showed a shift of proportions of different prey in the diet between midnight and dawn, in response to the change of abundance of these insects in light traps. In addition, there was a positive correlation between the diet of bats and the light trap collections at the ordinal level, in 9 of 12 comparisons when Orthoptera were included, and in all 12 comparisons if Orthoptera were removed.

INTRODUCTION

Various factors determine an animal's patterns of resource use. These include the activity of the forager in time and space, the spatiotemporal distribution of its food supply, and its interactions with other organisms. Flight and echolocation are two features that distinguish bats from other mammals, and are two important features in determining the resource use patterns of bats. Studies in the field or laboratory on wing morphology, flight performance, and the structure of echolocation calls allow predictions with regard to the habitats, foraging strategies, and prey resources that animal-eating bats (about 70% of total bat species) may exploit (e.g., Norberg and Rayner, 1987; Neuweiler, 1989; Fenton, 1990; Bogdanowicz et al., 1999).

The Family Molossidae is widely distributed throughout warmer parts of the Old and New Worlds (Koopman, 1993). Because of their high aspect ratio and high wing loading, species in this family are specialized for fast and continuous flight (Norberg and Rayner, 1987). However, due to their high wing loading, molossids are not very maneuverable. These bats tend to forage in open space, hawking for insects high above vegetation, where they employ long narrow-band calls of low frequency (mostly below 30 kHz) for long range detection (Norberg and Rayner, 1987; Neuweiler, 1989; Fenton, 1990). The foraging behavior and ecology of several species of molossids in Africa and Australia (e.g., *Tadarida aegyptiaca*, *T. fulminans*, *Chaerephon ansorgei*, *C. chapini*, *C. jobensis*, *C. nigeriae*, *C. pumila*, *Mops condylura*, *M. midas*, *Mormopterus beccarii*, *Otomops martiensseni*) have been studied in free flying conditions (Fenton and Thomas, 1980; Fenton, 1982b; Fenton and Rautenbach, 1986; Aldridge and Rautenbach, 1987; Fenton and Griffin, 1997).

The most common North American molossid, the migratory Mexican free-tailed bat *Tadarida brasiliensis mexicana* (Saussure, 1860), is widely distributed in the southwestern United States. They are particularly abundant in south central Texas with huge aggregations in several maternity colonies during summer (Davis et al., 1962). The maximum flight speed of T. b. mexicana emerging from a cave has been visually estimated at about 50 km per hour (Davis et al., 1962). Using radar, Williams et al. (1973) documented the movement of dispersing bats at speeds of more than 40 km per hour, and that the foraging dispersal of bat targets at high altitudes covers over 400 km^2. The bats are known to forage at heights of a few meters above the ground to over 1,200 meters (Caire et al., 1984; Griffin and Thompson, 1982; McCracken et al., 1996, 1997), where they use long narrow-band echolocation calls of low frequency (20 to 30 kHz, G. F. McCracken, pers. comm.; not ca. 40 to 45 kHz as previously reported by Simmons et al. 1978, 1979) to search for insects. Aspects of their feeding ecology, such as food habits and feeding rates, have been reported (Kunz et al., 1995b; Whitaker et al., 1996; also see Chapter II), but no previous studies have documented their foraging activity and resource use patterns in different habitats.

The areas in south central Texas, where large colonies of T. b. mexicana forage, are characterized by open and continuous cropland and ranches (McMahan et al., 1984; Jordan et al., 1984). However, the bats also forage in human residential areas where concentrated buildings and taller trees present a somewhat cluttered environment. The wing morphology and echolocation calls of T. b. mexicana suggest that these bats should frequent the more open areas and avoid areas with high human density. On the other hand, street lamps in residential areas attract large numbers of nocturnal insects, forming patches of prey at unusually high densities that in turn may attract foraging bats (Rydell and Racey, 1995).

The major purpose of this study was to document the foraging activity of T. b. mexicana, and to compare the habitat use of the bats in residential areas, croplands, and areas of natural vegetation. A second purpose was to investigate the resource use pattern of T. b. mexicana. These bats live in large aggregations and may have an intensive competition for food. They disperse over long distances and a great range of altitudes for foraging, and may encounter very different food resources. In addition, insect resources also change over time and space. I predicted that T. b. mexicana should be opportunistic in foraging, exploiting the most abundant prey available within their foraging range.

MATERIALS AND METHODS

Study Sites

I conducted field work from 30 May to 6 August 1996, and 16 May to 21 August 1997, at Frio Cave (29°25'N, 99°42'W, 354 m above the sea level) and adjacent areas in Uvalde County, Texas (Fig. 3.1). Frio Cave is located at the southern edge of the Edwards Plateau, and contains a large summer maternity colony of Mexican free-tailed bats. Major habitat types south of Frio Cave, where the majority of these bats disperse for nightly foraging include large areas of cropland and ranches, with isolated small towns.

The croplands are cultivated, mainly with corn, cotton, and sorghum (Texas Agricultural Extension Service, Texas A & M University). Ranch areas contain natural vegetation and pasture, which support livestock and a variety of wildlife. Major plants in ranch areas include blackbrush (Acacia rigidula) and mesquite (Prosopis glandulosa), and other woody plants such as live oak (Quercus virginiana), ashe juniper (Juniperus ashei), and bluewood (Condalia hookeri) (McMahan et al., 1984). These brush and woody plants form small clusters or are scattered individually within large areas of long or short grass and forbs. Less than a dozen small towns or villages are located within the foraging range of the bats from Frio Cave (ca. 50 km, Davis et al., 1962). Uvalde, the county seat, is about 14 km^2 in area, and has a population of about 15,000 (Profile of America, 1995). This town has concentrated public or private buildings and residences, many street lamps, and frequent traffic on several main routes. Vegetation includes mostly live oaks, other woody plants, and grass. The outskirts of Uvalde intermingle with cropland or

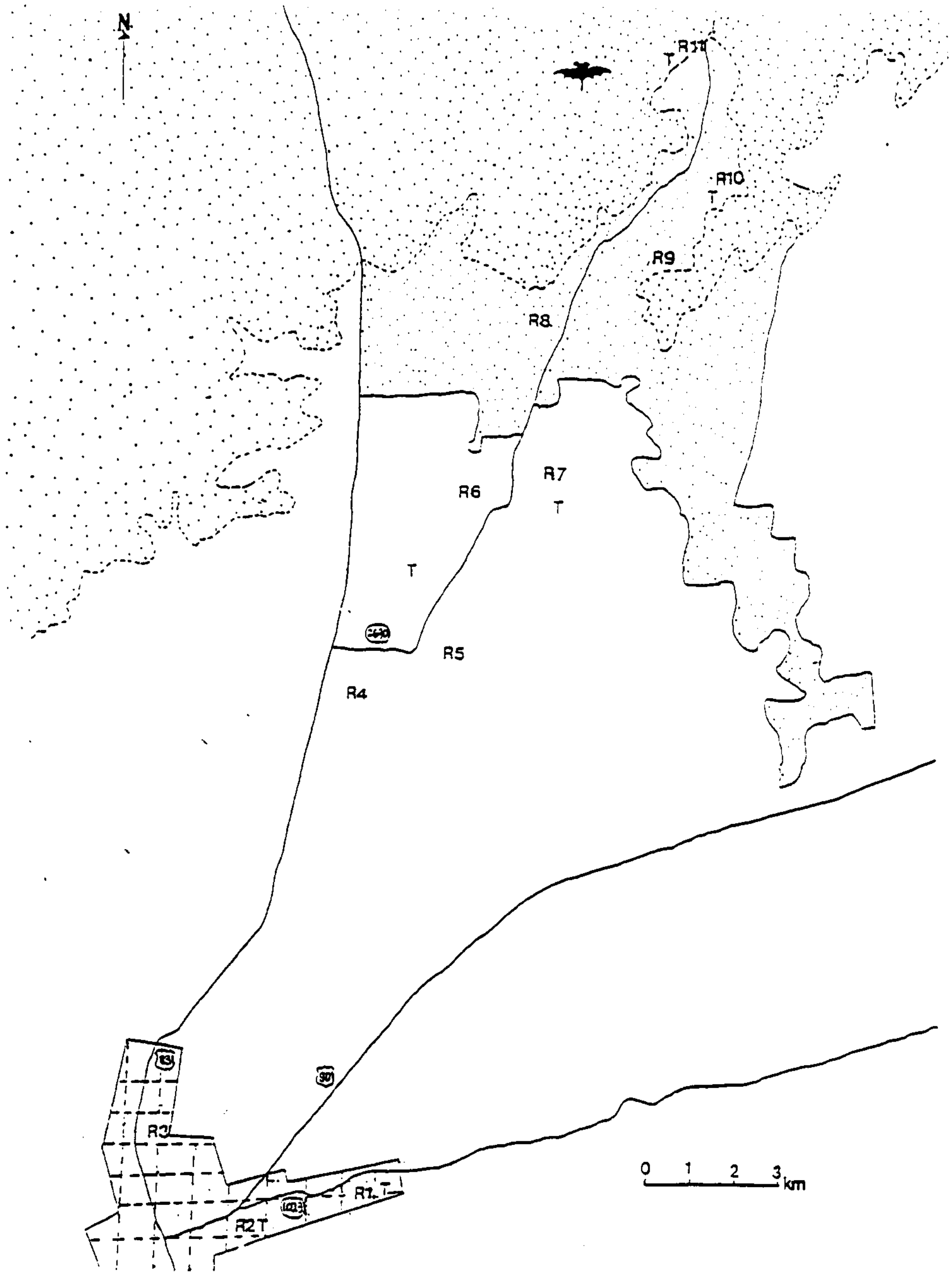

Figure 3.1. The location of Frio Cave and the study sites with associated habitats adjacent to Uvalde, Texas. Bat figure: Frio Cave; dashed line: the southern boundary of Hill Country region; dotted area: ranching areas; white area: cropland; grid area: town areas; R: bat activity recording sites; T: insect sampling sites.

ranches, and the nearest town from Uvalde is about 20 km in distance. All other towns within the 50 km range from Frio Cave are no more than several km^2 in area, with population sizes from several hundred to less than two thousand (Profile of America, 1995). These small towns are surrounded by large areas devoted to crops or ranching.

Bat Activity

I measured foraging activities by recording echolocation calls in the three habitats along a transect of about 40 km. Each night, I surveyed the transect twice, during the two peak feeding bouts of T. b. mexicana. The first session was from dusk (ca. 2100 h) to midnight, and the second was from ca. 0200 h to pre-dawn (ca. 0500 h). The transect included three sampling sites in towns, four sites in cropland, and four sites in ranch areas. The three town stops were in the NE, central, and NW sections of Uvalde, because the other towns are too small and are right beside large areas of cropland or ranches. The closet site to Frio Cave was about 3 km from the cave, and each consecutive site was spaced at about 3 to 4 km, except that sites R3 and R4 were at about 12 km apart. This is because a highway was avoided to reduce the noise, and no access was available to the croplands between these two stops (Fig. 3.1). To minimize bias due to temporal activity patterns of bats, I alternated the start and end points and the direction that I moved along the transect on each consecutive evening session and each consecutive pre dawn session.

I conducted both evening and pre-dawn sessions about once a week throughout the 1996 and 1997 summers. At each stop, I used an Ultrasound Advice S-25 bat detector set on heterodyne mode to monitor the echolocation calls of bats for five minutes, and recorded bat calls using an AIWA HS-F150 cassette recorder. The bat detector was tuned to 25 kHz at which T. b. mexicana emit calls with most energy (McCracken, pers. comm.). Within my study area, there are records of six other species of bats, including Myotis velifer, Nycticeius humeralis, Pipistrellus subflavus, Lasiurus borealis, L.

cinereus, and Mormoops megalophylla (Schmidly, 1991). The former four species all emit echolocation calls with most energy at above 40 kHz (Fullard et al., 1983; Neuweiler, 1990), and can be distinguished from T. b. mexicana. Information on the echolocation calls of M. megalophylla is unavailable, but records suggest that it is a rare seasonal migrant in the Edwards Plateau region (Schmidly, 1991). Lasiurus cinereus is the only known species with echolocation calls that could be confused with those of T. b. mexicana. This species is a spring-fall migrant, only males are summer residents and are rare in south central Texas (Schmidly, 1991).

Feeding buzzes consist of a series of bat calls that are emitted with an increased repetition rate as the bat approaching and attacking an insect. Feeding buzzes were distinguished from search-phase calls, and were tallied. Search-phase calls often were in such high numbers that they were difficult to count, presumably because more than one bat was emitting calls at the same time. Therefore, I used the proportion of signal-receiving time of the total recording time to obtain an estimate of percent activity time of bats. I used the numbers of feeding buzzes per unit of activity time to calculate the attack rate of the bats.

Insect Composition and Relative Abundance

I used light traps (the Universal Black Light Trap, Model 2851A with BL tube 2851U, BioQuip Products, CA) to assess the composition and abundance of nocturnal insects. Insects were sampled at two sites in each of the three types of habitats as described above. I alternately sampled each habitat once per week and, in total, 12 nights of samples were collected in each habitat in 1997. Light traps were set in two collecting sessions, from dusk (ca. 2030 h-2100 h) to midnight and from midnight to pre-dawn (ca. 0500 h). Insect collections were preserved in a freezer for later identification.

I identified most insects to family, however, because many specimens were damaged during freezing, moths were identified only to order unless obvious diagnostic characteristics were present. Other soft-bodied insects (e.g., mayflies and caddisflies) could often only be identified to order for the same reason. I measured relative frequency of occurrence (the number of occurrences of a particular taxon in samples divided by the total occurrences of all taxa in samples, multiplied by 100) for insects at both order and family levels. Insect collections were also oven-dried, quantified by mass at the ordinal level using an electric balance (to 1 mg), and were presented as relative mass. Collections from sites of the same habitat were pooled to obtain the total abundance in each habitat. I adjusted the mass of insect collections in each nightly collecting session according to the length of time that traps were on, about 3 hr in the first session and 5 hr in the second session. The insect collections provided as voucher specimen for dietary studies, and were used as a base line for the comparison with the diet composition of bats.

Food Habits

The materials and methods used for collecting fecal samples and to determine the diet of the bats are described in Chapter II.

Data Analysis

All means were presented as (± 1 SE) unless noted. All statistical tests were determined at the significance level of 0.05. I used non-parametric methods (Mann-Whitney U-test in two-sample comparisons and Kruskal-Wallis test in comparisons of three or more samples) to test for differences in the length of activity time, and in the mean number of feeding buzzes emitted by bats between recording sessions and among habitats. I used Smith's (1982) standardized measure, $FT = \sum (p_j a_j)^{1/2}$, to calculate the dietary breadth of the bats (Krebs, 1989), where P_j is the proportion of individuals found using prey item j, and a_j is the proportion of prey item j within the total prey items. The lower and upper 95% confidence limits of each measure were calculated as follows: 95% confidence limit = sin (arcsin FT ± $1.96/2(y^{1/2})$), where y is the total number of individuals studied. The overall correspondence between diets of bats in relative volume and the relative abundance of major insect orders in mass of the trap collections was examined using graphic analysis and Spearman's coefficient of rank correlation (Sokal and Rohlf, 1981). Because I have no knowledge of the habitat in which any particular bat foraged, the diet of the bats was compared with insect abundance based on the pooled data from all the three habitats.

