ROSS, Anthony, 1931–
ECOLOGICAL ASPECTS OF THE FOOD HABITS
OF SOME INSECTIVOROUS BATS.

University of Arizona, Ph.D., 1964
Zoology

University Microfilms, Inc., Ann Arbor, Michigan

ECOLOGICAL ASPECTS OF THE FOOD HABITS OF SOME INSECTIVOROUS BATS

by

Anthony Ross

A Dissertation Submitted to the Faculty of the

DEPARTMENT OF ZOOLOGY

In Partial Fulfillment of the Requirements
For the Degree of

DOCTOR OF PHILOSOPHY

In the Graduate College

THE UNIVERSITY OF ARIZONA

1964

THE UNIVERSITY OF ARIZONA

GRADUATE COLLEGE

I hereby recommend that this dissertation prepared under my direction by Anthony Ross

entitled Ecological Aspects of Food Habits of Some Insectivorous Bats.

be accepted as fulfilling the dissertation requirement of the degree of Doctor of Philosophy

E. Lendell Cockrum 5 May 1964

Dissertation Director Date

After inspection of the dissertation, the following members of the Final Examination Committee concur in its approval and recommend its acceptance:*

H K Gloyd May 4, 1964

Albert R Mead May 4, 1964

Floyd G. Werner May 4, 1964

L. C. Carruth May 4, 1964

*This approval and acceptance is contingent on the candidate's adequate performance and defense of this dissertation at the final oral examination. The inclusion of this sheet bound into the library copy of the dissertation is evidence of satisfactory performance at the final examination.

STATEMENT BY AUTHOR

This dissertation has been submitted in partial fulfillment of requirements for an advanced degree at The University of Arizona and is deposited in The University Library to be made available to borrowers under rules of the Library.

Brief quotations from this dissertation are allowable without special permission, provided that accurate acknowledgment of source is made. Requests for permission for extended quotation from or reproduction of this manuscript in whole or in part may be granted by the head of the major department or the Dean of the Graduate College when in his judgment the proposed use of the material is in the interests of scholarship. In all other instances, however, permission must be obtained from the author.

SIGNED: Anthony Ross

APPROVAL BY DISSERTATION DIRECTOR

This dissertation has been approved on the date shown below:

E. Lendell Cockrum

E. LENDELL COCKRUM
Professor of Zoology

5 May 1964
Date

ACKNOWLEDGMENT

First, I wish to express my deepest admiration for my major professor, Dr. E. L. Cockrum, for his guidance and consultation during the formative stages of this dissertation, and for partial financial support through his National Science Foundation Grant G-5209 (Biology of the Bats of the Southwest).

Secondly, I wish to thank the following persons who have, at various times during their stay at the University of Arizona (Tucson), been associated with me in various pursuits of this study: Thomas J. Cox (collecting of Molossid bats), Stephen P. Cross (collecting of Western pipistrelle bats), and Bruce J. Hayward (collecting of Cave and Allen's big-eared bats).

Finally, I wish to thank Clyde Jones (Department of Biology, University of New Mexico, Albuquerque) for presenting me with over two hundred and fifty digestive tracts of Hoary, Townsend's Big-eared, Allen's big-eared, Yellow, Red, Spotted, and Brazilian free-tailed bats.

TABLE OF CONTENTS

LIST OF TABLES

ABSTRACT

In this study observations were made pertaining to the food habits of seventeen species of insectivorous bats that are primarily inhabitants of the southwestern United States.

The types of insects used as food by these insectivores were determined by identifying insect remains obtained in three different ways: from digestive tracts (563 stomachs), from fecal pellets (of an undetermined number), and from insect fragments found under night roosts.

An attempt was made to correlate the prey selected by each species of bat studied with the prey's length, life form, type, ability to fly, nocturnal or crepuscular habits, and relative abundance. Echolocation in various bats is discussed in relation to hunting and food selection activities, and the role of competition in regard to the food habits of insectivores is considered.

It was found that most bats feed in a more or less defined size range of prey but many other factors are involved in the final selections.

Three methods for capturing of insects by these bats are discussed; the use of vision for detecting ground

and vegetation-dwelling prey, filter feeding on dense flights of crepuscular insects, and individual pursuit of a prey by echolocation.

INTRODUCTION

"It is common knowledge that bats eat insects, but there appears to have been little effort directed towards determining what these insects are" (Hamilton, 1933).

Bats, as a group, have a wide diversity of diets and may be thought of as carnivores in the strict sense (that is, feeding on other bats, rats, reptiles, and other animals), sanguivores, piscivores, insectivores, nectarivores, frugivores, and as omnivores. These designations represent only their general food habits and some appear to fall into two or more categories. This dissertation, for the most part, will consider only insectivorous bats.

It is tremendously impressive to see large numbers of bats, often in millions, occupying one roost. Such a situation is found in a large maternity colony near Morenci (Greenlee County, Arizona). The colony has been estimated by mammalogists to consist of between five and twenty million individuals of *Tadarida brasiliensis*, and is probably one of the largest colonies of these bats in North America (Ross, 1961a). At the same time one can not but be impressed by the abundance of insects, too. There is a tremendous number of species of insects, at least 800,000.

The population density that can be attained by some of these species is exemplified by grasshoppers. Some grasshopper infestations are reported to have covered 15,000 acres and, in the infested areas, the grasshoppers were so numerous that they consumed the crops of the region in seven or eight hours (Frost, 1959).

Presumably bats help regulate the numbers of some species of insects, but it is unlikely that bats are ever reducing factors, destroying the individuals of the population at a greater rate than they are being replaced. Nelson expressed this succinctly as follows: "Nearly all of the bats of North America north of the Tropics consume vast quantities of insects, but apparently do not exterminate any."

One can usually obtain the following data from an analysis of food items within a predator's digestive tract: the relative size of prey, whether flying or ground dwelling prey, the number of insects eaten, and the species of prey. Armed with this type of information one may then learn more about the feeding methods of the insectivore without direct observations. From species determination and knowledge of the habits of these insects, inferences may be drawn as to the feeding behavior of bats.

Fragmentation of the food by the bat made the effort to identify prey species at generic, specific, or subspecific levels unprofitable, if not impossible. Moreover, determination at this level would usually contribute little to the general elucidation of the feeding habits of the bat. Most important, from the standpoint of prey selection, appear to be whether life form, relative size, capability of flight, or other habit of the prey species are the determining factors in food selection. The contents of the digestive tracts of insectivores that have been collected over many months and over most of their range strongly indicates the insects that are being selected. After determining the size range and type of prey taken, generalizations may be made about the food habits of a particular species. At the same time one can not help being concerned as to why the predator does not make use of the other available insects in the same habitat and of similar size, life form, and habits. There are many causes for rejection of prey, such as wrong or offensive odor, too much water or fluid, too thick an exoskeleton, foul taste, or possibly markings that have a deterring psychological effect.

METHODS AND PRESERVATION

Food habits of various types of animals may be demonstrated by four methods: (1) direct observation, (2) contents of digestive tracts, (3) inspection of culled food parts, and (4) fecal or waste material. However, the following discussion is restricted to the application of these methods to nocturnal insectivores.

(1) By direct observations. For most nocturnal, flying raptors (ones that prey upon other animals) this can not at this time be attained.

(2) By examination of contents of digestive tracts. Although the prey may undergo considerable chewing by predators, requiring many long hours of restoration of the fragmented prey by the student, it is usually still identifiable; at least, to the ordinal level. This is due, in great part, to the indestructible nature of the chitinized exoskeleton of the arthropods that are usually recovered. Chitin is an aminopolysaccharide that, as far as can be determined, does not respond to the digestive enzymes of any vertebrate. As a matter of fact, the only natural decomposing agent reported for chitin is Bacillus chitinovorus (Snodgrass, 1935). It is true that the shape of the swallowed insect may be greatly altered (Koersueld, 1950); yet, the taxonomically important structures, invariably of a

chitinous nature, are usually still present and may be utilized for determination, even in their badly distorted condition, at least to the ordinal level.

The greater bulk of the material analyzed in this study was in the form of digestive tracts with contents intact. It is desirable to have digestive tracts preserved intact in not less than 70 per cent alcohol, using a greater volume of alcohol than that of the tract. One reason for preserving them intact is that, in many instances, one may determine the feeding times and periods by the relative fullness of the stomach, if the time of capture of the raptor has been noted. Also, keeping the digestive tract intact prevents the loss of small insect parts and serves to indicate the order of prey feeding, since the particles of a fragmented insect tend to remain together. The practice of drying the contents of digestive tracts is not recommended, especially if they are to be stored. One of the disadvantages of working with dried material (whether the digestive tract is intact or not) is that dermestid larvae (notorious museum pests) will feed on the dried insect-prey, reducing the hard parts to dust. With dried material there is also increased difficulty of unfolding various parts, such as wings of moths and flies. For best results dried material must be soaked for several weeks before one can work with it.

Of course, the predator should be killed immediately upon capture, preventing further elimination of undigested food-items.

To obtain information on feeding habits it is best to have a rough approximation of the feeding periods of the raptor so as to insure collecting them when the digestive tracts contain prey. For example, digestive tracts of bats secured during the day have little value for the stomachs usually are empty.

(3) By examination of culled food parts. Pallid and Leaf-nosed bats have the habit of feeding on large insects and eating chiefly only their abdomens. The remaining parts are dropped to the ground under their night roost (a retreat that is used primarily for nocturnal activities such as feeding). This habit has been noted for the Pallid bat especially by Dixon (1925) Borell (1942) and Ross (1961b). The parts beneath the roosts consist of head capsules, thoracic segments, legs and wings of the hard-bodied insects; wings and legs of the soft-bodied insects; and, in many cases, the wings only of large lepidopterous insects. Because of this habit species level determinations of prey are easily possible for such bats. However, some raptors cull parts from their prey while they are in flight; thus these parts are scattered over the countryside and lost.

(4) By the examination of fecal matter or waste material (e.g., owl pellets). Examinations of fecal matter

or waste materials are the least desirable type of food habit analyses, mainly because of the possibility of the contamination of the sample by wastes of other species of animals. This is particularly true if some other predator species forms pellets or scats of a similar structure or shape. Because of this factor the study of fecal pellets was avoided whenever possible.

However, when utilized, the examination of bat guano was greatly facilitated by the immersion of the fecal pellets in a solution of Photo-Flo and water to soften them (Ross, 1961b).

The taxonomic level to which insect remains from digestive tracts and pellets of a bat can be determined depends upon the type of insect taken, how thoroughly the bat chews, and how much of the insect is actually ingested. There is actually little difference as to the level of determination of an insect-prey whether it is recovered from digestive tract or a pellet. The degree of chewing is the main factor that influences the extent of prey identification. Insectivorous bats, as a group, chew their prey into smaller pieces than do most other insectivores. In contrast, insectivorous reptiles usually swallow their prey intact. Birds, on the other hand, appear to be intermediate in that sometimes they may fragment the prey, but never to the degree bats do. Birds do tend to flatten (and thereby elongate) soft prey (such as lepidopterous larvae) to the extent that one can not accept the measurements as indicative of their size in life.

The insectivorous bats utilized for this study were either (1) obtained by shooting over feeding grounds or in night roosts, or (2) captured by the use of mist nets (fine Japanese bird nets) over water. In the summer months in arid parts of the southwest man-made relatively permanent pools (often less than twenty feet across) are utilized by bats of the region as a source of water. Mist nets are especially useful for capturing larger molossids (_e.g._, _Eumops_) because of the lateness of their flight and paucity of known roosts. One may obtain an estimate of raptor species of an area by noting what is collected in mist nets. One of the better sites to observe the diverse types of insectivorous animals such as bats, nighthawks, and owls feeding in the same general area, but not necessarily at the same niche, is at a watering place.

A concerted effort was made to obtain digestive tracts, pellets, and droppings of insectivorous bats from different localities, different times during the night, and different times of the year. This was done because even a large number of digestive tracts from the same locality and same time of night would offer little help in determining the spectrum of an insectivore's food habit; it would be far better to have only one stomach each for many different nights and from many different localities. This spaced sampling allows for insect "turnover." That is, insects vary in number, species (adult forms), with season of year and even time of night; therefore the samples will vary.

When bats are captured for biological or taxonomical purposes, especially if this is done during the bat's feeding periods, it would be helpful to future investigators if their digestive tracts could be saved.

Contents of digestive tracts, guano, and insect fragments found beneath night roosts, were analyzed using a dissecting microscope. The particular microscope used had graduations of magnifications from a low of 7 to a high of 90X. The individual stomach was placed in a Syracuse watch glass and covered with 75 per cent alcohol. Usually an incision was made in the stomach wall and, by means of two fine jeweler's forceps, the insect remains were teased out.

Obtaining a determination of the type of insect on which a bat was feeding required a great deal of searching and placing together of fragments. These remains were mounted on one or more slides; they included such fragmented parts as wings, tarsi, legs, head capsules, and antennae. The medium used for mounting these parts on slides was "P.V.A." [polyvinyl alcohol] (Baker and Wharton, 1959, p. 10). Slides were made and kept until a composite picture of the insect was made and a reliable determination was established. Of course, many slides of unidentifiable fragments were made.

Determinations were made by means of taxonomic keys, by "picture-matching," and by matching the restored insect with known, determined museum specimens. The procedure used was dictated by the condition of the remains.

In this study, the following materials, pertaining to 17 species of insectivorous bats, were examined:

Macrotus californicus, California leaf-nosed bat: 41 digestive tracts, and insect remains dropped below night roosts. Collected in Arizona and Mexico.

Myotis velifer, Cave bat: 14 tracts. Arizona and Mexico.

Pipistrellus hesperus, Western pipistrelle: 130 tracts. Arizona.

Pipistrellus subflavus, Eastern pipistrelle: 1 tract. Indiana.

Lasiurus borealis, Red bat: guano; 25 tracts. California, Illinois, Indiana and New Mexico.

Lasiurus cinereus, Hoary bat: 139 tracts. Arizona and New Mexico.

Lasiurus ega, Yellow bat: 6 tracts. New Mexico and Mexico.

Nycticeius humeralis, Evening bat: 2 tracts. Indiana.

Euderma maculatum, Spotted bat: guano; 5 tracts. New Mexico.

Plecotus townsendi, Townsend's big-eared bat, 38 tracts. Arizona and New Mexico.

Plecotus phyllotis, Allen big-eared bat: guano; 25 tracts. New Mexico.

Antrozous pallidus, Pallid bat: guano; 22 tracts; and insect remains dropped below night roosts. Arizona.

Tadarida brasiliensis, Brazilian free-tailed bat: "ancient" guano; 91 tracts. Arizona, New Mexico and Mexico.

Tadarida femorosacca, Pocketed free-tailed bat: 2 tracts. Arizona.

Tadarida molossa, Big free-tailed bat: 1 tract. Arizona.

Eumops perotis, Greater mastiff bat: guano; 13 tracts. Arizona.

Eumops underwoodi, Underwood's mastiff bat: 6 tracts. Arizona.

FOOD HABITS OF INSECTIVOROUS BATS

"From this blanket of vegetation over the river valley, rise countless millions of insects, which provide food for the bats" (Stager, 1939).

"Campbell (1913) states definitely that bats will eat pieces out of hams and bacon left in smoke houses; I know of no other reference to such a habit, outside of nursery rhymes" (Grinnell, 1918).

In noting the food-items taken by raptors many writers try to connote their food values to the readers; however, this is not easily, if at all attainable. One could say "50 leafhoppers are equal to a medium-size grasshopper." This is not true, especially if weight is taken into consideration, for some forms have a heavier exoskeleton than others and there is no apparent food-value in chitin for raptors. Certain large beetles (with a heavy exoskeleton, too) are almost living "hollow shells," with very little digestible soft material.

Then, how does one compare, a 100 mm (length) by 4 mm (diameter) stringy "walking stick" with a juicy, rotund 25 mm (length) by 12 mm (diameter) Jerusalem cricket? Dice (1925) pointed out, "Even when the numbers of the several kinds of food individuals eaten can be accurately estimated, it will be misleading to compare food species which differ considerably in size." Even more, I suspect that it is misleading to compare kinds of insects even when they do not vary considerably in size. In fact, there are examples of similarly sized organisms, such as a worker ant and a winged reproductive ant (queen), in which one, the queen, contains a great amount of stored food that can not be equated with that of the other. There is no practical way in which the food value of the prey taken can be noted or stated; one may only make approximations, for what they are worth.

As I can not readily accept or contrive any method to show comparative food values, I have not utilized any bulk or volume measuring device. I have simply listed the number and kinds of insects encountered by (number of) digestive tract(s), or listed them as percentages of the total food-items. This last method was used in the analysis of insect parts dropped below the night roost (see Pallid bat).

In one bat (Western pipistrelle) the number of individuals of a given type of insect was not determined as they were too numerous to count. In this case, the relative frequency of a given prey species is expressed in terms of a percentage of the total size of the "food-ball." The greatly extended stomachs in this case would contain about fifty insects.

Although McAtee (1912) stated the following principle for birds, the general concept has wide application.

"The principal objection to the method of reckoning the contents of bird stomachs solely by the number of individual insects or seeds, is that the method takes no account of size of the objects, and hence conveys no idea to those unacquainted with the groups concerned of the relative importance of the food elements."

I have tried in varying degrees, to interpret the value of different types of prey but it will be up to the judgment of the reader to render the final interpretation.

In captivity bats have often been exposed to, and sometimes have accepted unusual food items. Engler (1943) fed two Western Skinks (<u>Eumeces skiltonianus</u>) and one Sonoran Desert Gecko (<u>Coleonyx variegatus</u>) to captive Pallid bats. He suggested that Pallid bats in nature also feed on lizards but there is no evidence to support this view. Stager (1939) fed beef heart and liver to the Cave bat. Further, Stager noted "cannibalism" in these bats. They apparently fed on two Leaf-nosed bats that were forced to share the same cage with them. Bishop (1947) and Krutzsch (1950) also report cannibalism in bats. Gates (1936) in keeping bats in captivity utilized a diet that did not include any of natural insect foods; but consisted of a mixture of bread, hard-boiled egg, cream cheese, and buttermilk. For other unusual foods see Klugh (1924), Sherman

(1930), Mathias and Sequela (1940), Ramage (1947), and Constatine (1952).

I have considered all of these food-items as "factitious prey." Briefly, factitious prey comprise organisms (or parts thereof) that are not selected or available to bats in nature, but that will be taken as food in captivity. Such factitious prey include fly pupae, small flies, mosquitoes, mealworms, beef hearts, and various lizards.

In the following discussion each species of bat will be taken up by phylogenetic ranking regardless of its food habits.

Macrotus californicus, California leaf-nosed bat.

The Leaf-nosed bat is active in Arizona throughout the greater part of the year. Southern Arizona appears to be at the northern fringe of its activity during the colder seasons of the year. During the very cold months (December to February), apparently, it feeds only during the evening period (feeding time not extending much past midnight).

The examination of contents of the stomach of this bat is not particularily fruitful as it is one that feeds primarily on the abdomens of the larger night-flying insects (size range, on the average, of 40 to 60 mm). However, an inspection of the stomach contents did indicate that these bats to a minor degree fed on lepidopterous larvae and small prey (about 20 mm in length) such as short-horned grasshoppers (Acrididae) and June beetles (Scarabaeidae). More startling is the fact that contents of the stomachs indicate that these bats are plant feeders too.

Observations of the insect remains found beneath the night roosts show that these insectivores captured and fed on tremendous quantities of larger insects such as short-horned desert grasshoppers (Acrididae, Trimerotropis sp.), long-horned grasshoppers (Tettigoniidae, Microcentrum californicus, Schistocerca vaga and other species), long-horned beetles (Cerambycidae, Derobrachus geminatus), sphingid and owlet moths (Sphingidae, Celerio lineata, Phalaenidae, Catocala sp.).

This bat has been reported as an insectivorous species by J. Grinnell (1914), H. W. Grinnell (1918), Howell (1920), Huey (1925), Stager (1943), and Vaughan (1959); and as a fruit-eating form by Burt (1938). The insect prey utilized tends generally to consist of large night-flying insects, including moths, grasshoppers, katydids, flies, beetles, cicadas, butterflies, dragonflies, and flying ants. Grinnell (1918) noted the following species of insects: June beetles (Scarabaeidae), Ligyrus gibbosus and Polyphylla decemlineate; ground beetles (Carabidae), Chlaenius sericeus. Huey (1925) reported Schistocerca, Trimerotropis [short-horned grasshoppers], Celerio lineata, Smerinthus cerisyi [sphingid moths], *Peridroma margaritosa* [owlet moth], cossid moth, *Cicada* (harvest fly), and a genus of Meloidae [blister beetle].

Huey (1925) thought that the bats took the foregoing presumed diurnal insects (grasshoppers and harvest fly) from their nocturnal resting places on willow trees and, in many cases, carried the prey back to the roost. His reason for supposing that these insects were resting on willow trees was obviously based only on finding some willow leaves "in the bottom of" the roost. He actually states that the insects were picked off their resting places on the leaves (presumably along with the leaves). It has never been shown that either these grasshoppers or their predators have any direct ecological association with willow trees. Further, the grasshoppers listed are very active at night and must be considered nocturnal forms; most certainly they can be captured in flight during the night. However, the Leaf-nosed bat does carry its larger prey, such as sphingid moths (*Celerio lineata*), gray bird locusts (*Schistocerca vaga*), and Palo Verde borer beetles (*Derobrachus geminatus*), back to a night roost.

Vaughan (1959) also states, "Some insects regularly eaten by *Macrotus* are almost certainly taken from the ground or from vegetation." In support of this statement he offers four main points:

(1) A food list. This list indicated that *Macrotus* feed on orthopteran insects, noctuid [=owlet] moths,

caterpillars, and beetles (Scarabaeidae and Carabidae). Then Vaughan goes on to say that the list of food items of Macrotus contains a preponderance of insects that either seldom fly, are flightless, or that fly in the daytime; and that this constitutes strong evidence supporting the view that this bat takes mostly insects that are either on the ground or on vegetation.

Unfortunately, Vaughan's list does not give generic determinations but most of the names listed appear to be similar to the more specific listings of Grinnell (1918) and Huey (1925), with the notable exception of lepidopterous larvae (caterpillars). Further, most of those listed by Huey are not diurnal, but are flying nocturnal forms. Other than the larval forms recovered from bat stomachs by Vaughan, the published listings of diurnal forms are based on reports of finding fragments on the ground beneath night roosts: "wings of several diurnal butterflies" (Howell, 1920) and "butterflies and dragonflies" (Vaughan, 1959). Such findings beneath night roosts, of course, offer no real association of presumed prey and bats.

(2) Huey's paper of 1925.

(3) Grinnell's isolated report (1918) that in 1908 C. H. Richardson found a female Leaf-nosed bat in a mouse-trap.