RESULTS

Bat Activity

A total of 2,640 minutes (44 hr) of recording from 24 nights were collected and analyzed. On average, I recorded 29.1 ± 1.4 sec of search-phase calls per min (ca. 48.5% of the recording time), and 0.7 ± 0.3 feeding buzzes per min, which translates into about 1.4 attack attempts per min of activity time. The activity time of bats and the feeding buzzes emitted fluctuated during the summer at each habitat. Activity time and the frequency of feeding buzzes of bats differed among habitats, but were not significantly different between the two summers or between the two nightly recording sessions (Table 3.1 and 3.2). In following analyses, the data from the two summers and from the two collecting sessions were combined for both the length of activity time and the number of feeding buzzes per min of recording time.

Bats showed the highest mean activity time in town habitats and the lowest in croplands ($H = 7.14$, d.f. = 2, $P < 0.05$) (Fig. 3.2 (a)). Bats also had the highest mean feeding buzzes per min in town areas, and the lowest in croplands ($H = 6.99$, d.f. = 2, $P < 0.05$) (Fig. 3.2 (b)). Separated into the three seasonal phases (I: late May-mid June, II: late June-mid July, III: late July-August), the pattern of higher bat activity in town areas

Table 3.1. Mean activity time of bats (seconds of recorded echolocation calls per min ± 1 SE) in the evening and morning recording sessions in the three habitats during the summers of (a) 1996 (11 nights) and (b) 1997 (13 nights). Sample sizes in parentheses after each year refer to the total recording time in minutes in each session, and those after each habitat type refers to the number of recording sites.

(a) 1996 (n = 605)

	Habitat			
Session	Town (n = 3)	Cropland (n = 4)	Ranch (n = 4)	Total
Evening	42.6 ± 4.22	8.7 ± 2.65	12.0 ± 3.31	19.4 ± 4.75
Morning	49.4 ± 3.67	13.2 ± 2.25	27.8 ± 6.07	28.3 ± 4.67
Total	45.7 ± 3.81	10.8 ± 2.39	19.5 ± 4.59	23.6 ± 4.57

(b) 1997 (n = 715)

	Habitat			
Session	Town (n = 3)	Cropland (n = 4)	Ranch (n = 4)	Total
Evening	36.1 ± 1.21	14.5 ± 2.69	23.5 ± 6.06	23.6 ± 3.18
Morning	38.5 ± 2.62	8.5 ± 2.63	24.4 ± 7.02	22.5 ± 4.27
Total	37.3 ± 1.22	11.5 ± 2.48	24.0 ± 6.52	23.0 ± 3.68

Three-factor ANOVA analysis: year, F = 0.01, P > 0.5; habitat, F = 38.38, P < 0.001; session, F = 3.97, P > 0.05.

Table 3.2. Mean number of feeding buzzes (± 1 SE) per recording minute in the evening and morning recording sessions in the three habitats during the summers of (a) 1996 (11 nights) and (b) 1997 (13 nights). Sample sizes in parentheses after each year refer to the total recording time in minutes in each session, and those after each habitat type refers to the number of recording sites.

(a) 1996 (n = 605)

	Habitat			
Session	Town (n = 3)	Cropland (n = 4)	Ranch (n = 4)	Total
Evening	2.4 ± 1.66	0.04 ± 0.02	0.09 ± 0.04	0.7 ± 0.5
Morning	1.9 ± 1.18	0.11 ± 0.04	0.2 ± 0.04	0.6 ± 0.38
Total	2.2 ± 1.44	0.08 ± 0.03	0.14 ± 0.04	0.7 ± 0.45

(b) 1997 (n = 715)

	Habitat			
Session	Town (n = 3)	Cropland (n = 4)	Ranch (n = 4)	Total
Evening	1.3 ± 0.45	0.4 ± 0.08	0.8 ± 0.28	0.8 ± 0.19
Morning	0.8 ± 0.29	0.1 ± 0.03	0.5 ± 0.11	0.4 ± 0.11
Total	1.0 ± 0.36	0.3 ± 0.05	0.6 ± 0.19	0.6 ± 0.15

Three-factor ANOVA analysis: year, $F = 0.28$, $P > 0.5$; habitat, $F = 9.24$, $P < 0.001$; session, $F = 0.76$, $P > 0.1$.

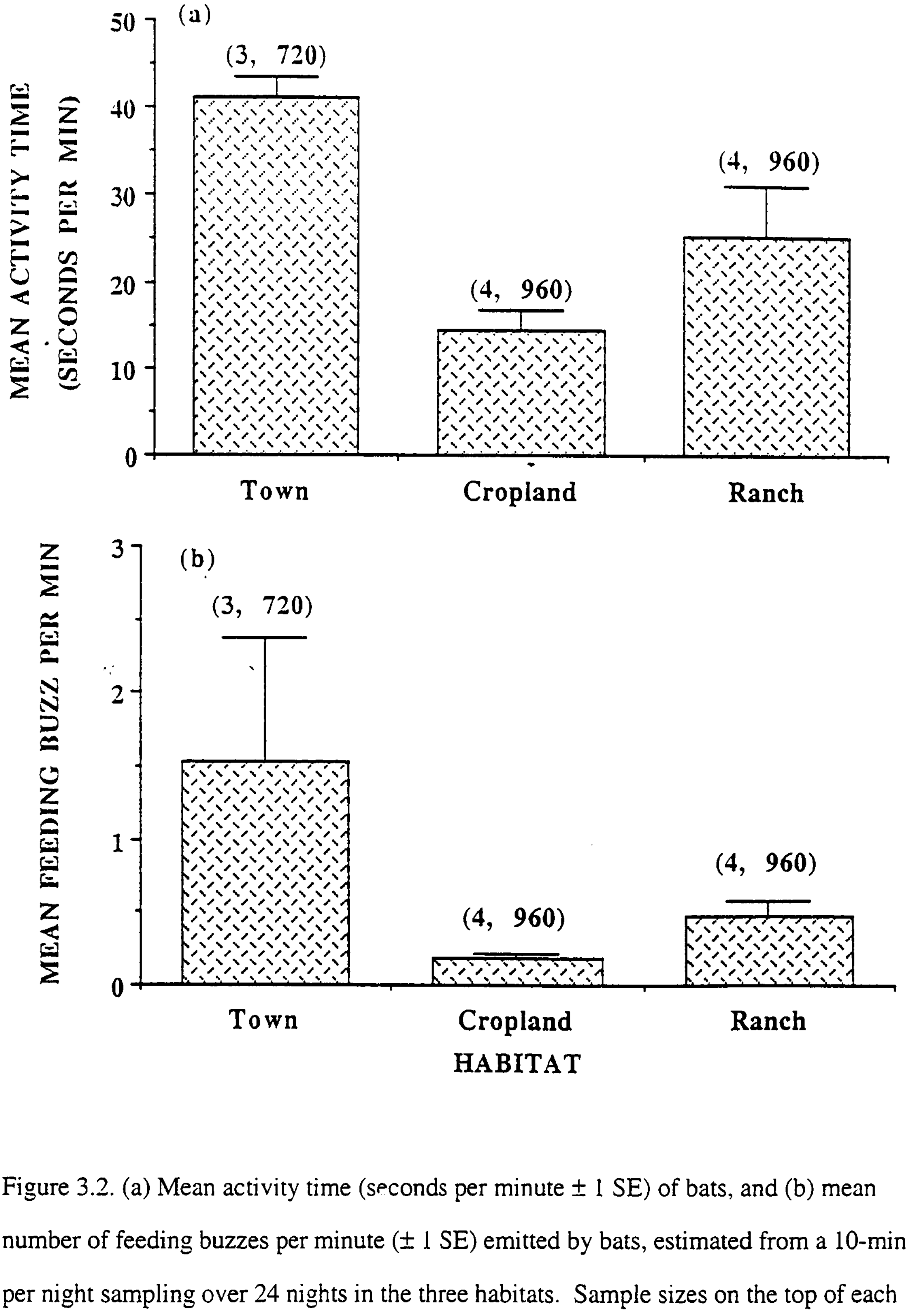

Figure 3.2. (a) Mean activity time (seconds per minute ± 1 SE) of bats, and (b) mean number of feeding buzzes per minute (± 1 SE) emitted by bats, estimated from a 10-min per night sampling over 24 nights in the three habitats. Sample sizes on the top of each column refer to the replicate sites within each habitat, and the total recording time in min.

than in the other two habitats was consistent. There were no significant differences among the three seasonal phases in activity time of the bats in each habitat (town: $H = 3.59$, d.f. = 2, $P > 0.1$; cropland: $H = 2.51$, d.f. = 2, $P > 0.1$; ranch: $H = 1.93$, d.f. = 2, $P > 0.1$) (Fig. 3.3), nor in mean numbers of feeding buzzes (town: $H = 3.68$, d.f. = 2, $P > 0.1$; cropland: $H = 0.97$, d.f. = 2, $P > 0.5$; ranch: $H = 3.42$, d.f. = 2, $P > 0.1$). Attack rates (the number of feeding buzzes per min of activity time), however, were higher in the evening session than in the pre dawn session in cropland ($U_{(4,4)} = 16$, $P < 0.05$) and in ranches ($U_{(4,4)} = 15$, $P < 0.05$), but not in town areas ($U_{(3,3)} = 7$, $P > 0.1$) (Fig. 3.4). Attack rates were not significantly different among the three seasonal phases in any of the three habitats (town: $H = 5.92$, d.f. = 2, $P > 0.05$; cropland: $H = 1.36$, d.f. = 2, $P > 0.5$; ranch: $H = 3.15$, d.f. = 2, $P > 0.1$) (Fig. 3.5).

Insect Composition and Relative Abundance

Light traps collected a total of 2191.2 g (dry mass) of insects from 15 orders, and 92 identified families or family groups, including both aquatic and non aquatic forms (Appendix I). Coleopterans, homopterans, lepidopterans (moths), hemipterans, hymenopterans, and dipterans were the most common insects in the collections. Each of these accounted for over 10% of the total occurrence of insects, and collectively these six orders accounted for 72.6% of the total occurrence. Trichopterans, orthopterans, and neuropterans were less common, and all other orders accounted for less than 5% of the total occurrence (Table 3.3). In relative mass, however, Coleoptera dominated the collections (ca. 57%), of which about 81.5% comprised of scarabaeids and carabids. Moths accounted for over 23% of the total mass collected, Orthoptera and Hemiptera each accounted for 8.9% and 7.7% respectively, and all other orders accounted for only 3.2%.

The three habitats had similar patterns of relative abundance in mass (%) among different insect orders (Table 3.4). Coleopterans dominated the total mass of collections,

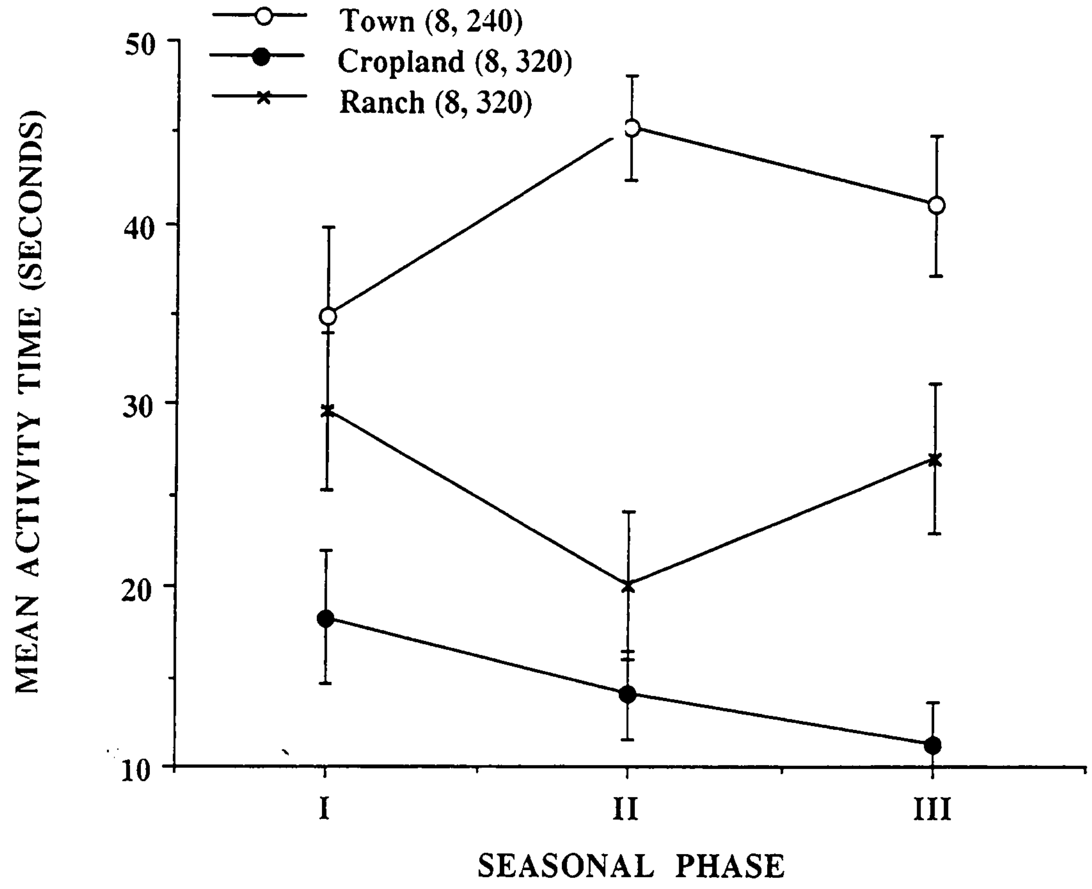

Figure 3.3. Mean activity time (seconds per minute ± 1 SE) of bats estimated from a 10-min per night sampling during seasonal phase I (late May-mid June), II (late June-mid July), and III (late July-August) in the three habitats. Sample sizes after each habitat refer to the number of nights and the total recording time in min in each season.