(4) Stager's (1934) report of a bat impaled on a desert shrub. Stager suggests that the bat may have become impaled while attempting to secure an insect on the shrub. If the

bat did indeed become impaled while foraging, it could just as well have been due to the animal's attempt to feed directly on the plant, a type of feeding to be discussed below. Also, I have seen Free-tailed bats impaled on spiny plants, obviously not while in the act of searching for food.

I, too, recovered three well-chewed lepidopterous larvae (unidentifiable) from one of 41 stomachs examined. Therefore, Huey and Vaughan are essentially correct in their conclusions, although their strongly worded assertions were, for the most part, based on faulty observations. I would suggest that Macrotus do occasionally take flightless insects from vegetation, probably without actively searching for them and, perhaps even while feeding directly on the plants. No truly ground dwelling forms of insects were found in any of the digestive tracts examined.

Vaughan (1959) states "Leaf-nosed bats seem to be totally insectivorous, and their food clearly reflects the bats' foraging habits." This is based on an unspecified number of stomachs that he collected in the summers of 1953 and 1954 in the Riverside Mountains, California.

However, Burt had previously (1938) reported that this species, besides feeding on insects, is also a fruit-eating form. This statement was based on examinations of stomach contents of bats taken in Sonora, Mexico. Both Grinnell (1918) and Allen (1939) reported this genus to be a transitional feeding group. Allen quotes Osburn's discussion that they [Otopterus (=Macrotus) in Jamaica] feed on Orthoptera, certain berries of breadnut, roseapple, and fustic. In personal communications both Alfred L. Gardner and Gordon VR. Bradshaw, mentioned that this species (M. californicus) feeds on various cactus fruits and Alfred Gardner observed them as they fed on pitahaya [or organpipe cactus] fruit (Lemaireocereus thruberi) at Bahia San Carlos, Sonora, Mexico.

From the analysis of digestive tract I found support for the contention that M. californicus has an omnivorous appetite. I have noted stomachs varying, in contents, from purely insect to purely vegetable. In the winter months I have even recovered what appear to be the green vegetative parts of plants. There appears to be no cycle to this variable diet, and certainly, it does not appear to depend on the relative abundance of the food items. One can find in the same sample of stomachs (taken at the same time and place) some that are filled with insects, while others are filled with fruit.

Although, I have previously stated that M. californicus preys on large (40 to 60 mm) night-flying insects, this must be considered a broad generalization. They also feed on smaller forms of flying grasshoppers, beetles and antlions, some as small as 20 mm, as well as foods of plant origin. Therefore, this bat can not be readily classified as to types of food or size of prey. This condition may well be correlated with the omnivorous food habits of Macrotus.

I reported in 1961(b) finding the head of an ant (Camponotus) embedded in the angle of a Leaf-nosed bat's mouth. The area of embedding suggests that the bat was feeding on the flying ant when it was bitten. Therefore, I suspect that these bats are also opportunistic in feeding, at least on flying ants. That ant jaws can be found on bats is explained by the fact that wounds were once stitched by the use of various species of ants. Apparently, if after the ant takes hold, all but the head is excised the mandibles will not release their grip (Gudger, 1925). This phenomenon probably accounts for the findings of embedded ant heads on bats.

Myotis velifer, Cave bat.

The Arizona populations of Cave bats are not usually residents in the state throughout the year. Before winter, most apparently migrate southward into Mexico, apparently to hibernate there.

Only fourteen digestive tracts from these animals were examined. One bat, taken from a hibernal in January, had a completely empty tract; so, for all practical purposes, only thirteen tracts were examined. The contents of these few stomachs indicated a trend of food preferences.

Although there appears to be little uniformity in prey selection as to type or size, most of the stomachs contained microlepidopterous insects of forms <u>circa</u> 10 mm in length.

Insect prey were taken in the following amounts: MOTHS (microlepidoptera) - 11 bats (1, 3, 4, 4, 5, 5, 6, 7, 10, 12, 14); BEETLES (Coleoptera) - leaf beetles (Chrysomelidae, 5 mm), 2 bats (1, 2), comb-clawed beetle (Alleculidae, 13 mm), 1 bat (1), long-horned beetle (Cerambycidae, 8 mm), 1 bat (1), June beetles (Scarabaeidae, <u>Phyllophaga</u>, 12 mm), 4 bats (1, 6, 10, 12), weevils (Curculionidae, <u>Colecercus</u>, 4 mm), 5 bats (6, 12, 13, 13, 14); FLY (Diptera, 7 mm) - 1 bat (1); ANTLIONS (Neuroptera, Myrmeleontidae, <u>Hesperoleon</u>, 25 mm) - 2 bats (1, 1).

The presence of weevils strongly indicates opportunistic feeding, as they were found only in the five animals taken at different times of the same night and location. All other samples were collected at more widely spaced intervals and localities.

In spite of the large number of coleopterous insects in the stomachs in these analyses, I consider the Cave bats to be primarily feeders on lepidopterous insects. All of the weevils were of the same species and probably were swarming at the period when taken. These weevils maintain a high density in the air only for a very short period.

Further, five of the stomachs primarily contained moths, and only two were filled with June beetles.

Pipistrellus hesperus, Western pipistrelle.

The Western pipistrelle is the smallest bat in the continental United States. It does not normally occur in colonies or caves; rather it roosts solitarily in rocky areas, usually in canyons. Pipistrelles are sometimes called Evening bats, for they are often seen flying overhead at twilight. The pipistrelle is one of the few insectivorous bats adapted to hunting in this still somewhat daylight period. In Arizona, at least, this species is active the greater part of the year.

In order to observe seasonal variation in prey selection, 91 digestive tracts of Pipistrelles taken in the vicinity of Tucson were examined and tabulated on a monthly basis (Table 1). However, although these bats were taken from the same locality, this does not necessarily mean that all were utilizing the same feeding ground.

As seen in Table 1, three groups of insects furnish the majority of the prey; leafhoppers, flying ants, and microlepidoptera (4 to 10 mm). Beetles are taken, but never to the extent noted for the other forms.

In Table 1 the leafhoppers are mainly of the genus *Draeculacephala* (4 mm), while the flying ants (Formicidae) are of the genera *Acromyrmex* (8 mm), *Neivamyrmex* (10 mm), *Camponotus* (8 mm), and *Formica* (6 mm). The pea weevils (Mylabridae) are of the genus *Callosobruchus*. The leaf beetles (Chrysomelidae) included the genus *Disonycha*. The ant-like flower beetles (Anthicidae) were primarily of the genus *Anthicus*. Sepsid scavenger flies were of the genus *Pandora*.

Only Bailey (1905, 1936) and Davis (1960) allude to the food habits of the Western pipistrelles and they note only that these bats were almost invariably stuffed with a well masticated mass of small insects.

E. L. Cockrum in personal communication reported that he observed *Myotis californicus*, *Myotis subulatus*, *Myotis volans* and *Pipistrellus hesperus* feeding together. These bats were capturing flies that were emerging from manure around a stable at the Southwest Research Station (Portal, Arizona) in November, 1958.

As a broad generalization, microlepidoptera (moths) are the main staple food in winter and leafhoppers during the spring. During and shortly after the summer rains, flying ants are utilized in great numbers. In its ability to seek out and feed on the swarming ants this bat is truly the most amazing of all raptors that I have observed. Probably this bat, of all bats in the region, is most adapted to feeding wholly, night after night, on opportunistic prey, such as flying ants. After the season for swarming ants has passed, however, it returns to feeding on leafhoppers.

Table 1. Types and percentages of insects taken throughout the year by Western pipistrelle in the vicinity of Tucson, Arizona.

The numbers at the top of the table under their respective months indicate the totals of bats examined in that month. In the column under each month are the percentages of insects found in a digestive tract. The number preceding the percentage represents the number of tracts containing this type of prey (number of tracts - per cent). The percentages used in this study indicate the relative proportion of that insect in a bat's stomach and not a definite number. For example, an entry of 50 per cent Homoptera and 50 per cent Coleoptera, would indicate that each of these two forms contributed half of the food ball; by actual count, however, there might have been only five beetles and as many as 50 true bugs for in many cases the actual count per stomach was too time consuming to make.

TYPES OF INSECTS

months # bats	Jan. 3	Feb. 10	Mar. 9	Apr. 2	May 7	June 10	July 9	Aug. 8	Sep. 13	Oct. 10	Nov. 8	Dec. 2
Hemiptera			1- 1						1- 1	unidentifiable		
Miridae		3- 3	1- 2		1- 1	2- 2						
Neididae									1- 1			
Homoptera	1-17	2- 3	1- 7			1- 3	1- 2			unidentifiable		
Cicadellidae		2- 7	5-34	2-33	6-62	7-24	2- 5	3-13	8-44	9-72	8-59	2-25
Coleoptera	2-33	4-10	1- 1		2- 3	3-11	2- 2		2- 4	unidentifiable		
Staphylinidae					1- 3	1- 1						
Cleridae					1- 3							
Nitidulidae						1- 5					1- 2	
Anthicidae				1- 7		1- 2	1- 3	3-13				
Scarabaeidae			1- 1			4-11		2-10	2- 5			
Chrysomelidae			1- 2	1- 8	4- 9	5-10	2- 7	5-20	2- 5		4-20	
Mylabridae					1- 4							
Apionidae						1- 1						
Curculionidae											1- 3	
Trichoptera		1- 1										
Lepidoptera	2-50	9-55	6-35	2-32	4- 7	4- 5	2- 7	3- 8	6-13	3-16	4-16	2-75
Diptera		4-14		1-10	1- 3	1- 1	1- 1	2- 5		unidentifiable		
Psychodidae											1- 3	
Chironomidae			2-11								1- 3	
Mycetophilidae										1- 1		
Sepsidae					1- 1						1- 1	
Drosophilidae			2- 6	1-10	1- 1	1- 2					1- 3	
Agromyzidae										2- 9		
Hymenoptera		1- 1			1- 3					unidentifiable		
Braconidae		2- 6				1- 2			1- 1			
Chalcidoidea						1- 1						
Formicidae						3-19	8-73	3-31	6-26	1- 2		
TOTAL	100%	100%	100%	100%	100%	100%	100%	100%	100%	100%	100%	100%

Although not listed in Table 1, a few years ago I examined the contents of the stomach of a Pipistrelle shot during February while foraging over a creek. This stomach contained numerous small crepuscular nematocerous dipterans. Among these flies were approximately 13 mosquitoes (Culicidae, Aedes). The pipistrelle, a small bat, might perhaps be able to maintain itself on mosquitoes. However, mosquitoes have not been encountered in later studies of the contents of digestive tracts of this or of any other species.

A few times when specimens were collected by shooting they were found to have head capsules and other insect remains still clinging near the mouth (Stephen Cross, personal communication). From stomach analyses it appears that, for some of the insects ingested, the head capsules and wings were not taken in. The condition appeared to be more prevalent in the morning feedings that involve individual pursuit of insects. For example, in no tract did I ever encounter the entire wings of a moth. This factor, alone, made impossible the identification of the microlepidopterans below the ordinal level.

In general, the sample sizes shown in Table 2 are small, but there are observable trends for the month of August. Very noticeable in two stomachs are the high percentages of dipterous insects (probably snipe flies, Rhagionidae; also drosphilids). Some of the bats were collected near a reservoir in the oak zone of the Galiuro Mountains (Graham County, Arizona). It seems that these bats sometimes select bodies of water over which they forage. Redington Road is northeast of Tucson, and the particular collecting locality is in the Upper Sonoran Life-zone. The Tucson and Twin Windmills (4.5 miles southeast of Kingman, Mohave County, Arizona) localities are quite similar ecologically, both essentially Lower Sonoran. This appears to be reflected in the prey selection shown in Table 2.