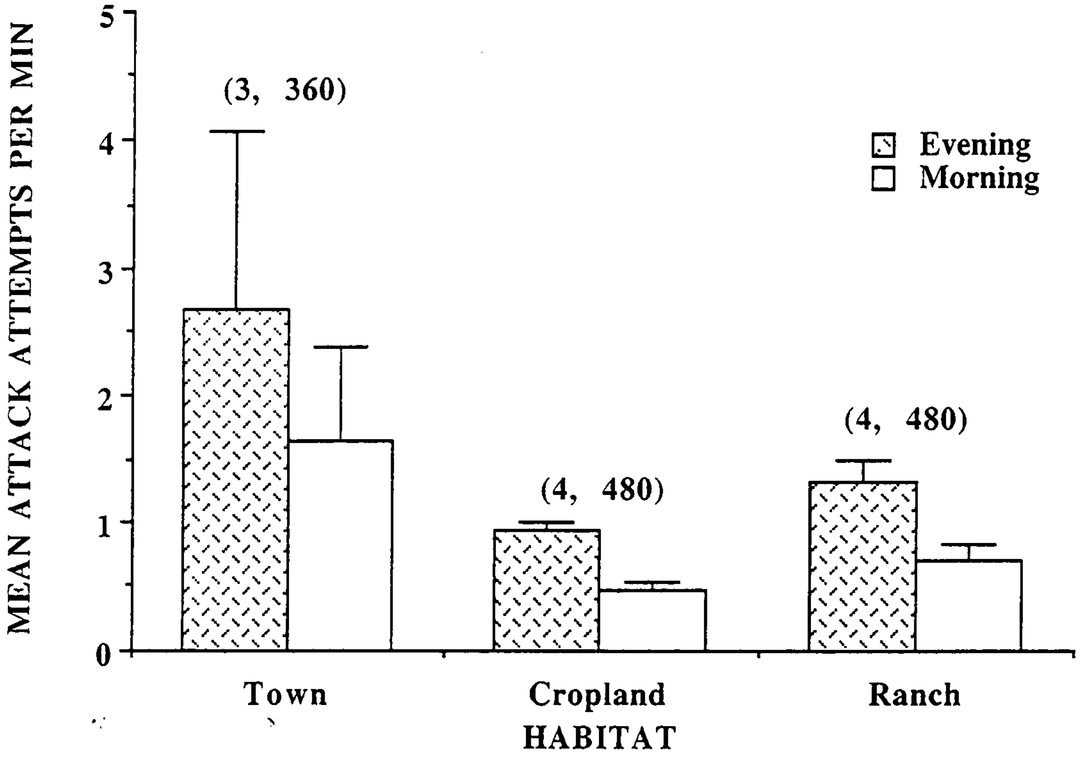

Figure 3.4. Mean attack rate (number of feeding buzzes per min of activity time ± 1 SE) of bats in the evening and morning recording sessions over 24 nights in the three habitats. Sample sizes on the top of each habitats refer to the replicate sites within each habitat, and the total recording time in min for each session.

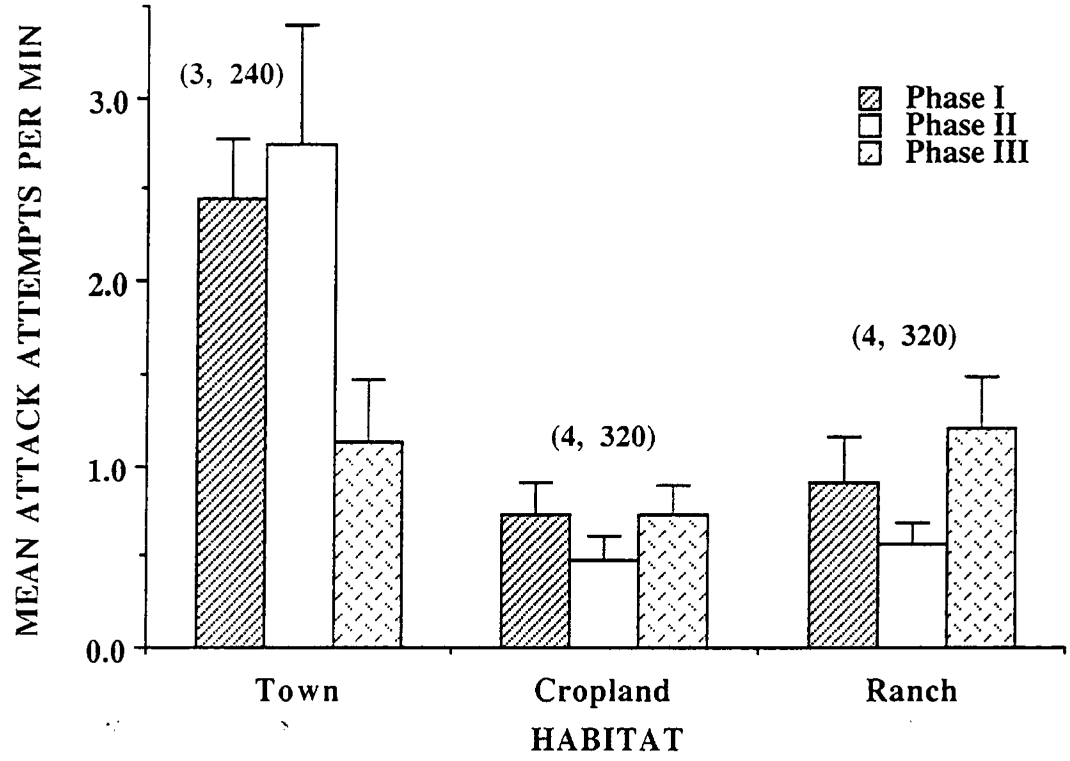

Figure 3.5. Mean attack rate (number of feeding buzzes per min of activity time ± 1 SE) of bats estimated from a 10-min per night sampling during seasonal phase I (late May-mid June), II (late June-mid July), and III (late July-August) in the three habitats. Sample sizes on the top of each habitat refer to the replicate sites within each habitat, and the total recording time in min for each seasonal phase.

Table 3.3. Insect taxa, relative frequency (%) of occurrence, and relative mass (%) of each insect order and family in the light trap collections in the three habitats over 12 nights. Relative frequency (%) of occurrence and relative volume (%) of each insect taxon in the diets of bats (n = 355 bats) are in parentheses.

Insect Taxon*	Relative Frequency of Occurrence Order	 Family**	Relative Mass (Volume) Order
COLEOPTERA	12.5 (18.5)		56.96 (28.58 ± 1.38)
Carabidae		19.3 (27.1)	
Chrysomelidae		12.0 (17.4)	
Curculionidae		8.1 (2.7)	
Dytiscidae‡		10.5 (1.6)	
Scarabaeidae		19.6 (16.3)	
Scolytidae		10.5 (0.1)	
Others		20.0 (34.6)†	
DIPTERA	11.0 (9.4)		0.23 (2.55 ± 0.29)
Drosophilidae		4.6 (1.7)	
Nematocera		30.0 (8.5)	
Schizophora		31.0 (6.3)	
Syrphidae		7.3 (1.1)	
Tephritidae		4.0 (20.0)	
Others		23.1 (62.5)†	
EPHEMEROPTERA‡	2.1 (1.1)		0.01 (0.34 ± 0.12)
HEMIPTERA	12.3 (18.9)		7.74 (18.16 ± 1.00)
Coreidae		0.8 (1.4)	
Corixidae‡		6.3 (3.2)	
Cydnidae		14.0 (4.0)	

Table 3.3 (continued).

Insect Taxon*	Relative Frequency of Occurrence		Relative Mass (Volume)
	Order	Family**	Order
Lygaeidae		14.4 (27.8)	
Miridae		17.6 (10.0)	
Nabidae		15.9 (9.2)	
Pentatomidae		14.1 (28.0)	
Reduviidae		8.9 (1.4)	
Tingidae		0.2 (0.6)	
Others		7.8 (14.4)†	
HOMOPTERA	12.5 (15.7)		1.00 (8.06 ± 0.67)
Cercopidae		9.5 (20.3)	
Cicadellidae		39.0 (49.6)	
Cixiidae		15.8 (13.5)	
Delphacidae		23.5 (7.2)	
Others		12.2 (9.5)†	
HYMENOPTERA	11.9 (7.2)		0.67 (5.19 ± 0.82)
Braconidae		17.1 (12.9)	
Formicidae		33.1 (35.7)	
Tiphiidae		21.8 (13.6)	
Others		28.0 (37.9)†	
LEPIDOPTERA	12.4 (18.7)		23.23 (34.33 ± 1.53)
NEUROPTERA	4.7 (5.4)		0.16 (1.78 ± 0.24)
Chrysopidae		25.4 (45.0)	
Hemerobiidae		23.9 (55.0)	
Others		50.7 (0.0)	

Table 3.3 (continued).

Insect Taxon*	Relative Frequency of Occurrence		Relative Mass (Volume)
	Order	Family**	Order
ODONATA	0.2 (0.2)		0.03 (< 0.005)
(Zygotera)			
ORTHOPTERA	8.3 (1.0)		8.89 (0.35 ± 0.13)
Gryllidae		67.9 (100.0)	
Others		32.1 (0.0)	
PLECOPTERA‡	0.0 (0.3)		0.0 (0.04 ± 0.02)
TRICHOPTERA‡	8.9 (0.8)		0.07 (0.39 ± 0.15)
OTHERS¥	4.7 (2.8)		1.01 (0.23 ± 0.13)
Total	100.0 (100.0)		100.00 (100.0)

* Only the insect orders and families that were also found in the diets of bats are presented. Orders or families that were not found in the bats' diets are listed as others.

** The relative percent frequencies (%) of occurrence at family level were measured within each insect order to which those families belong.

† Values in parentheses refer to all unidentified insect fragments of that associated order in diet of bats.

¥ OTHERS refers to blattellids, mantids, corydalids, Strepsiptera, and spiders. Values in parentheses refer to unidentified fragments in diet of bats.

‡ Insect taxa that are considered as aquatic, with almost all species having one or more aquatic stages, and adult forms are common around aquatic or semi-aquatic environments (based on Borror et al., 1989; Arnett, 1993; Merritt and Cummins, 1996).

Table 3.4. Relative abundance (%) of each insect order in mass assessed using light traps during the midnight and dawn collecting sessions in the three habitats (two replicate sites each) over 12 nights.

	Town		Cropland		Ranch	
Insect Order	Midnight	Dawn	Midnight	Dawn	Midnight	Dawn
Coleoptera	66.68	51.66	60.72	60.48	66.03	38.03
Diptera	0.39	0.35	0.08	0.13	0.29	0.33
Ephemeroptera	0.13	0.04	0.01	< 0.005	0.01	< 0.005
Hemiptera	9.81	2.41	16.60	1.26	6.83	3.33
Homoptera	3.81	3.03	1.05	1.00	0.90	0.57
Hymenoptera	0.63	0.88	0.21	1.11	0.27	1.31
Lepidoptera	13.03	35.11	17.87	29.47	18.65	32.20
Neuroptera	0.06	0.09	0.10	0.02	0.32	0.07
Odonata	0.00	0.00	0.01	0.00	0.01	0.02
Orthoptera	4.49	5.72	3.06	6.48	5.04	22.52
Trichoptera	0.27	0.20	0.08	0.03	0.09	0.03
Other*	0.69	0.51	0.22	0.02	1.56	1.60
Total	99.99	100.01	100.01	100.00	100.00	100.01

* Insects and other arthropods that were only occasionally collected and were not found in the diet of bats, including wood cockroaches, mantids, dobsonflies, Strepsiptera, and spiders.

and lepidopterans were the next. Collectively with the other four common orders, they accounted for over 75% of total mass assessed in the dawn collecting session and for over 92% in the midnight collecting session in ranch areas. These six orders also accounted for over 93% of total mass assessed both in midnight and dawn collecting sessions in town areas and croplands. Among the less frequently found insects, orthopterans were the only group that accounted for appreciable mass (from ca. 3% up to over 20%), ranking third or fourth among insect orders in total mass. Of the three habitats, town areas had the lowest relative abundance in mass ($G = 7.11$, d.f. = 2, $P < 0.05$). Insect abundance was similar in relative mass between the midnight and dawn collecting sessions in town areas (paired T-test: $t = 1.15$, d.f. = 11, $P = 0.28$), but not in croplands where the dawn session was over 25% less than at midnight ($t = 3.04$, d.f. = 11, $P < 0.01$). Insect abundance in ranch areas was not significantly less in the dawn session ($t = 1.43$, d.f. = 11, $P = 0.18$) (Fig. 3.6). Cropland and ranches showed a similar pattern of a lower insect abundance during the second seasonal phase, and a slight increase during the third phase; however, in all three habitats, the mean dry mass of insects did not differ among the three seasonal phases (town: $H = 5.16$, d.f. = 2, $P = 0.08$; cropland: $H = 0.38$, d.f. = 2, $P > 0.5$; ranch: $H = 0.78$, d.f. = 2, $P > 0.5$) (Fig. 3.7).

Dietary Breadth and Resource Use

The food habits of T. b. mexicana are described in detail in Chapter II. The bats' diet in 1997, the year insects also were collected, was similar to that in 1995 and 1996 (Chapter II). In 1997, the diet included 12 orders and 31 families and family groups of insects (Table 3.3). Lepidopterans, coleopterans, and hemipterans were again the three most common and abundant prey items (each over 15% in both relative occurrence and relative volume), followed by homopterans, hymenopterans, dipterans, and neuropterans (each over 5% in relative occurrence, and ca. 2% to 8% in relative volume). Other orders

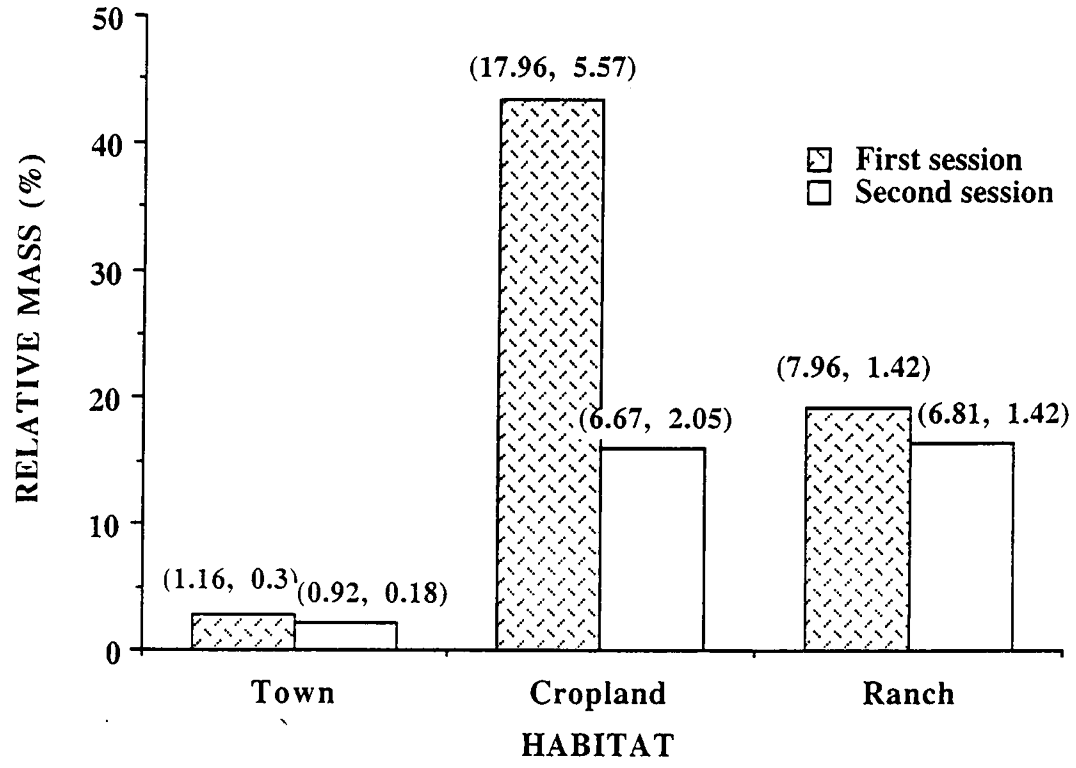

Figure 3.6. Relative abundance (%) in mass of insects assessed by light traps during the midnight and dawn collecting sessions in the three habitats over 12 nights. Numbers on the top of each column indicate the mean dry mass (g per trapping hr ± 1 SE) of insects. All six columns sum to 100%.