The remaining 15 stomachs, of the original 131, were either empty or did not yield additional determinations.

Since the insect prey is chewed quite thoroughly, the condition of the bat's teeth becomes important in an analysis of this nature. That is, if the teeth are greatly worn, the bat can not break up the insect as finely. Therefore, in stomachs from individuals with greatly worn teeth a more exact level of identification usually can be made. However, the insect remains are usually quite small fragments, that, looked at individually without any attempt to reconstruct the insect, are of little value. When a given bat feeds on an insect that is outside its normal prey size range, whether larger or smaller, the insect is poorly chewed. Apparently when the insect is "more than a mouthful" or undersized (and hence swallowed whole), normal mastication does not occur.

Table 2. Types of insects taken by Western pipistrelles at four different Arizona localities in the month of August.

Localities	North Tucson	Twin Windmills	Redington Road	Galiuro Mts.
Number of bats	8	15	5	4
INSECT PREY				
Homoptera				1- 6*
Cicadellidae	3-13	2- 4		
Coleoptera		4-16*		3-31*
Staphylinidae		2- 2		
Anthicidae	3-13	1- 1		
Scarabaeidae	2-10	6-12		1- 5
Chrysomelidae	5-20	10-24		
Lepidoptera	3- 8*	7-15*		1- 1*
Diptera	2- 5*	2- 2*		2-38*
Drosophilidae				1-19
Hymenoptera				
Formicidae	3-31	4-21	5-100	
TOTAL	100%	100%	100%	100%

* = unidentifiable

In the early evening the pipistrelle utilizes the dense crepuscular flight activity and swarming of many types of insects in order to readily obtain a stomach full. During the morning feeding, when the flights of insects are not as dense, it seems to select prey types more by individual pursuits.

When pipistrelles encounter large dense crepuscular flights of insects (such as leafhoppers) they appear to "filter feed". Filter feeding is a type of capture of insects that does not involve the pursuit of each individual. In this feeding the bat (with its mouth open) flies through a dense flight of small insects engulfing its victims by chance. Probably the bats echolocate in order to detect such flights, but it would seem hardly worthwhile to echolocate in pursuit of individual prey. Their stomach contents do not indicate random pursuit of individual prey, as the food ball contains pure "veins" of various types of insects. That is, if the food ball contains moths and leafhoppers, these are packed separately, not mixed as one might expect with random pursuit. The insect remains in the stomachs show that they have been captured from all angles (from the front, the sides, and the rear) as indicated by the teeth marks found on the bodies. One would expect more of a pattern (that is, consistently taken from the rear) to the capture of these insects if the bats were engaging in solitary pursuits.

These bats will feed on flying insects ranging in size from less than 1 mm up to 15 mm (the latter size estimated from insect fragments found in a few stomachs). However, the majority of the feeding occurs on insects in the size range of from 4 to 10 mm.

In general, the Western pipistrelles feed on crepuscular flying insects (e.g., leafhopper) and small nocturnal moths, but also indulge in opportunistic feeding on swarming insects such as flying ants. They usually feed within a size range of 4 to 10 mm, and with an average of 5 mm.

Pipistrellus subflavus, Eastern pipistrelle.

Although the Eastern pipistrelle is represented in this study only by a single stomach, the contents are interesting enough to be included. This stomach was sent to me by R. E. Mumford (Purdue University, Indiana).

I found the stomach content of this bat to be 80 per cent leafhoppers (Homoptera, Cicadellidae) and 20 per cent flying ants (Hymenoptera, Formicidae). This food selection is remarkably similar, both in types and sizes, to that of the Western pipistrelle.

Hamilton has noted (1930) that the Eastern pipistrelle can fill itself, in nature, within 15 to 20 minutes with small dipterous and coleopterous insects. Sherman recorded (1940) that it fed on Diptera, Anthomyiidae (flies), and Hymenoptera (Formicinae: winged reproductive ants).

Lasiurus borealis, Red bat.

Bats of this migratory species utilize trees for their day roosts.

The stomach contents of 21 of these bats were sent to me in individual vials by R. E. Mumford. They had been collected in 1958 (July to August) from various localities, primarily in Indiana.

The following insects were involved: TRUE BUGS (Homoptera) - 1 bat (1), leafhoppers (Cicadellidae), 2 bats (4, 6), spittlebugs (Cercopidae, primarily Philaenus pumaria, 6 mm), 15 bats (6, 10, 20, 30, 30, 40, 50, 50, 52, 53, 54, 54, 55, 56, 60); BEETLES (Coleoptera) - 4 bats (1, 2, 3, 3), ant-like flower beetles (Anthicidae), 1 bat (1), June beetles (Scarabaeidae), 2 bats (1, 1), leaf beetles (Chrysomelidae), 1 bat (2); MOTHS (Lepidoptera) - 2 bats (3, 4); FLIES (Diptera) - 2 bats (3, 4), near Pomace flies (Drosophilidae), 1 bat (4); FLYING ANTS (Hymenoptera, Formicidae) - 5 bats (1, 1, 6, 6, 21).

Lewis (1940) observed that, in Virginia, these bats feed on Angoumois grain-moths occurring over cribs containing old corn. Gould (1955) reports that Red bats actively feed on moths (among them the adult army worms, Pseudaletia unipuncta), beetles and other insects attracted to lights.

These feeding records are apparently based on sight observations.

Red bats appear to have food habits similar to those of the Pipistrelles in that they, too, actively search out and devour numerous crepuscular flying true bugs. At least in Indiana, spittlebugs appear to be the mainstay of their diet. These spittlebugs appear to be widespread and are considered an agricultural pest. Little is known of their habits but apparently like the Red bat, they are also migratory.

In an earlier paper (1961b) I reported on an analysis of guano from Red bats collected in California and gave: Orthoptera 30 per cent, Coleoptera 1 per cent, and Lepidoptera 60 per cent. Further, I noted "This bat appears to feed on small moths (mostly 10 to 16 mm in length), but takes other insects occasionally (some as large as 30 mm in length)." This determination was based on 10 pellets. More recently I examined four full digestive tracts sent to me by Clyde Jones which again contained only moths, among them members of the family Geometridae. However, due to the incompatibility between the Indiana and California-New Mexico analyses, not only to prey selection (which could be expected), but also as to size range (which is not expected), it seems that the food habits of the Red bat need further study. It has been noted that prey-selection varies greatly in widely distributed raptors, but not the general size range of prey selection. In regard to a predator that will accept many different kinds of prey-foods, one could expect the prey-species selection to vary nightly, but maintaining the same size range, *per se*.

Lasiurus cinereus, Hoary bat.

The Hoary bat, like other members of the genus, hangs in a solitary fashion in a tree by day. It too is migratory. However, there is no similarity as to insect-prey selection.

Clyde Jones presented me with 131 digestive tracts of these bats (nearly all of them extended with food), collected in various parts of New Mexico during the summer months (May, June and July) of 1960-62. Included also were a few collected the nights of 29 April (3), 29 August (1), and the 12th of October (1). The remaining eight Hoary bats examined by me were from southern Arizona.

The following insect-prey were encountered: GRASSHOPPER (Orthoptera) - 1 bat (1); TERMITES (Isoptera) - 3 bats (2, 2, 3); LACEWING (Neuroptera, Chrysopidae) - 1 bat (1); BEETLES (Coleoptera) - 4 bats (1, 2, 3, 3), June beetles (Scarabaeidae), 3 bats (1, 1, 2), leaf beetles (Chrysomelidae), 1 bat (2), long-horned beetle (Cerambycidae), 1 bat (1); MOTHS (Lepidoptera), primarily owlet moths (Phalaenidae), geometers (Geometridae), and gelechiids (Gelechiidae) - 136 bats (up to 25 specimens in a full stomach); FLYING ANTS (Hymenoptera, Formicidae) - 9 bats (1, 2, 3, 4, 4, 6, 15, 19, 24).

Poole's report (1932) on the stomach contents of this raptor (determined by F. M. Uhler), mentioned as prey a large stink-bug, Nezara probably hilaris, and a mosquito, possibly Culex. The only other "food" reported thus far is in the form of a "cannibalistic" act by one of these animals (Bishop, 1947).

As can be seen from my above determination, these bats are rather strict feeders on microlepidoptera. These moths ranged from 6 to 30 mm in size. However, the food was chewed too finely to allow me to estimate an average prey size, outside of stating that most of the insects taken were in the upper limit, ca. 20 mm in length. When Hoary bats feed on moths they exhibit excellent mastication; however, when chewing on relatively thick-bodied ants and beetles (apparently in the same overall size range) they ingest wings, heads, and various other large fragments. I have not yet encountered an entire wing or head of a moth. The hunting bat appears to approach the flying moth (of the proper length) from the rear, engulfing the abdomen and thorax in its mouth, then biting down and shearing off the head and wings, leaving these parts to fall to the ground. The constant direction of approach by these bats in these solitary pursuits indicates that they echolocate for each prey.

The termite remains are the first that I have encountered in examinations of the tracts of various bats. It is known that the wings of termites can be shed quite readily; in fact, pressure applied to the thorax will cause the wings to "pop" off. However, even without the wings, if the bats are preying on flying termites, one should recover either thoracic, tarsal, or abdominal fragments none of which were seen. On the other hand, the presence of termites in these stomachs was determined by finding their fragmented, but characteristic, wings.

The swarming behavior of termites (similar to that of flying ants) should provide them as natural prey for opportunistic feeding by insectivores; yet most bats do not appear to utilize them.

Although the food-prey list for the Hoary bat is not very extensive nor at a fine taxonomic level of determination, it is yet as complete as the much longer listing of prey selected by the Western pipistrelles, for a similar number of stomachs analyzed. Therefore, one may characterize the Hoary bat as a rather restricted feeder, primarily selecting individually pursued moths. Of course, this strictness is of a relative nature, for there are numerous types of moths, each with numerous individuals, that will fit the size range of prey for this bat.

Lasiurus ega, Yellow bat.

The stomach contents of six of these bats are indicated here only for comparison with the other two members of this genus. Three of these stomachs were secured by R. E. Mumford in his visit to New Mexico.

These six animals had fed on coleopterous insects (sap beetles, Nitidulidae, 5 mm, and leaf beetles, Chrysomelidae, 7 mm), true bugs (Lygaeidae bugs, Lygaeidae, 6 mm), moths (Lepidoptera); and one of them on flying ants (Hymenoptera, Formicidae, 12 mm).

One of the stomachs contained the remains of three (or possibly four) lizards, two of them embryos. In view of the apparent insectivorous habits of this species I would suggest that this was a case of a tree-climbing lizard (a gravid Sceloporus (?)) versus a tree-roosting bat. This bat was shot out of a tree during the day. In the contents of the stomach of the bat, besides remains of the lizards, were numerous head capsules of (non-flying) worker ants. Because of the lack of indication of chewing I strongly suspect that these insects had originally been ingested by the adult lizard.

Nycticeius humeralis, Evening bat.

Two stomachs of this species were provided by R. E. Mumford. One of them was almost empty, the bat having fed only on one flying ant (Hymenoptera, Formicidae) and one spittlebug (Homoptera, Cercopidae). The other had a full stomach, having fed to a great extent on coleopterous insects, among them June beetles (Scarabaeidae), and to a lesser extent on flies (Diptera), among them pomace flies (Drosophilidae).