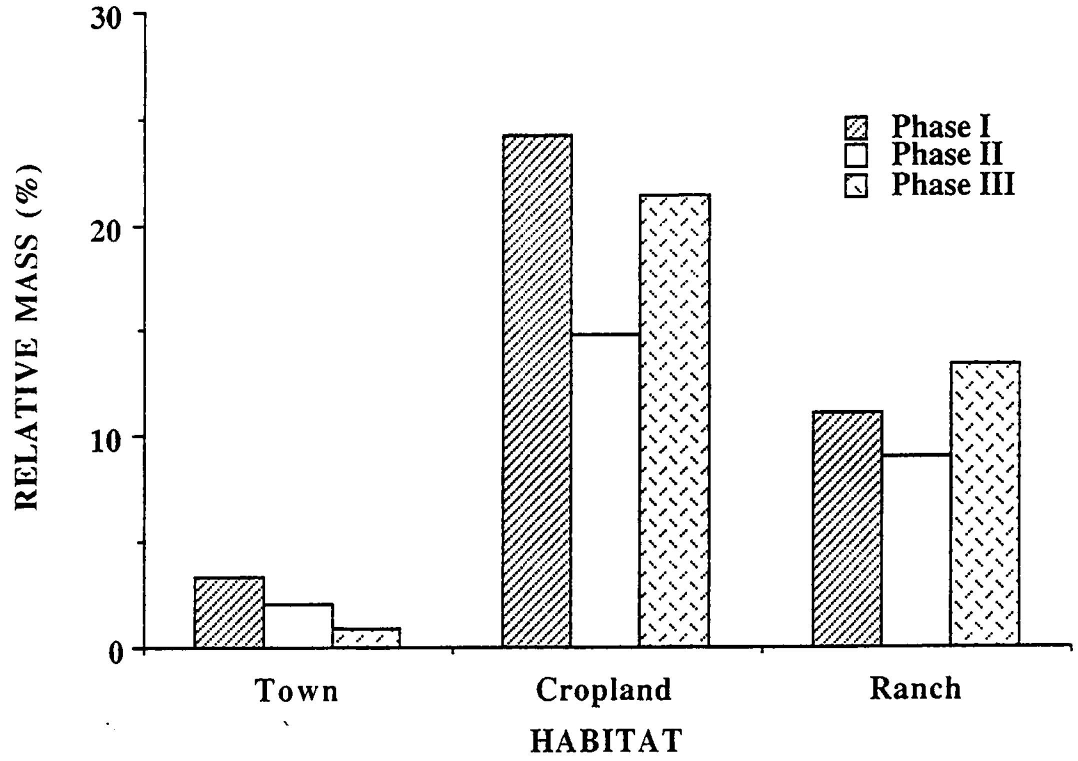

Figure 3.7. Relative abundance (%) in mass of insects assessed by light traps during seasonal phase I (late May-mid June, n = 3 nights), II (late June-mid July, n = 4 nights), and III (late July-August, n = 5 nights) in the three habitats. Sample sizes in parentheses refer to the number of nights sampled during each seasonal phase.

accounted for only 6% of the total occurrence and 1% of the total volume. At the family level, Carabidae, Chrysomelidae, and Scarabaeidae (Coleoptera), Tephritidae (Diptera), Lygaeidae and Pentatomidae (Hemiptera), Cicadellidae and Cercopidae (Homoptera), Formicidae (Hymenoptera), Gryllidae (Orthoptera), and Hemerobiidae and Chrysopidae (Neuroptera) were most common within each order. No families of ephemeropterans, lepidopterans, odonates, plecopterans, and trichopterans were identified in diets of the bats.

Dietary breadth measurements, based on relative mass in trap collections vs. relative volume in bat diets of each insect order showed a broad dietary breadth in all classes of T. b. mexicana during all three seasonal phases (Table 3.5). However, bats in the evening feeding bout tended to have a broader diet than in the pre-dawn feeding bout, and reproductive females in the second seasonal phase (late June-mid July), consisting mostly lactating females and a small proportion of females in late pregnancy, had a broader diet breadth than adults (males, post-lactating females, and non-reproductive females included) in the third seasonal phase (Table 3.5).

Graphic comparisons showed a close correspondence between the relative abundance of major insect orders in mass in trap collections and their percent volume in bats' diet (Fig. 3.8). While coleopterans dominated relative mass in the midnight collecting session, the relative volume of coleopterans was also the highest among prey items. However, as the relative abundance of lepidopterans increased during the dawn session, the proportion of coleopterans in diets decreased, and the relative volume of lepidopterans exceeded coleopterans. Hemiptera showed a temporal pattern similar to coleopterans, and Homoptera and Hymenoptera showed patterns similar to lepidopterans (Fig. 3.8). The temporal pattern of shift in proportions of these major prey orders in the diet and in trap collections was consistent during all the three seasonal phases (Fig. 3.9). When all the insect orders were included, I found a significant positive correlation at the

Table 3.5. Dietary breadth measurements for (a) the two feeding bouts and (b) different classes of bats in the three seasonal phases, based on relative abundance (%) of insect orders in mass assessed in light trap collections and relative volumes of these orders in diet of bats. P: pregnant, NP: all other non-pregnant individuals (including males), R: reproductive (pregnant and lactating females), NR: all other non-reproductive individuals, J: juveniles, A: adults.

(a)

Feeding Bout	Dietary Breadth*	95% Confidence Limit† (lower, upper)
Dusk to Midnight (n = 177)	0.943	0.915, 0.965
Midnight to Pre dawn (n = 178)	0.826	0.779, 0.867

(b)

Seasonal Phase	Bat Class	Dietary Breadth*	95% Confidence Limit† (lower, upper)
I: before summer	P (n = 44)	0.861	0.790, 0.918
	NP (n = 44)	0.865	0.789, 0.925
II: early summer	R (n = 72)	0.937	0.891, 0.971
	NR (n = 37)	0.913	0.845, 0.962
III: mid summer	J (n = 51)	0.871	0.795, 0.931
	A (n = 107)	0.822	0.751, 0.881

* Based on Smith's (1982) standardized measure, $FT = \sum (p_j a_j)^{1/2}$, where P_j is the proportion of individuals found using prey item j, and a_j is the proportion of prey item j within the total prey items.

† The lower and upper 95% confidence limits of each measure = sin (arcsin FT ± $1.96/2(y^{1/2})$), where y is the total number of individuals studied.

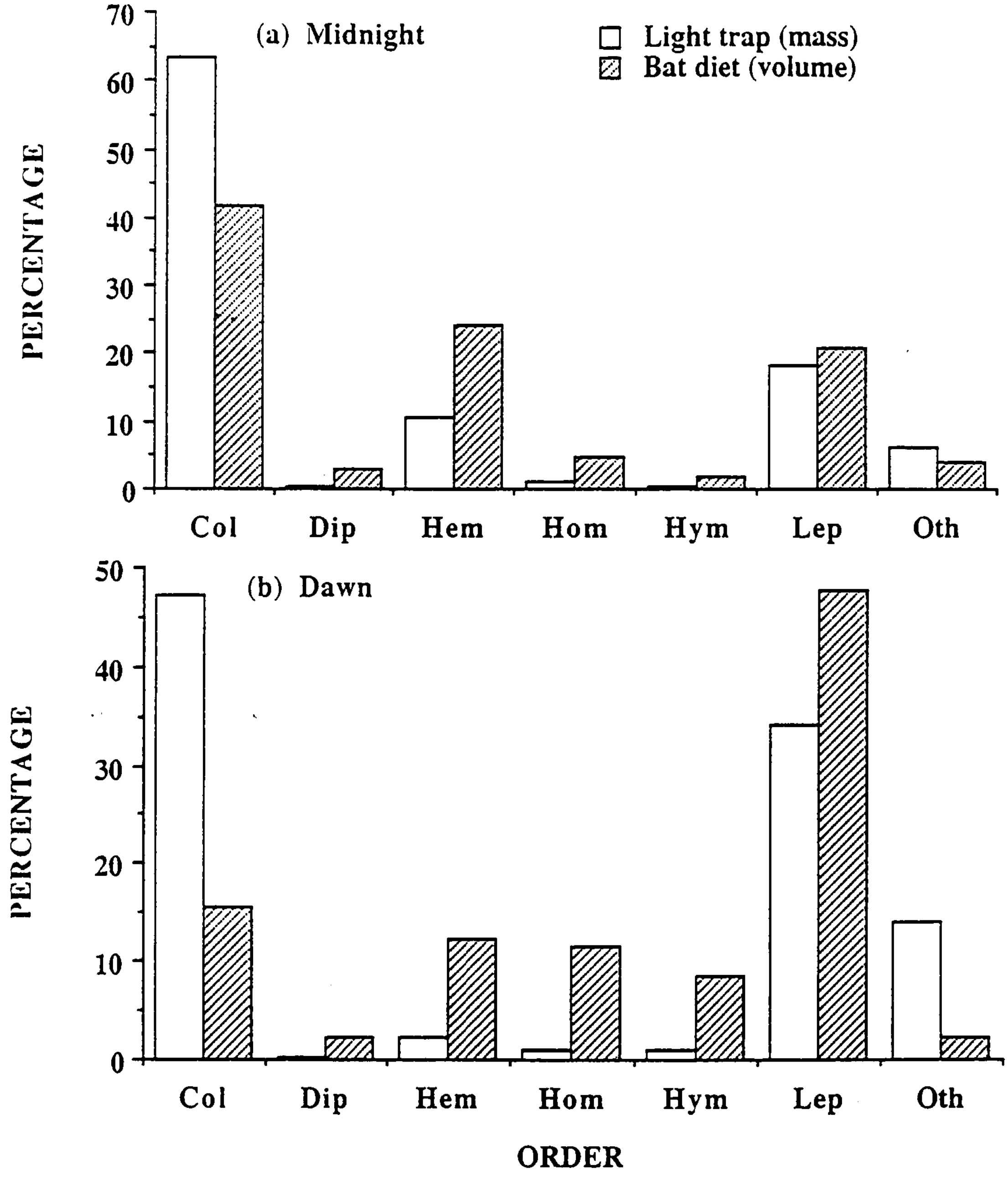

Figure 3.8. Graphic comparisons of relative abundance of six major insect orders and the combined minor orders (Oth) assessed by light traps (relative mass) and that in the diet of bats (relative volume) for (a) midnight (n = 177 bats) and (b) dawn (n = 178 bats) collecting sessions.

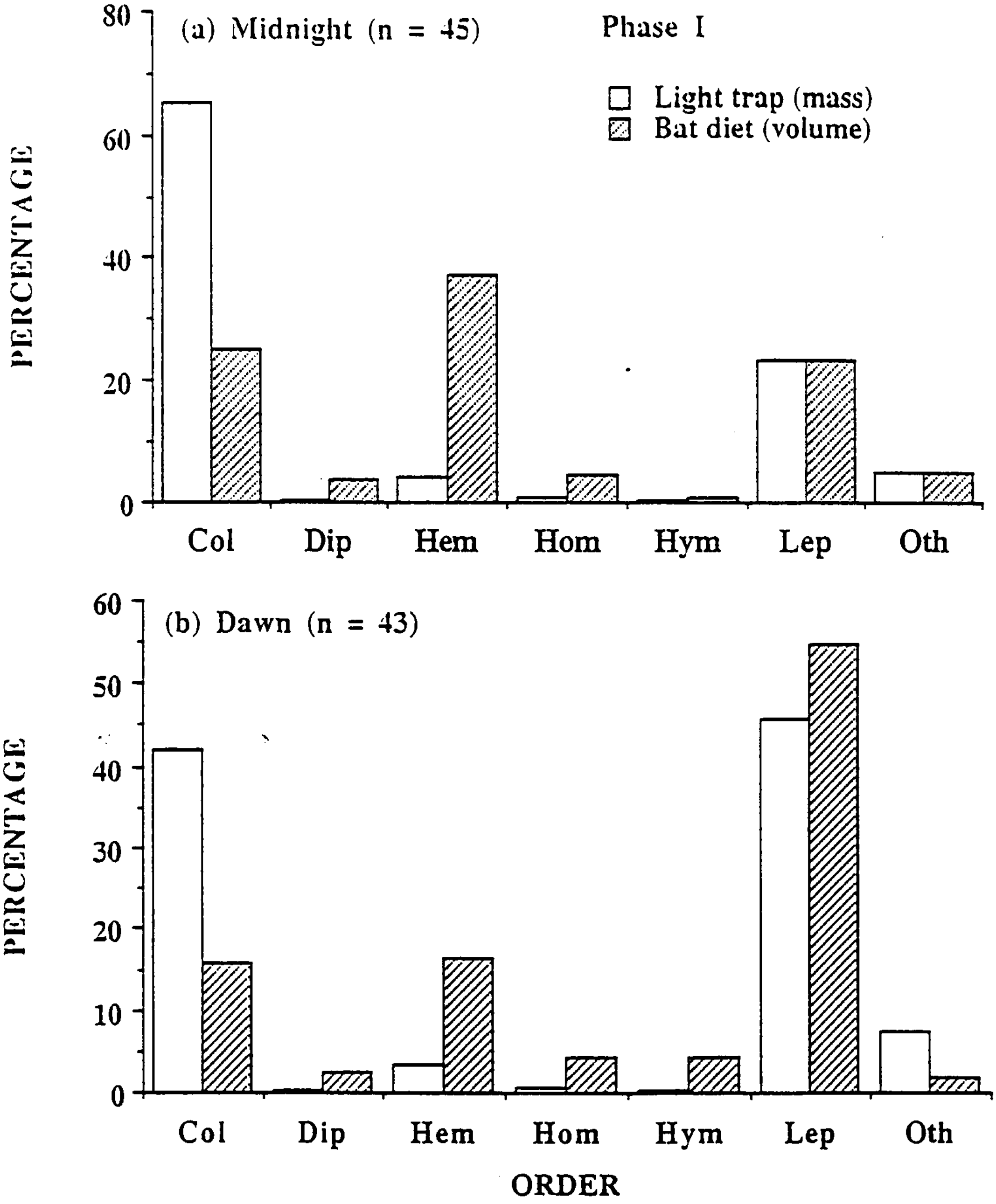

Figure 3.9. Graphic comparisons of relative abundance of six major insect orders and the combined minor orders (Oth) assessed by light traps (relative mass) and that in the diet of bats (relative volume) for (a) midnight (n = bats) and (b) dawn (n = bats) collecting sessions during the three seasonal phases, I: late May-mid June, II: late June-mid July, and III: late July-August.

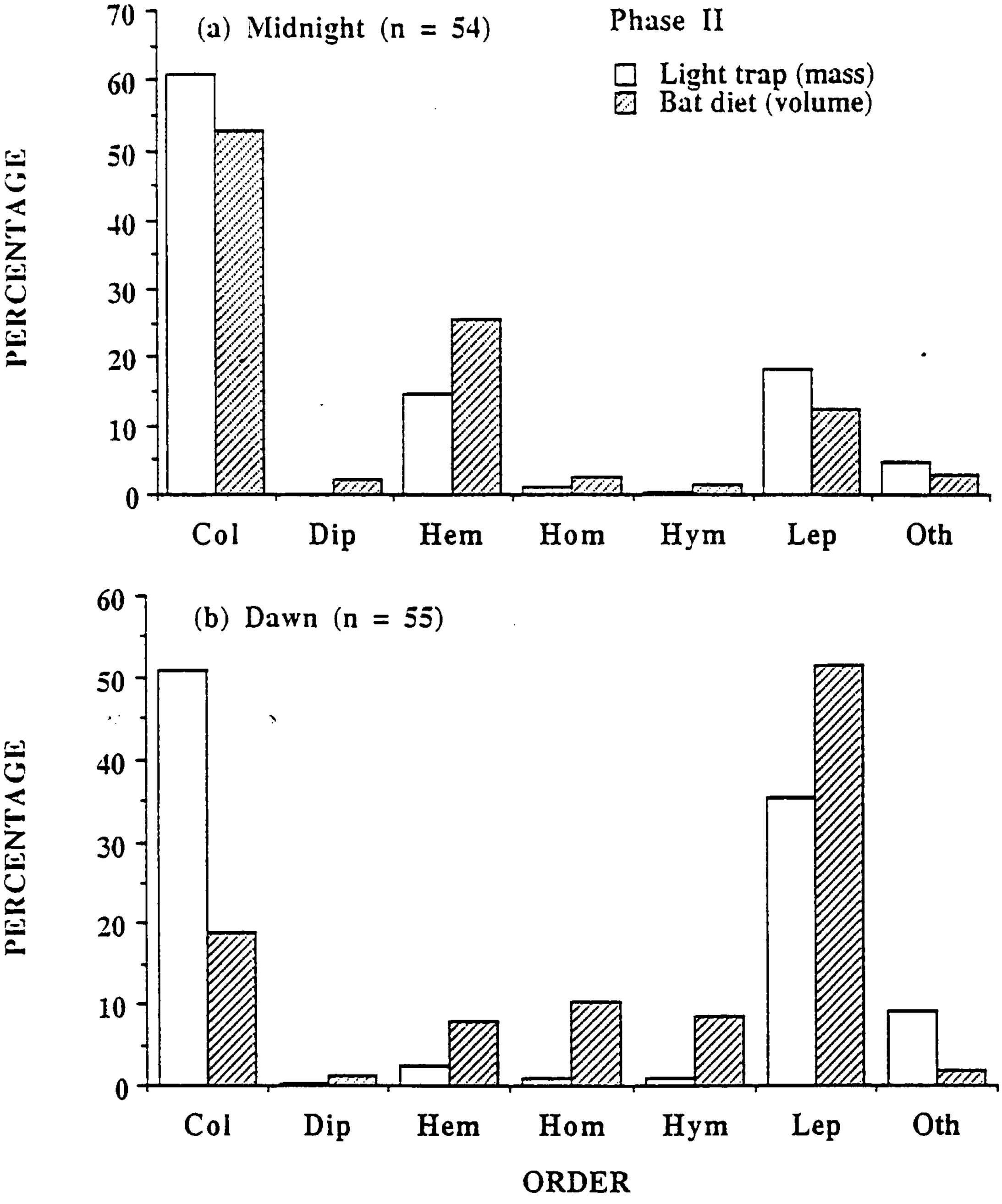

Figure 3.9 (continued).

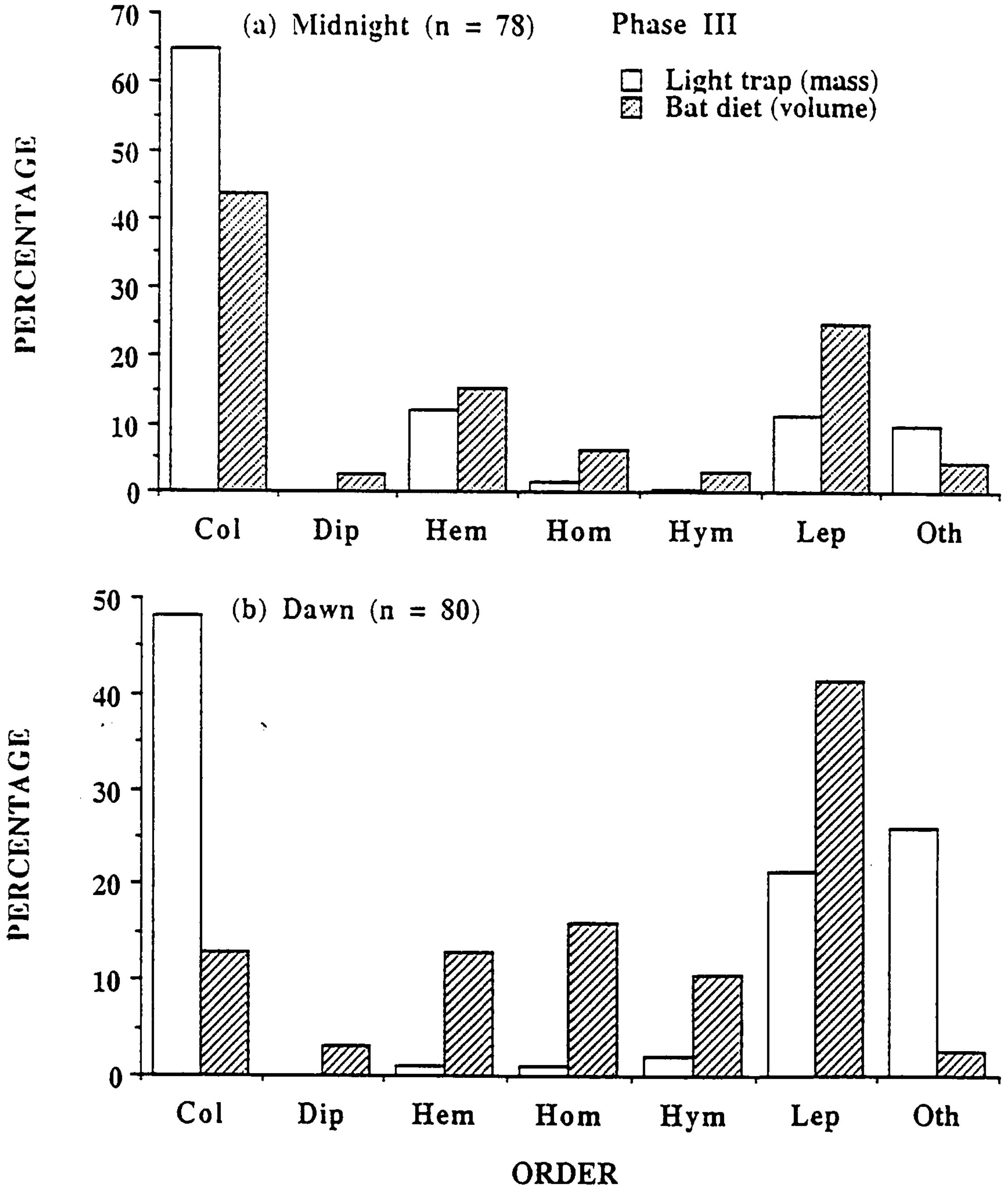

Figure 3.9 (continued).

Table 3.6. The correlation between the diet of *Tadarida b. mexicana* in relative volume (%) of insect orders and the relative abundance (%) in mass of insect orders, examined using Spearman's coefficient of rank correlation (r_s) for the two collecting sessions, each bat class present, and the three seasonal phases. See table 5 for the abbreviations for bat classes. (1): all insect orders included, (2) orthopterans removed. Sample sizes (n = bats) are in parentheses.

Seasonal Phase	Bat Class	Collecting Session	(1) r_s		(2) r_s	
I	P	Midnight (22)	0.78	*	0.94	***
		Dawn (22)	0.59	ns	0.81	*
	NP	Midnight (23)	0.78	*	0.92	**
		Dawn (21)	0.63	*	0.90	**
II	R	Midnight (36)	0.85	**	0.93	**
		Dawn (36)	0.61	ns	0.92	**
	NR	Midnight (18)	0.68	*	0.84	*
		Dawn (19)	0.76	*	0.87	**
III	A	Midnight (52)	0.67	*	0.79	*
		Dawn (55)	0.39	ns	0.77	*
	J	Midnight (26)	0.69	*	0.81	*
		Dawn (25)	0.66	*	0.90	**

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.005$

ordinal level between the trap collections and the diet of bats in 9 of the 12 comparisons. When Orthoptera were removed from the analysis, a significant positive correlation between bat diets and trap collections was found in all 12 comparisons (Table 3.6).

DISCUSSION

Bat Activities

In my study, Tadarida b. mexicana emitted an average of 0.7 feeding buzz per min (ranged 0.08 to 2.2 in different habitats), which is an order of magnitude higher than reported in different habitats in southwestern Arizona in an earlier study by Bell (1980) (mean activity of 0.06 to 0.09 bat passes per min). The levels of bat activity that I report also are higher than those reported in other studies of different species of aerial hunting insectivorous bats (e.g., Eptesicus fuscus, Lasionycteris noctivagans, Lasiurus borealis, and L. cinereus; Geggie and Fenton, 1985; Barclay, 1985; Acharya, 1995). While L. cinereus emits echolocation calls of a similar peak frequency as that of T. b. mexicana (ca. 25 kHz), and some recordings might have contained calls of this species, the rarity of L. cinereus compared to the superior abundance of T. b. mexicana in this region during summer would make the effects of mistaken identifications insignificant.

My data showed higher foraging activity of bats in town areas than in croplands and ranches. This suggests that T. b. mexicana can accommodate the somewhat cluttered environment of towns. However, the patterns of insect abundance in the different habitats do not correspond with the foraging pattern of the bats, because town areas had the lowest estimated insect abundance. The presence of street lamps in towns may be a major reason for this difference in insect trapping success. In more open areas such as croplands and ranches, light traps attract insects, both horizontally and vertically, from substantial distance. In town areas, the efficiency of light traps is interfered with by the presence of street lamps and other light sources. In addition, the attracting distance of light traps may be reduced by the presence of buildings and houses. However, comparisons between the two collecting sessions showed a similar relative insect abundance in town areas, but a dramatic decrease during the second session in croplands (Fig. 3.7). Similarly, the numbers of feeding buzzes emitted per min by bats were not different between the two sessions in town areas, but significantly decreased during the second session in croplands (Fig. 3.5). This suggests a positive relationship between bat foraging activity and insect abundance.

Tadarida b. mexicana is known to feed on swarming insects (Rose, 1967). Mercury-vapor street lamps, which produce a bluish-white light that is attractive to insects (Rydell and Racey, 1995), are used throughout Uvalde (at ca. 100 to 150 m apart in most town areas). It is documented that street lamps that attract high concentrations of insects in turn attract foraging bats of a variety of species, such as Eptesicus, Lasiurus, Nyctalus, Pipistrellus, and Verpertilio (Geggie and Fenton, 1985; Furlonger et al., 1987; Hickey and Fenton, 1990; Rydell, 1992a; Rydell and Racey, 1995; Hickey et al., 1996; Gaisler et al., 1998). Rydell and Racey (1995) concluded that bats that forage frequently around street lamps are often aerial-hawking species, like T. b. mexicana which are adapted for echolocation away from obstacles. Large numbers of T. b. mexicana may be attracted to insect concentrations that form in town areas around lights each night. Furlonger et al. (1987) found significantly higher bat activity at sites with lights than at sites without lights, and insect abundance attracted to a light source decreases with distance from the light, as does bat activity (Hickey and Fenton, 1990).

Foraging by bats in any habitats, whether light sources are available or not, should depend on the spatiotemporal distribution of insects. The vertical distribution of a variety of insects at night has been documented from ground level to several hundred meters above ground level (Callahan et al., 1972; Farrow and Dowse, 1984). The radar observations of Williams et al. (1973) have documented that the nightly dispersal of the bat colony at Bracken Cave can cover a minimum area of ca. 400 km^2. Other studies document that these bats forage as high as 1,200 m (Griffin and Thompson, 1982; McCracken et al., 1996, 1997). Given these minimum estimates of their nightly dispersion, the estimated 10×10^6 Mexican free-tailed bats from Frio Cave would have an average density of about one bat per 48,000 m^3 of air space. Their actual density may be even lower, because the colony size may not be as high as that was estimated almost four decades ago, nor is the entire colony out foraging at any given time.

However, foraging bats also are not uniformly distributed in the air. Tadarida b. mexicana is known to forage in small groups (Davis et al., 1962; Rose, 1967), and most bats may forage at altitudes of below 500 m above the ground. Reasons for this may include their attraction to insect concentrations around light sources in town areas. My data concern only habitat use patterns by Mexican free-tailed bats at lower elevations of no more than a few meters above the ground. Bats feeding at higher altitudes cannot be monitored using bat detectors at the ground level, because of the attenuation of echolocation calls in the atmosphere (Griffin, 1971). Thus, my estimates of bat activity in these three habitats are restricted to activity within tens of meters of the ground. Studying high altitude foraging by T. b. mexicana at a cropland site ca. 12 km from Frio Cave, McCracken et al. (1997) also recorded high bat activity at altitudes of 200 to 1,200 m above the ground. Future studies on foraging activity of T. b. mexicana must consider their activity at high altitudes as well, and the vertical distribution of activity at different altitudes (e.g., Fenton and Griffin, 1997; McCracken et al., 1997).

Dietary Breadth and Resource Use

Tadarida b. mexicana feeds on a variety of insect prey and has a broad diet. At the ordinal level, only three insect orders collected in trap collections, Blattaria (cockroaches), Mantodea (mantids), and Megaloptera (dobsonflies), were not found in the diet of the bats. Each of these orders was each represented by one family, only occasionally appeared in the trap collections, and accounted for less than 5% of the total occurrence and about 1% of the total mass (Table 3.3). At the family level, however, the bats' diet included only about 30% (30 out of 92) of the insect families found in the trap collections. This does not reflect the actual food resource use at the family level of T. b. mexicana, because the insect families detected in the diet of bats are influenced by the ability to identify fragments of different insects in feces. Moths and other soft-bodied insects are more difficult to identify to family, and the food resource use by T. b. mexicana at the family level has been underestimated.