Too little in the way of pertinent material is available to warrant any type of summation for this species.

<u>Euderma</u> <u>maculatum</u>, Spotted bat.

In my earlier analysis (1961b) only 18 pellets of this rare bat were examined and, because of the condition of the insect remains, determinations could be made to ordinal level only. The remains of 21 adult moths, approximately 8 to 12 mm in length, were found in these pellets.

In an analyses of five full digestive tracts of these bats, provided by Clyde Jones, I again only recovered moths in a size range approximately 5 to 11 mm. The food was too finely chewed for further approximations.

Durrant (1935) records that a Spotted bat was kept alive for a short period of time by a schoolteacher in Utah. He states, "At first it would take no food, so she fed it flies by force, with the aid of tweezers. Following a few forced feedings it took to flies readily." Apparently, according to Durrant, the bat was kept alive for twenty days

(Oct. 20 to Nov. 19) on this diet. On Nov. 19 this bat died, and Durrant attributed its death to cold exposure.

Dr. Vorhies in Arizona in the same year (1935) reported on the death of another Spotted bat, noting that it "had been fed with flies and fresh meat, but it did not eat."

Hall (1939) reports that a Spotted bat died in California after a week of captivity in which it did not feed.

Plecotus townsendi, Townsend's big-eared bat.

This species, also called the Lump-nosed bat, hibernates in the winter months.

Clyde Jones presented to me most of the digestive tracts utilized in this study.

Unfortunately, about 20 of the 38 stomachs were relatively empty; only six were actually full of food. Although most of these stomachs were empty, there were always some pellets in the lower intestines, from which some information could be gleaned.

The following list of insect-prey was obtained from fragments found either in the formed pellets of the lower intestines or in the stomachs proper: LACEWING (Neuroptera, Chrysopidae, Chrysopa) - 1 bat (1); JUNE BEETLES (Coleoptera, Scarabaeidae, Aphodius, 4 mm) - 2 bats (2, 10); MOTHS (Lepidoptera) - 35 bats; NEMATOCERAN FLY (Diptera) -

1 bat (1); SAWFLY (Hymenoptera, Diprionidae) - 1 bat (1).

Townsend (1887) observed that the "Great-eared" bat (Corynorhinus = Plecotus) fed on the "dermestes" which abound in the fur establishments of the Hudson's Bay Company in northern California. Howell (1920) notes that Plecotus is known often to pick insects from leaves and other resting places. However, he offers no corroboration for this statement. Allen (1939) states, "Curiously, no remains of moths were discovered [in reference to Hamilton's analysis of the food habit of Eptesicus fuscus (1933)], although their characteristic wing-scales were found in the droppings of the Lump-nosed bat (Corynorhinus)."

Since these bats are highly successful in avoiding mist nets over watering holes or the like, and since they fly too late in the evening to be readily seen and shot, a collector is unable to obtain samples during or shortly after their feeding periods. Also they appear to utilize night roosts different from their day roost. For these reasons, a satisfactory analysis of their food is difficult or next to impossible.

For the greater part of its diet Townsend's bat appears to be restricted, to preying on the smaller microlepidopterans. It appears to feed in a range of 3 to 10 mm, with an average of perhaps 6 mm. Again, as in the Hoary bat, the fine mastication and the pre-ingestion discarding of wings and head capsules of the moths limit determination to an ordinal level.

Plecotus phyllotis, Allen's big-eared bat.

This Big-eared bat, with habits like those of Townsend's is successfully avoiding capture, at least during feeding periods, and is uncommon in collections. However, Clyde Jones gave me twenty digestive tracts of this species collected in various sites in New Mexico (years 1960-2). Five specimens were taken in Arizona (7500 ft., Sierra Ancha, Gila Co.) by Bruce Hayward.

The following insects were recovered from these bats: ROACH (Orthoptera, Blattidae, 7 mm) - 1 bat (1); BEETLES (Coleoptera) - unknown beetle, 1 bat (1), soldier beetle (Cantharidae, 8 mm), 1 bat (1), June beetles (Scarabaeidae, 6 mm), 1 bat (3), leaf beetles (Chrysomelidae, 7 mm), 1 bat (2); MOTHS (Lepidoptera, 6-12 mm) - 25 bats (2 to 15); FLEAS (Siphonaptera, Myodopsyllidae, Myodopsylla collinsi, 3 mm) - 1 bat (2) [See the Discussion about this occurrence.]; FLYING ANTS (Hymenoptera, Formicidae, Eccton subgenus Labidus, 16 mm, other unknown, 6 mm) - 4 bats (4, 5, 7, 10).

From this limited sample, with apparent opportunistic feeding having occurred (i.e., ants), it still appears that microlepidopterans are the staple item of the diet.

<u>Antrozous</u> <u>pallidus</u>, Pallid bat.

The Pallid bat is active in the summer months, and appears to hibernate in winter.

In this study insect parts dropped below night roosts, guano and stomach contents were examined from four different plant-life zones to determine if there is any evidence of regional food selection.

The following insects are noted for Locality 1 (Mine, 20.8 road miles south of Oracle, on Control Road, Pima Co., Arizona, 4 September 1959, night roost; collector, G. VR. Bradshaw. This mine is in the Upper Sonoran zone.): GRASSHOPPERS (Orthoptera): - long-horned grasshoppers (Tettigoniidae), <u>Stenopelmatus</u> sp.*, 4%, <u>Microcentrum californicus</u>, 4%; BEETLES (Coleoptera) - ground beetles (Carabidae), <u>Pasimachus</u> <u>californicus</u>†, 4%, darkling beetles (Tenebrionidae), <u>Euschides</u> <u>convexus</u>†, 4%, June beetles (Scarabaeidae), <u>Orizabus</u> <u>clunalis</u>, 20%, <u>Plusiotis</u> <u>gloriosa</u>, 20%, long-horned beetles (Cerambycidae), <u>Prionus californicus</u>, 4%, <u>Archodontes</u> <u>aridus</u>, 4%, <u>Prionus</u> sp., 15%, <u>Derobrachus</u> sp., 4%; MOTHS (Lepidoptera) - hawk moths (Sphingidae), <u>Chlaenogramma</u> <u>jasminearum</u>, 4%, <u>Celerio lineata</u>, 4%, lappet moths (Lasiocampidae), <u>Dicogaster coronado</u>, 9%.

The following insects are noted for Locality 2 (Mine tunnel, 1 mile north of Paradise, Cochise Co., Arizona, summer accumulation of insect parts, at night roost, 1958; collector, E. L. Cockrum. The determination of the insect fragments from this locality were made 6 December 1958 by F. G. Werner, Department of Entomology, University of Arizona. This tunnel is in a canyon with a pinyon-juniper association.): GRASSHOPPER (Orthoptera) - short-horned grasshoppers (Acrididae), Trimerotropis sp., 1%, long-horned grasshoppers (Tettigoniidae), Stenopelmatus sp.*, 1%, Capnobotes fuliginosus, 4%; BEETLES (Coleoptera) - ground beetles (Carabidae), Calosoma sp., 1%, carrion beetles (Silphidae), Nicrophorus sp., 1%, June beetles (Scarabaeidae), Plusiotis gloriosa, 8%, Polyphylla sp., 20%, long-horned beetles (Cerambycidae), Archodontes sp., 9%, Prionus sp., 10%, Derobrachus sp., 10%, Nothopleurus, 9%; MOTHS (Lepidoptera) - hawk moths (Sphingidae), Celerio lineata, 1%, giant silkworm moths (Saturnidae), Telea polyphemus, 1%, owlet moths (Phalaenidae), Catocala sp., 6%, lappet moths (Lasiocampidae), Dicogaster sp., 14%, Dicogaster coronado, 1%, Gloveria arizonensis, 3%.

The following insects are noted for Locality 3 (Second Mine, second stream crossing, 5.4 miles east of Oracle Junction, 6.6 road miles south of Highway 77 (Burney Mine Road), Pinal Co., 11 October 1959; collector, G. VR. Bradshaw. Mountainous grassland with oak, cottonwood, sycamore.): GRASSHOPPERS (Orthoptera) - short-horned grasshoppers (Acrididae), Trimerotropis sp., 2%, Schistocerca sp., 5%, long-horned grasshoppers

(Tettigoniidae), Stenopelmatus sp.*, 2%, Microcentrum californicum, 10%, Capnobotes fuliginosus, 2%; TRUE BUGS (Hemiptera) - giant water bugs (Belostomatidae), Abedus sp., 4%, leaf-footed bugs (Coreidae), Thasus acutangularis, 2%, Acanthocephala granulosa, 3%; TRUE BUGS (Homoptera) - cicadas (Cicadidae), Diceroprocta apache, 2%; NERVE WINGED INSECTS (Neuroptera) - antlions (Myrmeleontidae), Hesperoleon sp., 1%; BEETLES (Coleoptera) - ground beetles (Carabidae), Calosoma sp., 20%, Calosoma scrutator, 1%, darkling beetles (Tenebrionidae), Euschides convexus†, 4%, Edrotes ventricosus†, 1%, June beetles (Scarabaeidae), Orizabus clunalis, 6%, Plusiotis gloriosa, 2%, Polyphylla spp., 8%, Trox sp., 1%, long-horned beetles (Cerambycidae), Prionus californicus, 8%, Archodontes sp., 5%, Nothopleurus sp., 4%; MOTHS (Lepidoptera) - hawk moths (Sphingidae), Celerio lineata, 3%, Protoparce sp., 2%, giant silkworm moths (Saturniidae), Telea sp., 1%, tiger moths (Arctiidae), Apantesis proxima, 1%.

The following insects are noted for locality 4 (D. G. Hibbs Ranch, ca. 24 miles north of the Mexican border, east base of Baboquivari Mountains, 3800 feet, Pima Co., Arizona, 16 October 1959; collector, E. L. Cockrum. Mesquite shrubs are the dominant plants in this area.): GRASSHOPPERS (Orthoptera) - short-horned grasshoppers (Acrididae), Arphia sp., 2%, Xanthippus sp., 1%, Schistocerca vaga, 23%, Taeniopoda eques, 1%, long-horned grasshoppers

(Tettigoniidae), Stenopelmatus sp.*, 1%, Capnobotes fuliginosus, 2%; TRUE BUGS (Hemiptera) - leaf-footed bugs (Coreidae), Thasus acutangularis, 50%; TRUE BUGS (Homoptera) - cicadas (Cicadidae), Diceroprocta apache - 1%; BEETLES (Coleoptera) - darkling beetles (Tenebrionidae), Euschides convexus†, 9%, June beetles (Scarabaeidae), Cotinus sp., 1%, long-horned beetles (Cerambycidae), Oncideres rhodosticta, 8%. [* = wingless, † = flightless.]

In addition to the insect fragments, remains of one scorpion (Hadrurus sp.) of the family Vejovidae were identified from Locality No. 4.

This was the only scorpion encountered in this study; and, as scorpions are fairly abundant in Arizona, it appears that they are not a normal part of the diet of the Pallid bat, even though there are published reports of such a feeding habit. Perhaps scorpions are captured while these bats are searching the ground for similar life-forms, such as Jerusalem crickets.

It is interesting that Pallid bats at Locality 3 were feeding on predaceous water bugs (Abedus), but there is a stream in this area. These bugs leave the water to mate, at which time they fly or crawl over the ground looking for mates. They are large bugs, approximately 30 mm or more in length.

At Locality No. 4 one would expect a high percentage (50) of the very large (35 mm) bug (Thasus) in the prey, for it is one of the more abundant insect in this association. However, it is a very foul-smelling insect.

The stomachs and guano of Pallid bats from these areas indicate that these bats do not feed on the smaller insects, since all of the insect fragments found were over 17 mm in length. Only the cerambycid Oncideres (Locality No. 4) was in the 17 mm range, while the other insects were much larger. My study of the Pallid bat's food habits also indicates that it does not feed on immature (larval or flightless nymphal) forms which are found on vegetation, and its preference for flightless forms is limited to the large ones found on the ground (Ross, 1961b).

Other informative reports of food-items for this bat are as follows: Grinnell (1918) reports for California that most numerous among the "kitchen middens" were heads and legs of Jerusalem crickets and wings of sphinx moths. Specifically listed are Prionus californicus [long-horned beetle], Stenopelmatus [Jerusalem cricket], Deilephila [=Celerio] lineata [sphingid moth], Microcentrum [long-horned grasshopper], Ligyrus gibbosus [June beetle], and Gryllus [field cricket]. Hatt (1932) listed Schistocerca [short-horned grasshopper], Stenopelmatus fuscus [Jerusalem cricket], Polyphylla decimlineate [lined June beetle], and Anuroctonus phaidodactylus [scorpion]. Borell (1942) reported Melanoplus differentialis and Schistocerca shoshone [both are short-horned grasshoppers], June beetle, and a ground beetle. Orr (1954) notes that these bats fed on Stenopelmatus probably fuscus [Jerusalem cricket], Polyphylla probably decimlineate [lined June beetle], Romaleum simplicicolle, Prionus californicus [both are long-horned beetles], and Eleodes acuticauda [darkling beetle].

Apparently this bat feeds on all of the larger night-flying insects (20 to 70 mm in body length, wingspans up to 160 mm) and flightless insects (20 to 50 mm in length) that are available in these zones, with no indication of food selection as to types. The fact that it feeds on nocturnal flightless insects (e.g., Stenopelmatus, Euschides) in such large numbers would indicate that the bat alights on the ground and actively searches for these insects (Grinnell, 1918, Nelson, 1918, Howell, 1920, Hatt, 1923, Burt, 1934, Engler, 1934, Huey, 1936, Orr, 1954, Ross, 1961b). Orr (1954) also noted that this species feeds on Stenopelmatus in California and Arizona.

From several direct observations of the Pallid bat's ability to search for flightless prey, it can be stated that it appears to move at random over the area (at levels of six inches to three feet), scouting until it locates a prey (presumably by sight), then dropping abruptly to the ground to search for it, and then carrying it (usually a large flightless arthropod such as a Jerusalem cricket, June beetle, or a scorpion) off in its mouth. This behavior has been reported also by Nelson (1918) and Burt (1934).

William Musgroove (personal communications) reports of similar observations for this bat in the Kingman, Arizona area.

It is then interesting to speculate also on the ability of a Pallid bat to echolocate with a large Jerusalem cricket in its mouth. Perhaps it emits the pulses through its nostrils, as Griffin (1958) notes for Plecotus. However, Orr (1954) records that by using an ultrasonic amplifier it was found that during flight these bats emit a very narrow beam of sound from the open mouth.

Sherman's report (1935) on D. T. H. Hubbel's determination of the prey of a Seminole bat mentions that this species too had preyed on a flightless insect. The prey was determined as a field cricket, Gryllus assimilis (Fabr.) variant pennsylvanicus Burmeister. This variant has reduced wings; however, this is not the condition for other members of this species. Since this stands as the only report of this type of preying for this bat, it should be accepted with reservation.

Tadarida brasiliensis, Brazilian free-tailed bat.

Brazilian free-tailed bats are especially noted for the spectacular numbers which will inhabit an individual cave-roost and for the tremendous accumulation of guano below such roosts.

In 1961(b) I reported on the examination of the contents of seven stomachs of this species. I listed the following insects: Homoptera: bugs, 1 per cent, Diptera: Dolichopodidae, 4 per cent, Lepidoptera: moths, 95 per cent. Apparently, most of the moths belong to the family Gelechiidae. In conclusion it was stated, "Most of the insects were approximately 5 to 9 mm in length. Apparently, these bats feed on moths and occasionally take other prey captured without selectivity."

Since this original analysis I have examined 84 digestive tracts of these bats from Mexico, other areas of Arizona, and New Mexico.

The following insects are noted in this second investigation: TRUE BUGS (Hemiptera, among them, grass bugs, Corizidae) - 6.4%; LEAFHOPPERS (Homoptera, near Cicadellidae) - 15%; ANTLIONS (Neuroptera, Myrmeleontidae, Hesperoleon sp., 25 mm) - 1.6%; BEETLES (Coleoptera, among them, June beetles, Scarabaeidae; and flea beetles, Chrysomelidae, 2 mm) - 16.8%; MOTHS (Lepidoptera, some leaf miners, Nepticulidae) - 34%; FLYING ANTS (Hymenoptera, various species, among them, Camponotus sp.) - 26.2%.

In 1961 I analyzed 29 samples of "ancient" guano of Brazilian free-tailed bats for the Geochronology Laboratories, University of Arizona, Tucson. These samples were from Tramway Cave (U. S. Guano Corporation, Grand Canyon of Colorado River, Arizona) near a guano mound called

"Greasy Hill." They were taken down to a depth of seven feet. Although I do not have dates, this material doubtless involves several thousands of years. The only noticeable difference between this ancient guano and fresh guano was found in samples taken from the lower depths that had been crushed by the weight of the guano above. But even in this finely granulated material the presence of chitin could still be demonstrated by chemical analysis, which showed that the bats were primarily selecting moths and beetles at a rate similar to that observed for "modern bats."

Grinnell (1918) observed that these bats contained the remains of insects, such as flies and small beetles that were too finely triturated for identification, and that in captivity they ignored all food offered to them.

The first serious investigation of the food habits of this species was undertaken following the claims made by Campbell (1925) in regard to this bat's natural control of the malaria-carrying mosquitoes. His book, Bats, Mosquitoes, and Dollars (1925), is filled with imaginative remarks. It seems to me that little in this book can be regarded as fact, and statements by the author must have been based on conjecture rather than personal experience.

This study was instigated by Storer (1926). Two samples obtained from Campbell's bat roost were analyzed, and the following insects were noted: Sample 1 - chiefly, remains of moths (90%), but also traces of ground beetles (Carabidae), 2; leafchafer (Serica sp.?), 1; weevil, 1; leaf beetle (Chrysomelidae), 1; and an unidentified beetle; ant (Dolichoderus sp.), 1; water boatmen (Corixidae), several; stink bug (Pentatomidae), 1; green blow fly (Muscidae), 1; and small dragonfly, 1. Sample 2 - chiefly, remains of moths (90%); leafhopper (Jassidae [=Cicadellidae]), 1; water boatman (Corixidae), 1; Corizus sp., 1; bug (Heteroptera), 1; leaf beetles (Chrysomelidae), 2; weevil, 1; ground beetle (Carabidae), 1; unidentified beetle, 1; and ant, 1.

Storer blasts Campbell's deliberate asseveratio falsi by noting that no mosquito remains whatever were found and indeed only a trace of a single insect belonging to the whole order Diptera (the one Green Blow Fly).

Storer, further states: "The conclusion seems inevitable, therefore, that the bats in the San Antonio roosts were not feeding upon mosquitoes at the time when the above-mentioned samples were taken. Nor is there any evidence to show that this species [Tadarida mexicana = T. brasiliensis] of bat elsewhere feeds upon mosquitoes." Nelson's discussion of Campbell's conjectures (1926) includes this statement: "The assertions that bats will eradicate or even noticeably reduce the numbers of mosquitoes, and with them malaria, are shown by studies of their food and general habits to be misleading and without foundation." Goldman (1926) disagrees also with Campbell's assertions.

Bailey (1931) reported that a series of stomachs of Free-tailed bats yielded 95 per cent moths, the other 5 per cent being carabid beetles, hymenopterous insects, and a few crane flies. For the colony at Carlsbad Cave, New Mexico he noted only moths and beetles in their diet. However, he apparently succeeded in feeding them large gray "candle moths" [?].

The stomach analyses seem to indicate that these bats are group feeders, that is, they hunt in foraging groups. Two groups (10 and 13 respectively), collected consecutively at varying intervals in mist nets, showed similar feeding on various forms such as true bugs (Homoptera and Hemiptera) and flying ants (Hymenoptera). These stomachs were equally distended with prey forms of corresponding percentages, in similar layers in the food balls.

Apparently, the insect-prey has to be concentrated (swarming, or dense flights), as indicated by this stomach analysis. The appearance of the food ball is quite similar to that noted for the filter feeding <u>Pipistrellus hesperus</u>.

No flies (Diptera) were encountered in this recent analysis, and the other reports of finding flies (Grinnell, 1918, flies; Storer, 1926, one Green Blow Fly; Bailey, 1931, few Crane Flies; Ross, 1961b, 4 per cent Long-legged Flies, Dolichopodidae) do not include mosquitoes. However, many of the larger two-winged flies are in the right size range for prey selection by these bats; yet, dense flights of these insects are limited to the earlier crepuscular periods, and the Brazilian free-tailed bat is a late emerger.

<u>Tadarida femorosacca</u>, Pocketed free-tailed bat.

Only two digestive tracts of these relatively uncommon Free-tails were examined. They are included here only for comparison, as both specimens were taken on the same night (in mist nets) and in the same locality as the <u>Eumops perotis</u> and <u>Tadarida molossa</u> to be considered shortly.

One of the stomachs contained only macrolepidopterans (probably hawk moths, Sphingidae), while the other contained microlepidoptera (85 per cent) and beetles (Coleoptera, 15 per cent).

Krutzsch (1944) reported that wings and hard parts of insects were in the fresh droppings of these bats.

The analyses of these stomachs furnishes little enlightenment as to possible food habits.

<u>Tadarida molossa</u>, Big free-tailed bat.

Only one specimen of this species was taken along with the preceding. An analysis of its stomach content indicated that it also had fed on macrolepidoptera (apparently hawk moths, Sphingidae).

Eumops perotis, Greater mastiff bat.

The Mastiff bat is the largest of the bats found in the continental United States. It is a colonial species that selects a large crevice in a cliff for a roosting site.

In 1961(b) I reported on the food habits, from an examination of the contents of four stomachs and 43 pellets of these bats. The following insect fragments were noted in that study: Odonata: Aeshnoidea, 1%. Orthoptera: Acrididae, 10%. Hemiptera: Miridae, 10%. Coleoptera: Scarabaeidae, Cremastocheilus sp., 1%, Tenebrionidae, 5%, Curculionidae, 5%. Lepidoptera: moths, 10%. Hymenoptera: Halictidae, 36%, Formicidae, 12%, Megachilidae, 5%, Anthophoridae, 5%.

I then noted that the food habits of this bat apparently are unusual in that 58 per cent of the diet consists of hymenopterous insects. This large bat is also unusual in that it feeds on rather small insects (most of them approximately 8 mm in length). The habits of the insects on which this bat had been feeding (low-flying, weak-flying forms) indicate that E. perotis normally feeds from near ground level (3 to 4 feet above the surface) to treetop level.

Howell (1920) in discussing the lack of success he had in feeding captive bats of this species and their apparent fear of large insects (such as Jerusalem crickets) asked, "then for what is the huge mouth?"