Despite the limitations of fecal sample analysis, the rankings of the relative importance of different insect orders in the bats' diets and in the trap collections are similar (Table 3.3). The relative frequency of occurrence and relative volume of each insect order in the bats' diet were similar to the relative abundance of insects as assessed by traps, and there was a similar temporal pattern of shift of relative abundance in bat diets and insect collections between the two collecting sessions (Fig. 3.8 and 3.9). These results, as well as the correlation between insect collections and diets of bats of all classes (Table 3.6), suggest that T. b. mexicana is largely an opportunistic forager. In addition, my data indicate that reproductive females, which have higher energetic demands, had a broader diet during the second seasonal phase, corresponding with the lower relative insect abundance in the second phase (Table 3.5 and Fig. 3.7). These observations are compatible with predictions based on an opportunistic foraging mode (Morse, 1982).

Three orders and many families of insects collected in light traps are not in the bats' diet, and some families of insects that occurred in the diet are not present in proportion to their presence in the insect trap collections. Thus, it is possible that T. b. mexicana is largely opportunistic in foraging at the ordinal level, but more selective of a certain families of insects. However, this apparent selectivity may also be due to other factors. Foraging of insectivorous bats is subject to constraints associated with their body size, wing morphology, and echolocation design, which in turn may affect their resource use patterns (Barclay and Brigham, 1991, 1994). Flying fast and foraging in open air using long, narrow-band, low frequency echolocation calls may exclude T. b. mexicana from locating and pursuing very small insects (e.g., many members in Nematocera) unless these insects are in dense swarms. Non-flying insects will not be encountered by T. b. mexicana, unless they are in the air by passive means (see Chapter II). Tadarida b. mexicana is not known to forage over water, thus adults of most aquatic insects may not be available to them. The few aquatic insects found in the diet of T. b. mexicana (i.e., corixids, dytiscids, ephemeropterans, trichopterans) are known to actively fly at night, or form dense mating swarms (Borror et al., 1986; Merritt and Cummins, 1996).

Many nocturnal insects have developed defense mechanisms to escape from predation by bats. Auditory organs capable of detecting high frequency ultrasounds have been found in at least seven insect orders, including Coleoptera (e.g., tiger beetles), Diptera (e.g., tachinids), Homoptera (e.g., cicadas), Mantodea (praying mantises), Neuroptera (e.g., green lacewings), Orthoptera (e.g., crickets and katydids), and are well studied in Lepidoptera (Miller, 1975; Fenton and Fullard, 1979; Michelson and Larsen, 1985; Fullard, 1987; Spangler, 1988; Yager et al., 1990; Stumpner and Lakes-Harlan, 1996). Insects also may have other defense mechanisms. For instance, in laboratory settings, Goldman and Henson (1977) found that the neotropical insectivorous bat Pteronotus parnellii actively pursued some insects (e.g., noctuid moths, scarab beetles, and pentatomids), but totally ignored or terminated the pursuit before making contact with other moths (e.g., arctiids) and lampyrid beetle (fireflies). Dunning et al. (1992) found that arctiid moths are less likely to take evasive action to ultrasound stimulation than other tympanate moths (e.g., noctuids); however, bats eat arctiid moths in a lesser proportion than are available. The click sounds emitted by arctiids as a bat is approaching may serve as a startle to foraging bats (Bates and Fenton, 1990) or provide acoustic aposematism associated with their distasteful odor (Dunning and Kruger, 1996).

Insects that do not coincide with the bat's foraging time and space or that are beyond the capability of bats to detect and/or to catch are not available as food resources. However, these insects can still occur in the light trap collections. These factors should be taken into account when interpreting a selectivity of food (Whitaker, 1994). It is nearly impossible to accurately assess the food supply available to insectivorous bats; both because of the potential bias associated with all types of collecting devices (Kunz, 1988), and in the case of T. b. mexicana, because the bats disperse and forage over a large area. However, the use of light traps may provide the most realistic assessment of the insects available to T. b. mexicana. These bats feed not only in the night but also before the dusk and after the dawn (McCracken et al., 1997; Lee, pers. obs.), and around street lamps and other light sources which attract both nocturnal and diurnal insects. In addition, light traps can attract insects from higher altitudes where T. b. mexicana forage, instead of only collecting insects at ground level. Our knowledge of insect behavior and their distribution in time and space is limited, and the knowledge on response and defense of many nocturnal insects (e.g., fireflies, Goldman and Henson, 1977) to insectivorous bats is either incomplete or totally lacking. While any conclusions on the food preference of T. b. mexicana based solely on comparisons of diets with the results of insect trapping must remain speculative, the data presented here are fully consistent with the conclusion that T. b. mexicana is opportunistic in its exploitation of available insect resources.

IV. THE IMPLICATIONS OF FORAGING BEHAVIOR AND ECOLOGY OF MEXICAN FREE-TAILED BATS FOR INSECT PEST MANAGEMENT AND CONSERVATION BIOLOGY

Abstract. The implications of foraging behavior and ecology of Mexican free-tailed bats (Tadarida brasiliensis mexicana, Molossidae) for insect pest management and conservation were discussed. The temporal and seasonal variation of moth consumption in the diet of the bats showed a clear correlation with the availability of large migratory populations of agriculturally injurious moths. The evaluation at the ordinal and family levels, considering the diversity of insect prey of the bats, also suggested that the insect-eating by the bats might be agriculturally beneficial. Together with other lines of evidence, the data suggest that Mexican free-tailed bats have a potentially significant contribution in regulating agricultural insect pests. The decline of Mexican free-tailed bat populations, and their seasonal and patchy distribution, warrant conservation concerns and efforts. Protection of important cave roosts in both the summer and winter ranges should be implemented. Integrated pest management programs should be practiced in a larger spatiotemporal scale to reduce or regulate the usage of conventional chemical insecticides. Both efforts require educating the public regarding the ecological role and economic value of these bats, and the necessity of the conservation of these bats.

INTRODUCTION

A major finding of my studies is that Tadarida brasiliensis mexicana has a very diverse diet, with substantial dietary variation in time, space, and among bats of different sex, age, and reproductive status. In addition, different lines of evidence suggest that T. b. mexicana uses an opportunistic foraging strategy, given their constraints on wing morphology and echolocation structure. Opportunistic foragers are flexible and good at exploiting resources available to them within their foraging range. Similar examples are found in other taxa that also feed on the wing (e.g., swifts, Morse, 1980; cliff swallows, Brown and Brown, 1996). This behavior may in part explain the success of Mexican free-tailed bats in terms of their distribution and abundance. On the other hand, it provides implications for considering the role of this species in insect pest management.

IMPLICATIONS FOR INSECT PEST MANAGEMENT

Insectivorous bats (e.g., the big brown bat; Whitaker, 1993; 1995) can be significant predators of agricultural pest insects. Taking into account the foraging dispersal of T. b. mexicana on both horizontal and altitudinal scales, their diverse diet and opportunistic foraging patterns, and the fact that they forage near major agricultural areas, large colonies of T. b. mexicana may have a substantial impact on populations of agricultural insect pests. Previous studies on the nitrogen and carbon isotopic composition of the guano of this species from Carlsbad Caverns, New Mexico, and Eagle Creek Cave, Arizona, also suggest that agricultural insect pests constitute a major portion of the bats' diet. In these studies, the contribution of C_3 plants to the guano was three times that of C_4 plants (Des Marais et al., 1980; Mizutani et al., 1992). In the vicinity of these major cave roosts, native plants comprise of about equivalent numbers of C_3 and C_4 species, however, crop species in the vicinity are largely C_3 plants (e.g., cotton and alfalfa) during the summer (Des Marais et al., 1980).

Many lepidopterans, particularly moths of the most diverse and abundant family Noctuidae, are serious agricultural pests. For instance, corn earworms, Helicoverpa zea (Boddie), are the most severe agricultural pest in the United States in terms of damage caused, and they rank second only to boll weevils in the amounts of pesticides used for their control (Pfadt, 1985a). Although my fecal sample analysis could not determine the species or families of moths eaten by T. b. mexicana, many agriculturally important moth families (e.g., arctiids, gelechiids, noctuids, pyralids) were captured in the foraging areas of T. b. mexicana (see Chapter III), and the dietary studies do show that the bats prey heavily on moths. In addition, the temporal and seasonal variation of moth consumption in the diet of the bats shows a clear correlation with the availability of moths and provide support for the hypothesis that T. b. mexicana prey on migratory moths (see Chapter II).

The migration of moth populations is a dynamic annual phenomenon which covers a large area, and is often influenced by local weather patterns (Westbrook et al., 1995). However, moth consumption in the diet of T. b. mexicana over the summer of 1995 at Bracken, JRBC, and Frio Cave (see Chapter II for sampling and analysis methods) shows a temporal variation that corresponds very well to the timing of the emergence and migration of corn earworms from Mexico. Shifts in the temporal patterns of moth consumption also correlate to the local emergence and decline of corn earworms in later season (Fig. 4.1; also see Chapter II). Even apparent anomalies to these pattern, for instance, the unusually low moth proportion in the diet at dawn on June 5, 1995 (Fig. 4.1), support the migratory moths hypothesis. In this case, on the night of June 4, there was a strong easterly wind which would have inhibited the migration of moths from the Lower Rio Grand Valley into the south central Texas (Westbrook, pers. comm.).

Local weather and fluctuations in the populations of other moths might be responsible for other apparent anomalies in the bats' diet. For instance, the expected pattern of variation in moth consumption between the midnight and dawn sessions largely persisted in early June in the samples collected at Frio Cave in 1996 and 1997; however, the seasonal shift of this temporal pattern became less clear later in the season in 1997 (Fig. 4.2). Weather might have played a crucial role in the observed differences between years. The mean monthly precipitation in south central Texas during May and June of 1997 was among the highest for these months over the past three decades (ca. 260 mm; Division 9, National Oceanographic and Atmospheric Administration, 1968-1998). In

Figure 4.1. Moth consumption by Tadarida b. mexicana from (a) Bracken (n = 270), (b) JRBC (n = 270), and (c) Frio Cave (n = 300) in the midnight and dawn collecting sessions in the 1995 summer. The approximate timing of emergence and migration from Mexico, and local emergence and decline in south central Texas, of corn earworms (CEW) is at the bottom (based on Wolf et al., 1990). Asterisks indicate significant differences in moth consumption in relative volume (%) between the midnight and dawn collecting sessions ($P < 0.05$). Midnight sampling on 6/7 and 6/8 at Bracken, and both midnight and dawn sampling on 6/28 at Bracken and on 7/24 at Frio were interrupted by storms.

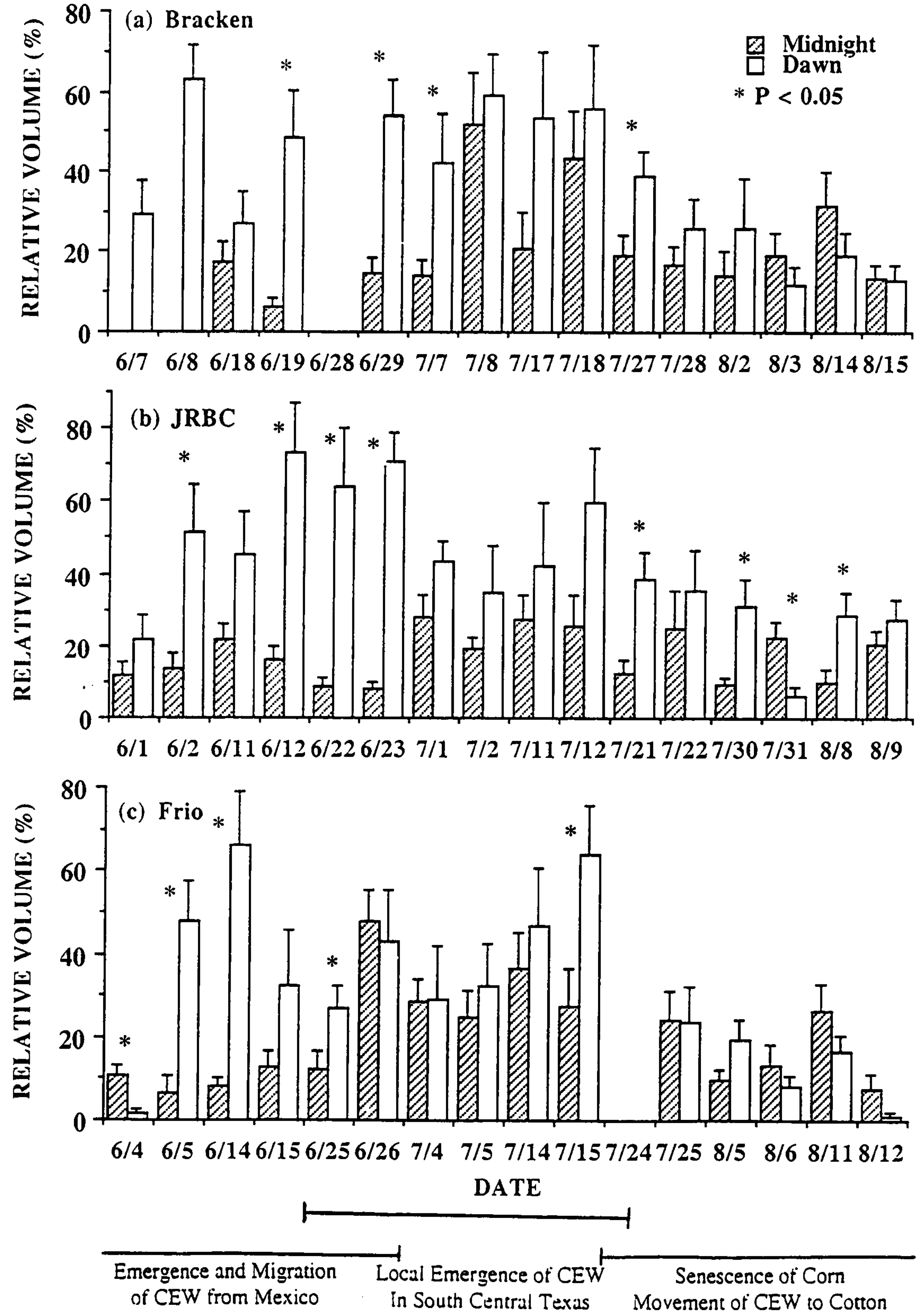

Figure 4.1 (see the previous page for the legend).