I, too, wondering why the huge mouth if it only feeds on small insects (8 mm), undertook another study of this species. Because digestive tracts, taken during the feeding periods, are rather hard to secure, the contents of only nine more stomachs were analyzed.

Primarily, these nine stomachs contained only the remains of macrolepidoptera (large hawk moths, Sphingidae up to 60 mm in length?). In agreement with the feeding process noted for other bats, only the abdomens of these moths were ingested, the heads, thoracic segments, and wings are dropped to the ground. There is no evidence for the conjecture that these bats may use a feeding roost, as was noted for Leaf-nosed and Pallid bats, which also take large prey. Only one of these specimens contained anything other than sphingids: the lower intestine yielded pellets containing two true bugs (Homoptera, near Cicadellidae), a large cicada (Homoptera, Cicadidae), and a planthopper (Homoptera, Fulgoridae).

This latest food listing appears to be more in line with what one might expect from a functional standpoint with regard to the bat's large size and big mouth. I have re-examined my earlier report and the material that it was based on, and can not contradict what I have published, but I will be distrustful in the future of any report based in whole or in part on guano analysis, at least when it involves bats.

Krutzsch (1955) refers to this bat as apparently a feeder on insects and his discussion of its food habit, based on a superficial analysis of droppings found below roosting places, reports chitinous insect parts that were so finely masticated as to be unidentifiable.

Vaughan (1959) similarly notes that Eumops is an insectivorous bat, whose droppings invariably consist of small fragments of insects. He further implies that these bats normally forage at 200 to 2000 feet above the ground; a conclusion based for the most part on his listening for the bat's "cheeps" and then by the loudness of the noise estimating the distance of the bat from himself. It must be strongly considered that insect density decreases very rapidly with gains in altitude; however, he too has noted this. Therefore, he suggests that insects (mainly those that are weak fliers) are swept up to these heights by uplifting currents of air. Yet, sphingid moths must be considered strong fliers that normally would not be uplifted thus. They mainly 'flitter' around night-blooming flowers. In fact, these moths are often mistaken at first glance for bats in the darkness of night. Therefore, I have noted nothing in these analyses that would deter one from accepting my first impression for the foraging heights used by this bat (*i.e.*, near ground to treetop level).

Eumops underwoodi, Underwood's mastiff bat.

Although little is known of the biology of this species, it is very similar in size and shape to the Greater mastiff bat.

Analysis of the content of six digestive tracts of these bats indicates the following insects: SHORT-HORNED GRASSHOPPERS (Orthoptera, Acrididae, some *Trimerotropis pallidipennis*, 40 to 60 mm) - 31%; TRUE BUGS (Homoptera) - leafhoppers (Cicadellidae, 6 mm), 12%, planthopper (Fulgoridae, 20 mm), trace; BEETLES (Coleoptera, some Chrysomelidae; and Scarabaeidae, 6 to 10 mm) - 47%; MOTHS (Lepidoptera) - 10%. From the foregoing it may be seen that these bats had fed on a diversity of insects, both in size and kinds. However, all samples were taken in the same evening at the same mist net. Because of the diversity of food habit observed, it does not seem safe to offer suggestions as to the specific feeding habit of this bat.

DISCUSSION

"Moths and beetles seem generally to form the great bulk of the food [for bats], but many other insects also are eaten, and in case of an unusual abundance of any nocturnal species, these might be expected to figure in the food. . . . In evaluation of their services as insect destroyers it is to be borne in mind that they feed almost entirely on night-flying species" (Nelson, 1926).

From what I have learned in this study I would modify Nelson's statement (now a quarter century old) only by including nocturnal ground-dwelling insects as prey for some bats and ranking grasshoppers on a par with the beetles.

Just how insectivorous bats evolved has been the subject of much discussion. Allen (1939) wrote that no doubt all bats were originally insect eaters and inherited this trait directly from their hypothetical ancestors of the Order Insectivora. He further states that the molars of insect-eating bats resemble those of moles and shrews.

Allen notes that "These sharp cusps and ridges of the opposing teeth act as scissors to cut up the insect food into such minute fragments that it is often difficult to find in the stomach contents bits large enough to identify. . . .

In insect-eating bats the long canines seize and pierce the prey, which is then reduced to minute fragments by the sharp-edged premolars and by the bladelike crests that connect the cusps of the molars. These latter perform the chief work of cutting up the food and are placed farthest back under the muscle masses of the jaw, where the greatest power can be applied."

The above statements seem to me an oversimplification for, whether the bat feeds in the air or takes the prey back to a roost, the manner of chewing depends on the bat's mouth gape as well as the size and hardness of the insect. However, for insect-eating bats these statements have a general validity.

Bats, although primarily nocturnal in their foraging habits, begin this activity at varying intervals after sunset. The smallest bats, such as the Pipistrelles, emerge early in the twilight period, while the largest bats, such as the Mastiffs, tend to be the last to commence foraging. Apparently Mastiffs may delay leaving the roost for several hours after sunset.

Small species of bats, which are usually crepuscular, appear to fill their stomach more quickly than do larger species. Many times the smaller bats will have retired from foraging before the larger bats even begin. This appears to be true even though the small ones feed on smaller insects than do the larger ones. However, many of the dense flights of insects occur during the twilight while the nocturnal insects do not show this tendency to congregate in dense flights. Although the size of the stomachs of larger species of bats are just as impressive when they are filled, it takes the bats longer to achieve this condition with pursuit of individual prey (also some of these species carry the insect to a convenient night roost). Even in the larger species (e.g., Myotis, Macrotus) the fully engorged female will appear as if she were in late stages of pregnancy, while really she is non-gravid.

In many insectivorous bats and owls there seems to be a rhythm of feeding during the night. During periods of feeding activity prey is accumulated and stored temporarily in the stomach (of a bat). If one can collect these raptors during the correct intervals he may ascertain, with high confidence, the number and kinds of individuals eaten during the last feeding period. However, shortly after digestion, remains of prey may still be isolated for analysis from the lower intestines. Although digestion does not affect the level of taxonomic determination in an analysis to any great extent, it will affect the knowledge of the relative numbers and kinds of organisms taken, if the food-items have already passed through the system.

Seemingly the majority of insectivorous raptors have two feeding periods which can be characterized in the following manner: the first begins with the onset of twilight, or shortly thereafter; apparently the more efficient feeders in a given species are satiated by 10:00 P.M., while the feeding period appears to continue until around 12:00 P. M. for others less efficient. Then there is a period of relative inactivity until around 3:00 A. M. when feeding begins again, with the hunters obtaining their fill by 4:30 A. M., and with some activity into the early daylight hours for the stragglers. On the other hand, these early morning feeding periods, when utilized, do not seem to be as productive for the hunters; many return with partially filled stomachs and insects taken at random. This randomness of prey selection seems to indicate that even the usually dense-swarming insects are more scattered in their flight. The feeding periods indicated above are based on correlating the amounts of food found within the digestive tracts of various raptors with the times of their capture.

In a paper on the activity of the Screech Owls, Allard (1937) suggests that the feeding periods of these birds are timed to the activities of certain moths and other animals in their diet. It is reasonable to adjudge that nocturnal predators (such as owls and bats) have adapted their activity to coincide with the periods of greater abundance of prey.

Pye's evaluation of echolocation for bats (1961) is as follows: "It has now been established beyond all doubt that it is the means by which bats navigate and find their food." I do not doubt that most bats echolocate to some degree; however, from a conservative point of view, Pye's statement is too inclusive for data available. The primary investigator of the echolocation phenomenon of bats is Dr. E. R. Griffin.

Griffin's studies mainly involve only two species, Myotis lucifugus and Eptesicus fuscus. In many of his echolocating experiments he uses food-items such as mosquitoes and fruit flies. Apparently these food-items are of a size range much smaller than normally selected by these bats. Pittman in his study of the feeding habits of Myotis lucifugus (1924) states: "They were offered flies and various other insects but preferred the noctuid [=phalaenid] moths which were at the time very plentiful. . . . Apparently eight to ten moths constituted a meal. . ." Although Pittman does not indicate any size range nor the species involved, noctuids in general are larger and heavier than the insects used by Griffin. If it is taken into consideration that 8 to 10 of these moths constitute a meal for this bat then they must have been a rather large species of noctuids. Gould (1955) reports that Myotis lucifugus will habituately attack moths as large as Crymodes devastator that have a body length of 30 mm.

It is even noted by Griffin et al. (1960) that even at best only a small fraction [which could be as low as 1

(?)] of his experimental animals, Myotis lucifugus, released into a room filled with flying mosquitoes undertook serious hunting. Furthermore, bias must be seriously considered when 90 per cent (or more) of the bats are discarded in his experiments because they failed to meet the requirement of pursuing unnatural prey. It might be earnestly considered that the 10 per cent (or less) of these kept and used in his experiments were not representative forms. This consideration is based on the condition that these bats could and would feed on mosquitoes of a size range smaller than the lower limit of normal prey detection by this species as indicated by Pittman (1924).

Griffin (1959) writes this about echolocating bats: "When they are hunting insects their ears receive a more complicated mixture of sounds than merely their original chirp plus a single echo returning from a single insect and having the same wave form at a lower energy level. What is really impinging upon their ears is a whole series of echoes from everything within several feet - the ground, other insects, and every bush, twig, tree trunk, leaf, or blade of grass." Then among the questions he asks of the above is, "how do they hear the difference between echoes that mean food to be caught and those that mean obstacles to be dodged?" His answer amounts to this: although from our vantage point these obstacles seem to be insurmountable, the bat indeed does overcome them as evidenced by their full stomach.

To me it appears that bats, when searching for prey are in a relatively unencumbered medium not surrounded by the myriad of obstacles envisioned by Griffin. It appears that many species feed about the trees, or circling the outside area of the trees and, even when they hunt in denser vegetation, there is usually free space of three to four feet surrounding the foraging bats. They may, therefore, receive a solitary echo from an individual insect. Furthermore, when the bats are in their roost or engaged in other non-insect-hunting activities, they may not even be echolocating. If they are, they only echolocate to determine exit routes. I have been in the roosts of insectivorous bats (with a multitude of kinds and numbers of bats) with tremendous numbers of flying insects that were not being molested in the slightest (Ross, 1960a). Nelson (1926) reported a similar observation. Then, too, if one considers that the bats are selecting in a given size range, they should be able to dismiss many other obstacles and organisms that are to be found in the habitat.

As stated by Griffin (1958), in regard to trying to attract bats to artificial prey, "it becomes obvious after several evenings, that pebbles which were too large or too small were less likely to be pursued.... If the bat reacted at all, the result was a sharp turn or dive toward the pebble, and often it would be pursued with what appeared to be just as much fervor as a real insect." He further reports that no pebbles were ever taken or swallowed by the bats.

Therefore, an olfactory function, as well as vision in some forms, may be an involvement that finally decides the issue of the acceptability of the prey, regardless of the prey's length falling within a given size range. Bats do not prey on all insect species of correct size range and life form that are available to them in a habitat. However, the prey being of the correct size range probably takes precedence. As a generalization, decreasing sizes of bats take smaller prey. However, the range of the prey size selection may be just as large as noted for the larger bats, and the spectrum of insect species used for food-items may be greater than that of the larger bats. An example of this concept would be the Pallid bats that are non-specific feeders of flying insects that have body lengths of 20 to 70 mm, while the food preference of Pipistrelles are small insects of 4 to 10 mm in length.

Poulson (1929), while feeding bats different types of foods, observed that there was a quick response in many of the rejections, even noting a case where a bat, after receiving an apparently foul tasting moth, reacted by "coughing and spluttering in the most ludicrous manner."