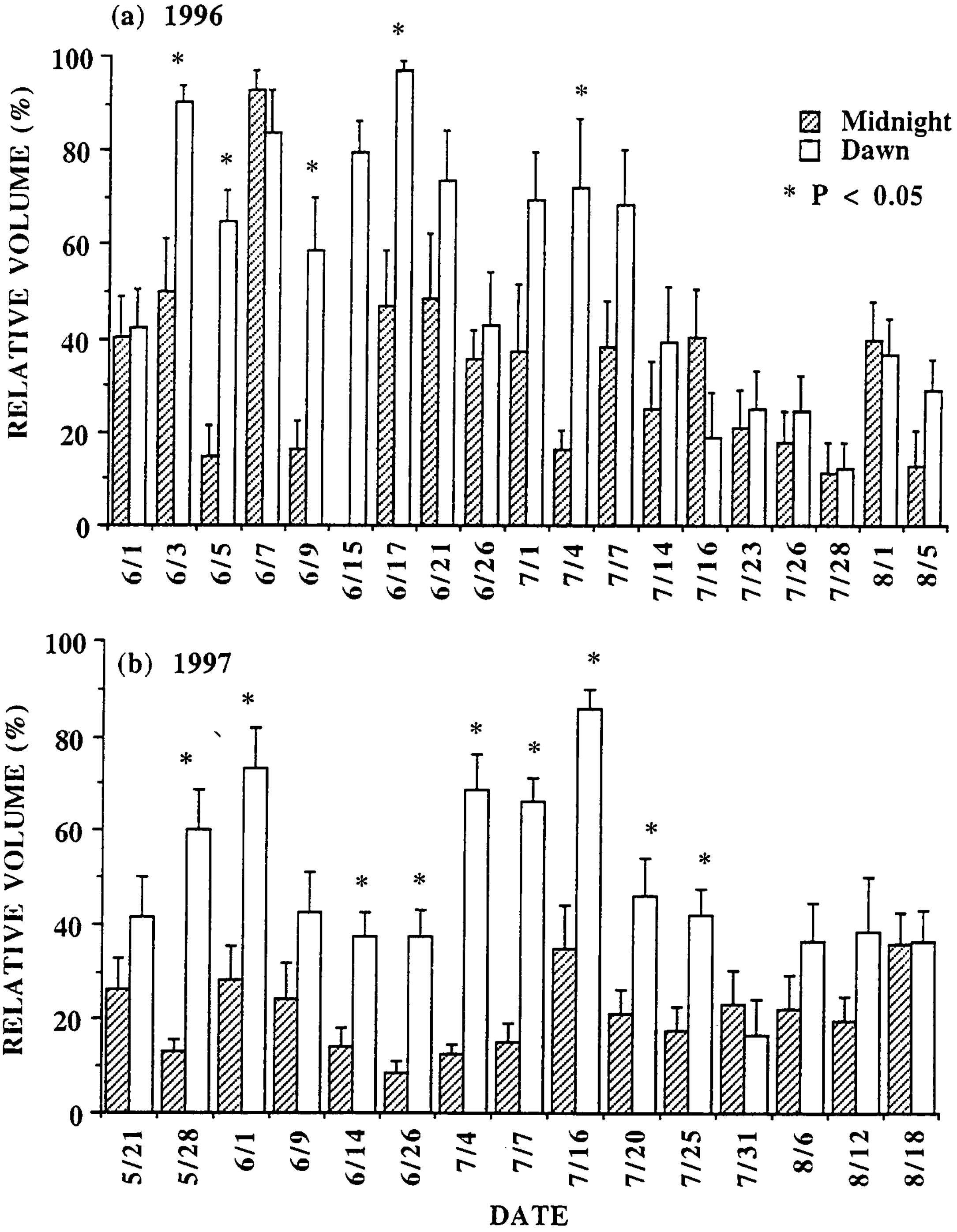

Figure 4.2. Moth consumption by Tadarida b. mexicana from Frio Cave at midnight and dawn in the (a) 1996 (n = 355) and (b) 1997 (n = 355) summers. Asterisks indicate significant differences in moth consumption in relative volume (%) between the midnight and dawn collecting sessions ($P < 0.05$).

Uvalde alone, the mean monthly precipitation during May and June of 1997 (ca. 125 mm) was about 1.6 times that of 1995 and 9.2 times that of 1996. Heavy rainfall, hail, and excessive moisture can cause the death of larvae and pupae of insects by direct mechanical damage, drowning, interfering with their feeding, and the spread of viral, fungal, and bacterial diseases (Andrewartha and Birch, 1954; Hughes et al., 1984; Wellington et al., 1999). The exceptionally high precipitation during May and June of 1997 in south central Texas may have significantly decreased the local residential populations of corn earworms and other migratory moths that otherwise would have been available as potential prey during the evening feeding bout of the bats (Westbrook, pers. comm.).

Other lines of evidence, including the strong correspondence between timing and movement of migratory moth populations and the colony location and foraging range of T. b. mexicana (Wolf et al., 1990, 1994; Westbrook et al., 1995), the flight patterns of the bats as observed by Doppler radar (McCracken, 1996), and high altitude monitoring on bat echolocation calls using tetroons, tethered kites, and hot air balloons (McCracken et al. 1996, 1997) all are consistent with the migratory moths hypothesis. These studies suggest that these migratory crop pests, such as corn earworms and fall armyworms, Spodoptera frugiperda (J. E. Smith), are highly significant food resources for T. b. mexicana. The potential contributions of T. b. mexicana to insect pest management are only now being realized.

The major limitation of fecal analysis is that insect fragments cannot be consistently identified to species. This limitation applies particularly to moths, which could only be identified to the order, and to some other insects as well. For example, my dietary analysis found spotted cucumber beetles (Diabrotica undecimpunctata howardi Barber) in the diet of T. b. mexicana, which at both the adult and larva stages (i.e. the southern corn rootworm) also cause severe agricultural damage (Burkhardt, 1985). However, in most samples only the family level (i.e., Chrysomelidae) could be confirmed, and an estimate of the consumption on spotted cucumber beetles by T. b. mexicana was not possible.

A recently developed method using polymerase chain reaction (PCR) to detect insect species-specific genetic markers may prove promising in providing more direct evidence for the consumption of particular insect species. Currently, McCracken's laboratory has tested two genetic markers, using 21 bp primers derived from an intron region taken from a published sequence of a neuropeptide gene (preproHez-PBAN) (Davis et al., 1992) from H. zea. During trial feedings of big brown bats (Eptesicus fuscus) and follow-up analysis of feces, PCR tests using these primers amplified the expected 173 bp fragment from DNA extracted from the feces of bats that were fed H. zea, but not from the feces of bats that were fed tobacco budworms, Heliothis virescens (Fabricius), a closely related species. This suggests sequence divergence that may be sufficient for species identification of corn earworms in fecal samples of bats (Pride, 1996). Recently, these primers have been used to amplify the corn earworm fragment from fecal samples that I collected in the field (Vege, pers. comm.). Future studies should demonstrate whether these genetic markers can be used to establish the frequency of predation on corn earworms, as well as other insect prey, by T. b. mexicana.

Because T. b. mexicana have a diverse diet, an evaluation of their role in regulating agricultural insect pests must consider the diversity of insects that they eat. Johansen (1985a) estimated the overall agricultural importance of each insect order, and assigned a series of "+" or "–" to indicate an order's beneficial or injurious effect on agriculture. I use his categorization to assess the impact of the overall diet composition of the bats (Table 4.1). Most minor orders (< 3% in importance) in the bats' diet, except Orthoptera (more injurious) and Neuroptera (slightly beneficial), are essentially neutral in terms of their beneficial or injurious effects to agriculture. On the other hand, most major orders (> 5% importance) in the bats' diet, except Hymenoptera, have a greater negative

Table 4.1. Relative importance of each insect order in the diet of *Tadarida b. mexicana*, and its estimated overall agricultural significance.

Prey Order	Relative Importance† in the Diet (%)	Agricultural Significance‡	
		Beneficial	Injurious
Coleoptera	24.42	++++	-----
Diptera	5.47	++++	-----
Ephemeroptera	0.61	*	*
Hemiptera	16.54	+++	----
Homoptera	11.32	*	-----
Hymenoptera	8.71	+++++	--
Lepidoptera	26.46	*	-----
Neuroptera	2.42	++	*
Odonata	0.17	+	*
Orthoptera	1.07	*	----
Plecoptera	0.12	*	-
Trichoptera	0.88	*	*

† Relative importance (PI) = (PF + PV)/2 (Bauerova, 1986); PF: relative frequency (%) of occurrence, PV: relative volume (%) (see Chapter II). The PI values of all prey orders do not sum to 100%, because that of the unidentified fragments is not listed.

‡ Asterisk indicates minor importance, and the number of plus or minus signs indicates the extent of major agricultural importance in benefit or injury (modified from Johansen, 1985a).

than positive effect. I assigned each plus or minus sign a numerical value of +1 or -1, respectively, and each asterisk (minor importance) a value of zero. The net predation effect (NPE) of the bats can be estimated as:

$$NPE = \sum [PI_i (BAI_i + IAI_i)] \qquad (1)$$

where PI is the relative importance (%) of each insect order i in the bats' diet, and BAI and IAI are the beneficial and injurious agricultural significance of each order i, respectively. From this equation, free-tailed bat predation has a NPE value of -2.09 (or -208.6%), which suggests that, evaluated at the ordinal level, the insect-eating by T. b. mexicana is agriculturally beneficial. Future studies on diet of Mexican free-tailed bats in different places (e.g., Mexico), or diet of other species of insectivorous bats, may apply similar approaches and provide a comparative analysis on the agricultural significance of insect-eating by bats.

Evaluation at the family level would probably lead to a similar conclusion. Many insect families in the diet of T. b. mexicana have many species known as serious agricultural or forest pests (Table 4.2). These include: among coleopterans, chrysomelids (e.g., spotted cucumber beetles, Diabrotica undecimpunctata howardi Barber, and allies), curculionids (e.g., boll weevils, Anthonomus grandis grandis Boheman, and allies), and scarabaeids (e.g., June beetles, Melolonthinae); among hemipterans, lygaeids (e.g., chinch bugs, Blissus leucopterus leucopterus (Say), and allies), mirids (e.g., tarnished plant bugs, Lygus lineolaris (Palisot de Beauvois), and allies), and pentatomids (e.g., harlequin bug, Murgantia histrionica (Hahn), and a variety of stink bugs); among homopterans, cercopids and cicadellids; and tephritids of dipterans (Pfadt, 1985a; Miscellaneous publications of Texas Agricultural Extension Service, Texas A&M University). Many other dipterans (e.g., culicids and species of the Calyptratae group) are vectors of a variety of diseases to humans and livestock, and can cause indirect agricultural loss.

Table 4.2. Major orders and families of insect pests that attack agricultural crops in Texas and adjacent areas.

Crop Type†	Major Insect Pest Order (major families)†
Alfalfa & Clover	Coleoptera (Curculionidae*, Meloidae)
	Hemiptera (Miridae*, Pentatomidae*)
	Homoptera (Aphidae, Cicadellidae*)
	Hymenoptera (Eurytomidae)
	Lepidoptera (Noctuidae, Pieridae, Pyralidae)
	Orthoptera (Acrididae*, Gryllidae*)
Corn	Coleoptera (Carabidae*, Chrysomelidae*, Curculionidae*, Nitidulidae, Scarabaeidae*)
	Diptera (Anthomyiidae‡)
	Hemiptera (Lygaeidae*)
	Homoptera (Aphidae, Cicadellidae*, Fulgoroidea: planthoppers*)
	Lepidoptera (Noctuidae, Pyralidae)
	Orthoptera (Acrididae*)
Cotton	Coleoptera (Curculionidae*)
	Hemiptera (Miridae*, Pentatomidae*, Pyrrhocoridae)
	Homoptera (Aleurodidae, Aphidae)
	Lepidoptera (Arctiidae, Gelechiidae, Lycaenidae, Lyonetiidae, Noctuidae, Tortricidae)
	Orthoptera (Acrididae*)
Pasture	Homoptera (Cicadellidae*)
	Hymenoptera (Formicidae*)
	Lepidoptera (Noctuidae)
	Orthoptera (Acrididae*)

Table 4.2. (continued).

Crop Type	Major Insect Pest Order (major families)
Pecan	Coleoptera (Curculionidae*)
	Hemiptera (Coreidae*, Pentatomidae*)
	Homoptera (Aphidae, Psyllidae)
	Hymenoptera (Formicidae*)
	Lepidoptera (Arctiidae, Notodontidae)
Small Grains	Coleoptera (Chrysomelidae*, Elateridae, Scarabaeidae*, Tenebrionidae)
	Diptera (Cecidomyiidae‡, Chloropidae‡)
	Hemiptera (Lygaeidae*)
	Homoptera (Aphidae, Cicadellidae*)
	Hymenoptera (Formicidae*)
	Lepidoptera (Noctuidae)
	Orthoptera (Acrididae*)
Sorghum	Coleoptera (Chrysomelidae*, Elateridae, Scarabaeidae*, Tenebrionidae)
	Diptera (Anthomyiidae‡, Cecidomyiidae‡)
	Hemiptera (Coreidae*, Lygaeidae*, Pentatomidae*)
	Homoptera (Aphidae, Cicadellidae*, Fulgoroidea: planthoppers*)
	Hymenoptera (Formicidae*)
	Lepidoptera (Noctuidae, Pyralidae)
	Orthoptera (Acrididae*)
Soybean & Vetch	Coleoptera (Bruchidae, Curculionidae*)
	Hemiptera (Miridae*, Pentatomidae*)
	Homoptera (Aphidae, Cicadellidae*)
	Lepidoptera (Arctiidae, Noctuidae)
	Orthoptera (Acrididae*, Gryllidae*)

Table 4.2. (continued).

Crop Type	Major Insect Pest Order (major families)
Tree Fruits & Small Fruits	Coleoptera (Buprestidae, Chrysomelidae*, Curculionidae*, Cerambycidae, Scarabeidae*, Scolytidae*)
	Diptera (Anthomyiidae‡, Cecidomyiidae‡, Tephritidae*)
	Hemiptera (Coreidae*, Lygaeidae*, Miridae*, Pentatomidae*)
	Homoptera (Aleyrodidae, Aphidae, Cercopidae*, Cicadellidae*, Coccidae, Diaspididae, Psyllidae)
	Hymenoptera (Tenthredinidae)
	Lepidoptera (Gelechiidae, Pyralidae, Sesiidae, Tortricidae)
Vegetables Elateridae,	Coleoptera (Curculionidae*, Chrysomelidae*, Coccinellidae, Meloidae, Nitidulidae, Scarabeidae*)
	Diptera (Agromyzidae‡, Anthomyiidae‡, Otitidae‡, Psilidae)
	Hemiptera (Coreidae*, Miridae*, Pentatomidae*, Tingidae*)
	Homoptera (Aphidae, Cicadellidae*, Psyllidae)
	Lepidoptera (Gelechiidae, Noctuidae, Oecophoridae, Plutellidae, Pyralidae, Sesiidae)
	Orthoptera (Acrididae*)

* Families found in the diet of T. b. mexicana.

‡ Families belonging to insect groups found in the diet of T. b. mexicana.

† Compiled from Don Fronk (1985), Johansen (1985c, 1985d) and the miscellaneous publications of the Texas Agricultural Extension Service (Bohmfalk et al., B-933; Randolph and Garner, B-975; Cronholm et al., B-1220 (a) ; Fuchs et al., B-1220 (b) ; Knutson and Ree, B-1238; Boring and Patrick, B-1251; Drees et al., B-1300;Sparks, B-1305; Morrison et al., B-1366; Allen and Hoelscher, B-1401; Drees and Way, B-1501).

Although no families of lepidopterans were identified in my dietary analysis, most moths families that I collected in the foraging range of T. b. mexicana (e.g., arctiids, gelechiids, noctuids, pyralids) have many members which are serious agricultural pests. In major orders, only Hymenoptera has an overall higher beneficial than injurious agricultural importance. This is due to the role in pollination of bees and derived commercial products, such as honey and beeswax, and to that many solitary species of wasps are parasites of agricultural injurious insects (Pfadt, 1985a; Borror et al., 1989; Romoser and Stoffolano, 1998). However, most hymenopterans found in the diet of T. b. mexicana are formicids, which are also considered injurious to various crops (e.g., pecan, sorghum, small grains, and pasture; Table 4.2). The limitation of fecal sample analysis prevents an estimation on the agricultural significance of insect predation by Mexican free-tailed bats to a further degree. However, as our ability in determining the diet of insectivorous bats to a lower taxonomic level (e.g., genus or species) improves by methods such as the genetic markers, a more precise estimation can be achieved.

IMPLICATIONS FOR CONSERVATION BIOLOGY

Rare or endangered species, or species with restricted distributions, typically attract public's attention and conservation efforts. As a consequence, the conservation needs of widely distributed and abundant species may be overlooked, even these species are declining, and even if they play an important ecological role (Pierson, 1998).

Tadarida b. mexicana plays important roles in the natural and agroeconomic ecosystems of the southwest. This study and evidence from other studies suggest that foraging by Mexican free-tailed bats may have a significant impact on agricultural insect pests. In addition, their cave-dwelling habits and huge colonies result in large guano deposits and an unique habitat and atmosphere that are only suitable to highly adapted species. Guano is not only an important source of fertilizer (Keleher, 1996), but also a vital living place for many invertebrates and thousands of species of microorganisms which are found nowhere else. Many of these microorganisms may have great potential values. They produce enzymes that may detoxify industrial waste, produce natural insecticides and detergents, and are potential sources of new antibiotics (Steele, 1989). Stratified guano deposits also have been used to monitor environmental pollution (Clark et al., 1995).

At least three features of this species that are associated with their ecology and their current status deserve conservation attention. Tadarida b. mexicana has a seasonal and patchy distribution, and their populations are in decline. Most Mexican free-tailed bat populations migrate each year, with wintering colonies in Mexico, and maternity colonies inhabiting in the southwestern United States during the summer. Although widely distributed over the southwestern United States and Mexico, their populations reside in a limited numbers of caves in Texas, New Mexico, Arizona, Oklahoma, and northern Mexico (McCracken et al., 1994). Populations have declined dramatically since the 1950s (McCracken, 1986), both in Mexico (in seven of eight caves surveyed, e.g., Ojuela Cave in Durango, T. Bartolo Cave in Nuevo Leon, and Abra Cave in Tamaulipas; Clark et al., 1995) and in the US (e.g., the Eagle Creek Cave in Arizona, Carlbad Caverns in New Mexico, and Valdina Farms Sinkhole in Texas; Wahl, 1989). These declines are due, in large part, to disturbance and destruction of important cave roosts by fires, dynamiting, gun shots, and mining. The loss of populations in some caves has been as severe as the extirpation of the entire colonies.

In addition, their diverse diet, including the consumption of many agricultural pests, expose these bats to significant pesticide loads. Acute toxicity may result in immediate death of bats, or, residues may accumulate in their bodies (Clark et al., 1988). Accumulated residues in turn can affect metabolic rates and energy balance (Swanepoel et al., 1999), cause a loss of coordination (Clark, 1986), and result in an indirect mortality particularly during annual migrations or during weaning of juveniles (Geluso et al., 1976). Evidence in support of pesticide poisoning has been found in major colonies of *T. b. mexicana* (e.g., Carlsbad Caverns, Geluso et al., 1981; Clark and Krynitsky, 1983), and in large colonies of other insectivorous bat species (e.g., the endangered grey bat, *Myotis grisescens*; Clark et al., 1988). However, determining the impact of pesticide poisoning on bat populations can be difficult because the effects may be subtle, depending on levels and types of pesticide exposure (Clark et al., 1995).

The current decline in populations of *T. b. mexicana* has brought the conservation needs of this species to focus. *Tadarida b. mexicana* is currently listed in Appendix I (Endangered) by the Bonn Convention for the Conservation of Migratory Animals of 1994. The conservation needs of these bats led to the formation of the US-Mexico binational initiative for their conservation, and eventually to a conservation coalition, the Program for the Conservation of Migratory Bats (Programa Para la Conservacion de Murcielagos Migratorios de Mexico y Estados Unidos de Norteamerica, or PCMM), involving government agencies and research institutes and universities of both Mexico and the US, and Bat Conservation International (Anonymous, 1994; Walker, 1995).

Disturbance and destruction of cave roosts in the past have caused immediate, mass catastrophe to populations in several important cave roosts. In recent years, conservation efforts have provided protection from the federal government, conservation organizations, and private land owners, by restricting entrance to important free-tailed bat cave roosts and through proper management of habitats surrounding the caves. Protected roosts include Carlsbad Caverns National Park, Bracken Cave (Bat Conservation International), James Rive Bat Cave (The Nature Conservancy of Texas), and Ney and Frio Caves (private land owners). Protection and management program are also in place in several important wintering cave roosts of *T. b. mexicana* in Mexico (Moreno, pers. comm.). Importantly, the protection and management of cave roosts and essential habitats depend on educating the public regarding the necessity and significance of the conservation of these bats.

Bats will continue to face the potential threat from insecticides, as long as insect pests continue to damage human agriculture and chemical pesticides are used in insect control. However, it is possible to reduce and regulate the usage of chemical pesticides in both quantity and the areas under exposure. The application of integrated pest management (IPM) at a larger spatiotemporal scale is an alternative to relying solely on conventional chemical pesticides, and this application has proved economically efficient and environmentally friendly (Johansen, 1985b; Pfadt, 1985b; Kogan et al., 1999). A properly designed IPM program integrate insect pests, plant species, other insects, predators of pests, weather factors, and different pest management tactics, such as biological, genetic, cultural, physical, and chemical control (Croft et al., 1984; Kogan et al., 1999). The application of integrated pest management can lessen the impact of pesticides not only on *T. b. mexicana*, but also on beneficial and non-target insects, and other vertebrates.

My data suggest that *T. b. mexicana* could have a significant role in insect pest management. Thus, estimation of their economic value to our society could play an important role in the conservation of *T. b. mexicana*. Nevertheless, the task of evaluating the economic value of *T. b. mexicana* in feeding on insects is more complex than identifying one or a few major pest species that are eaten. Indeed, it is very difficult to estimate the economic value of different insects to human society (Borror et al., 1989), and *T. b. mexicana* eat a variety of insects. While many of their prey families include agricultural pests, *T. b. mexicana* also prey on insect families in which many include members of predators or parasitoids of other insects, many of which are pests. These beneficial insects include braconids, carabids, chrysopids, formicids, hemerobiids, some muscoids, myrmeleontids, nabids, reduviids, syrphids, tachinids, all species of Odonata, and some ephemeropterans, plecopterans, and trichopterans (Borror et al., 1989; Merritt and Cummins, 1996). For a specific example, *Winthemia* *quadripustulata* (Fabr.), a species of fly in the Family Tachinidae, regularly parasitizes the larvae of *Helicoverpa* *zea* (Burkhardt, 1985). This family is a member of muscoid flies (Schizophora) that have been found in the diet of *T*. *b*. *mexicana*.

Some insects are agriculturally beneficial, but are destructive to humans in other respects, such as vectors of pathogens (e.g., assassin bugs as vectors of chagas disease). Many insects play an ecological role that is often ignored or the values of which are difficult to estimate, such as by scavenging or by destroying plants undesirable to humans. Insects that play these roles may be the same ones classified as destructive (e.g., callifords and chrysomelids; Borror et al., 1989). Furthermore, the distinction between beneficial and destructive or pest versus non-pest insect is often arbitrary and mostly from a specific economic point of view. Some similar species from the same family that have the almost identical ecological roles may be treated as pests, whereas others may be considered neutral or even beneficial. Good examples are the Colorado potato beetle (*Leptinotarsa* *decemlineata* (Say)), the dock beetle (*Gastrophysa* *cyanea* Melsheimer), and *Chrysolina* *quadrigemina* (Suffrian) (Rolston and McCoy, 1966). The first species defoliates the potato and is a pest; the second species defoliates dock which dose not interest humans, and therefore is not a pest; and finally the third species is introduced to control Klamath weed, a pest plant to ranchland. In evaluating the economic value of insect predation by *T*. *b*. *mexicana*, we also must recognize these conflicting values, and that these values may change. This complexity can make valuation of the role of these bats very difficult. However, researchers and conservationists should not be discouraged, and all efforts should still be spent in making the most realistic and closest valuation possible.

Populations decline and species become endangered or go extinct because of different proximate reasons, such as destruction of physical habitat, displacement by introduced species, alteration of habitat by chemical pollutants, hybridization with other species or subspecies, overharvesting, and natural catastrophes (Wilson, 1992). However, the ultimate cause of the loss of biodiversity is the continuously growing human population and our unrestricted and often unnecessary development, consumption, waste, and destruction of natural resources (Ehrlich, 1988). Conservation efforts may win a battle for some particular species, at some place and time; however, unless humans change their attitudes toward the nature and the current trend of human population growth slows down or stops, all efforts may eventually fail.

Education is the final hope. Individuals in every nation of the world should take any opportunity, and the mass media should be encouraged, to educate the public, politicians and government decision makers, and children at schools. We should do so through the understanding of principles of ecology, economic values of biodiversity to ourselves, human demography, and the consequences of overpopulation. Philosophical and religious thinking can be influential and helpful if applied properly. However, most importantly, it is the responsibility of the biologists to inform the public to recognize and appreciate every species' own value as a part of the chain of life through the evolutionary history of the earth. The earth cannot sustain a human population of over 6 billion as we now use and waste natural resources, without causing environmental problems and the loss of biodiversity. I believe that humans have the intelligence and capability to change the current situation and to prevent the conservation crisis from getting worse. The question is if most people would be willing to change. The answer to that question will be a determinant to the long term success of all our conservation efforts, including efforts for Mexican free-tailed bats.

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APPENDIX

Appendix I. Insect orders and families identified in trap collections from Uvalde areas, TX.

BLATTARIA
- Blattellidae (wood cockroaches)

COLEOPTERA
- Anthicidae (antlike flower beetles)
- Brentidae (brentid weevils)‡
- Carabidae (ground beetles)‡
- Cerambycidae (longhorned beetles)
- Chrysomelidae (leaf beetles)‡
- Cicindelidae (tiger beetles)
- Cleridae (checkered beetles)
- Coccinellidae (lady beetles)
- Curculionidae (weevils)‡
- Dytiscidae (predaceous diving beetles)‡*
- Elateridae (click beetles)
- Elmidae (riffle beetles)
- Haliplidae (crawling water beetles)*
- Hydrophilidae (water scavenger beetles)*
- Lampyridae (fireflies)
- Meloidae (blister beetles)
- Mordellidae (tumbling flower beetles)
- Phengodidae (glowworms)
- Scarabaeidae (scarab beetles)‡
- Scolytidae (bark beetles)‡
- Silphidae (carrion beetles)
- Staphylinidae (rove beetles)
- Tenebrionidae (darkling beetles)

DIPTERA
- Anthomyiidae (anthomyiid flies)
- Asilidae (robber flies)
- Calliphoridae (blow flies)
- Culicidae (mosquitoes)
- Dolichopodidae (longlegged flies)‡
- Drosophilidae (vinegar flies)‡
- Empididae (dance flies)
- Muscidae (house flies)
- Nematocera (other than culicids)
- Otitidae (otitid flies)
- Sarcophagidae (flesh flies)
- Stratiomyidae (soldier flies)
- Syrphidae (flower flies)‡
- Tabanidae (deer flies)
- Tachinidae (tachina flies)
- Tephritidae (fruit flies)‡

EPHEMEROPTERA‡*

HEMIPTERA
- Alydidae (alydid bugs)
- Belostomatidae (giant water bugs)*
- Berytidae (stilt bugs)
- Coreidae (coreid bugs)‡
- Corixidae (water boatmen)‡*

Appendix I. (continued)

- Cydnidae (burrower bugs)‡
- Hydrometridae (water measurers)*
- Lygaeidae (seed bugs)‡
- Miridae (plant bugs)‡
- Nabidae (damsel bugs)‡
- Notonectidae (back swimmers)*
- Pentatomidae (stink bugs)‡
- Reduviidae (assassin bugs)‡
- Saldidae (shore bugs)‡*
- Tingidae (lace bugs)‡
- Veliidae (broad-shoulded water striders)

HOMOPTERA

- Acanaloniidae (acanaloniid planthoppers)
- Aphidae (aphids)
- Cercopidae (spittlebugs)‡
- Cicadellidae (leaf hoppers)‡
- Cicadidae (cicadas)
- Cixiidae (cixiid planthoppers)‡
- Delphacidae (delphacid planthoppers)‡
- Flatidae (flatid planthoppers)‡
- Membracidae (treehooppers)

HYMENOPTERA

- Apidae (bumble bees and allies)
- Braconidae (braconids)‡
- Formicidae (ants)‡
- Halictidae (sweat bees)
- Ichneumonidae (ichneumons)
- Pompilidae (spider wasps)
- Siricidae (horntails)
- Sphecidae (sphecids)
- Tiphiidae (tiphiid wasps)
- Vespidae (hornets)

LEPIDOPTERA‡

- Arctiidae (tiger moths)
- Noctuidae (noctuids)
- Pyralidae (pyralid moths)
- Sphingidae (Sphinx moths)
- Yponomeutidae (ermine moths)

MANTODEA

- Mantidae (mantids)

MEGALOPTERA*

- Corydalidae (dobsonflies)

NEUROPTERA

- Ascalaphidae (owlflies)
- Chrysopidae (green lacewings)‡
- Hemerobiidae (brown lacewings)‡
- Myrmeleontidae (antlions)‡

ODONATA*

- Zygoptera (damselflies)‡

ORTHOPTERA

Appendix I. (continued)

- Acrididae (short-horned grasshoppers)‡
- Gryllidae (crickets)‡
- Tettigoniidae (katydids)

STREPSIPTERA
- Halictophagidae

TRICHOPTERA‡*
- Hydropsychidae (net-spinning caddisflies)
- Leptoceridae (long-horned caddisflies)
- Psychomyiidae (tube-making caddisflies)

Total: 15 orders and 92 families.

‡ Taxon that is also found in the diet of *T. b. mexicana*.

* Insect taxa that are considered aquatic, with almost all species having one or more aquatic stages, and adult forms are common around aquatic or semiaquatic environments (Borror et al., 1989; Arnett, 1993; Merritt and Cummins, 1996).

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