There are three basic methods utilized by bats to capture prey. (1) Vision. This is apparently used by *Macrotus californicus* and *Antrozoous pallidus* in securing some of their food-items. Superficially the eyes of these

two species appear to be better developed than the eyes of the insectivorous bats. The use of their eyes would readily account for their ability to locate ground-inhabiting (Pallid) and vegetation-dwelling prey (Leaf-nosed).
(2) Filter feeding. Notable examples of this type are seen in Pipistrellus hesperus and Tadarida brasiliensis. This type of feeding, without individual pursuit of a given prey, is indicated by the contents of the stomachs of these bats. The food balls contain pure veins of a given species of insects indicating that the bats had been feeding on insects that have dense flights. These insectivores usually ingest all of the smaller insects. Examinations of the bodies of these food-items clearly demonstrate that they were captured from all angles of attacks by these bats, thereby indicating a randomness of capture that would be expected in a filter feeding method. These bats may echolocate to find dense flights of insects. (3) Individual pursuit. Examples of this type of capture are afforded by Lasiurus cinereus and Plecotus spp. The bat will approach the intended prey from the rear engulfing the abdomen. These bats are specifically echolocating for their intended victims.

Gould would not agree with the above statements as to methods of feeding for he maintains (1955) that all insectivorous bats use random pursuit; although he does admit that small insects offer some difficulty in echolocation-detection. Furthermore, he computed evaluation of feeding habits on gram(s) per insect, instead of size range of prey. His studies emphasize the weight of one milligram insects and the resulting weight of the bat's food ball. He then goes on to state that a bat could not achieve the weight gain (of the stomach content) from filter feeding because of the high percentage of misses, low density per liter of insects, and the bat needs hundreds of these almost weightless insects to show this gain. Unfortunately, most bats do not feed on such insects, nor can one generalize for all insectivores from the finding with one (Myotis lucifugus). Gould has the customary comment about analyzing the food ball of a bat when he notes, "only a very small fraction of the stomach contents escape reduction to an unidentifiable 'soup ...'"

In a later paper, however, Gould (1959) finds support for his visual observations of the feeding efficiency of bats by noting a similar correlation "obtained through a stomach analysis, of 500 insects caught per hour." If the particular bat to which he refers was Myotis lucifugus it must have been a very unusual individual. In all of my studies of digestive tracts, I have never observed one that remotely approached such a rate of ingestion. The closest to it was the Western pipistrelle, which is one that fills quickly (within ca. 30 minutes) on small insects (usually ca. 5 mm in length), and even with the stomach in the most extended condition, in its greatest engorging, it will have accumulated only 80 insects.

Hamilton (1933) who analyzed the fantastic total of 2,200 pellets of the Big Brown Bat (Eptesicus fuscus), was one of the first to give a rather complete coverage of the food habits of a bat in percentages by orders of insects.

It is interesting that he states, "ten pellets were passed in sequence before a fragment large enough to warrant even remote identification was found . . ." Just above, in his paper, he notes the method of obtaining these pellets, which leaves one wondering how the sequence was determined: "A half-pint jar was filled with what were thought to be relatively fresh droppings; that is, those that were free from any dust and were reasonably bright and clean. It is not likely that those collected were dropped before early June."

I have found in analysis of the pellets already formed in the lower intestines of bats, and also in pellets of guano, that there may be one or more remains of prey per pellet, or each pellet may contain a mixture of fragments of various insects; most likely, the type of pellet depends on the amount of chewing before swallowing. I have observed guano from the smallest (Western pipistrelle) and medium-sized (Brazilian free-tailed), to larger bats (Pallid) and find the above condition to be fairly consistent.

Unfortunately, the contents of the few tracts of the Big brown bats that I examined were full only of flying ants (Camponotus sp.). Roeder and Treat (1961) in a paper on the detection and evasion of bats by moths unfold an interesting story of unheard and unseen "aerial dogfights" being staged in the darkness, particularly by the owlet moths or Noctuidae [=Phalaenidae]. These moths appear to have developed protective countermeasures that permit the detection of chirps of bats. These countermeasures consist of a pair of "ultrasonic ears" (tympanic membranes), containing sound-detecting apparatus, that when stimulated by the sound of a bat's echolocation pulse triggers an erratic flight pattern. This flight pattern, which often allows the moth to escape, has been referred to as "survival by evasion."

In their conclusion Roeder and Treat state that: "Several families of moths lack ears and show no response to ultrasonic stimuli. Some of these, such as the sphinx or hawk moths and the larger saturniid moths, are probably too much of a mouthful for the average bat, and might find no survival advantage in a warning device. Others are of the same size and general habits as the noctuids and might be expected to suffer attacks by bats. Included in this group are some common pests such as the tent caterpillar. It will be interesting to learn whether these forms owe their success in survival to some structural or behavioral countermeasure that compensates for the lack of a tympanic organ."

Two major weaknesses mar Roeder and Treat's conclusions: (1) Owlet moths are preyed upon not only by insectivorous bats, but also by non-echolocating raptors such as the insectivorous owls. For example these moths form one of the staple food items of the Flammulated Owl (<u>Otus flammeolus</u>) (Ross, unpublished manuscript). If owlet moths evolved "ultrasonic ears" to detect echolocating bats and left themselves open to attack by silent predators such as owls, then the survival value of evasion loses some of its enchantment.

Roeder and Treat assume that the larger moths, which do not have "ears" suitable for detecting the echolocation cries of bats, are too large to serve as food. That sphingids are preyed upon by "larger" bats, such as the Pallid and Leaf-nosed, has been well documented (Grinnell, 1918; Huey, 1925; Orr, 1954; Gould, 1955; Vaughan, 1959; and Ross, 1961a). Of course, Roeder and Treat qualify their position by saying the larger moths would not be preyed upon by the "average bat." I assume that their "average bat" includes <u>Myotis lucifugus</u> and <u>Eptesicus fuscus</u>. I would agree with them that sphingids would be too much of a mouthful for a bat with the small gape of <u>M. lucifugus</u>. <u>Eptesicus fuscus</u>, however, is probably capable of feeding on such large moths. Further, I would be inclined to wonder right along with Roeder and Treat as to why other insects, and not only other moths, have not developed such warning devices. After all, many insects, other than owlet moths, do have tympanic organs.

Of course, one of the most difficult problem is to assess the values of the multitude of environmental factors, in most cases unknown, operating on any species.

Again, I would emphasize that raptors are regulators, not reducers, and apparently many forms compensate via a countermeasure of having a high reproductive potential.

The last portion of the above statement is often severely criticized with the implication that it should be considered as a "general textbook" concept. Yet, the majority of those that criticize it offer that the number of young is under "precise" genetic control, or otherwise strictly regulated, and therefore can not change to meet heavy environmental pressures. They proceed to state various clutch or litter sizes of vertebrates, especially birds (see Klopfer, 1962), noting that the number of eggs or offspring is small and stable. As true as the above might be for vertebrates it must be realized that invertebrates such as insects are preyed on too. I am sure that most of us are aware of the fantastic reproductive potential of insects.

Sprague (1938), commented on bats using their ectoparasites as food: "It is possible, inasmuch as both species were heavily parasitized with bat-flies (Streblidae) and mites, that the bats, being aroused by the warm weather, undertook to feed upon the parasites of one another and in doing so, also consumed quantities of hair. Insect remains in the stomachs were confined to a few antennae."

In all of my studies and from the literature of food habits, I have not observed any further suggestion pertaining to the habit of bats feeding on their own ectoparasites (Ross, 1960b, 1961b). In regard to the last sentence of the quote, about the antennae, I am quite sure that Sprague did not intend to imply that those antennae belonged to the streblid flies; as these structures can only be observed (much less located) with the high magnification of a compound microscope.

On the other hand, I have on one occasion recovered the intact bodies of two fleas from the stomach of a Big-eared bat (Plecotus phyllotis). These fleas were of the species Myodopsylla collinsi, which are common enough ectoparasites of the Little brown bats (Myotis sp.) in Arizona (Bradshaw and Ross, 1961). There is no record of their occurrence on the Big-eared bat. They appeared to have been "snapped up," with little or no attempt to chew them. It is conceivable that they invaded the fur of the Big-eared bat, perhaps from an association with the Little brown, and that the former responded with their extermination by ingestion.

Because of the overwhelming number of insects in a given area, it is hard to consider competition for food between species of bats, or between bats and birds, as more than incidental. One may often see crepuscular bats and birds feeding at the same time on apparently the same type of insects, but they may be selecting different size ranges or different species of prey. An example of prey-size range selection could be offered by description of the feeding habits of a hypothetical bat; this raptor feeds on prey of from 15 to 45 mm -- with 30 mm being the optimal -- but can and will on occasion take an insect up to 100 mm. However, other species of predators may overlap the above range in part of their prey selection, but usually the staple food-items are far removed taxonomically (although these hunters may appear to occupy the same habitat). Of course, on opportunistic food items (e.g., swarming ants) all raptors will be taking these temporarily abundant insects at the time, but feedings together occur at irregular intervals.

It has been suggested that bats and certain birds (such as swallows) may compete for food. Van Gelder and Goodpaster (1952) report such competition between the violet-green swallows (Tachycineta thalassina) and the Western pipistrelles. They even noted that both predators attempted on one occasion to secure the same object of food at the same time. What is hard to understand about their report is that, although they shot six bats and one violet-green swallow apparently while making the above observations, they seem to have made no attempt to verify these "sight" feeding observations by comparing the contents of the digestive tracts.

Hall (1946) mentions that he had seen Western pipistrelles and nighthawks flying together toward a good feeding ground.

A similar observation was reported by John Wright (personal communication) where he and Clyde Jones observed several (four?) swallows pursuing and diving at a bat (presumably an Eptesicus fuscus) that was flying in early evening on 10 July 1960, along Jemez Creek, Jemez Mountains, Sandoval County, New Mexico.

Davis (1939) notes the common occurrences of Pipistrelles and cliff swallows (Petrochelidon albifrons) in the same feeding areas, but he indicated there was no overlapping in selection of prey.

In an attempt to gain a better understanding of the possible competition between birds and bats, the author analyzed contents of 183 stomachs of three species of owls (Otus asio, 114; O. flammeolus, 46; O. trichopsis, 23). These owls and the Pallid bat were selected for this comparative study because all occur in the same varied habitats, share the same general nocturnal feeding periods, and have wide distributional ranges.

The Pallid bat perhaps echolocates in order to obtain much of its prey, while the owls must depend on vision, and possibly hearing, to locate their prey. Yet, it is reasonable to assume that they both must use vision to locate ground-wandering prey.

However, in my study, except for the mutual selection of Jerusalem crickets (of the owls, primarily prey for O. asio), these predators have few food-items in common. All three species of owls are efficient predators on scorpions. The contents of the digestive tract of one owl yielded 12 scorpions besides a tremendous amount of other prey. The flightless darkling beetles (Euschides, Edrotes, Eleodes), that are fairly abundant in the diet of the Pallid bat, are almost completely lacking in the diets of the owls as are most types of tenebrionids. Jerusalem crickets, however, are widely utilized by both owls and bats. The large screech owl, O. asio, feeds on a wide spectrum of prey species, in a size range approximating that of the prey of the Pallid bat; but most are large, ground-dwelling arthropods. Both O. trichopsis and O. flammeolus take much more in the way of flying forms, but in many instances of a size range below or just within the lower limit of that noted for the Pallid bat.

To summarize the feeding habits of the Pallid bat, it is a very generalized feeder on the larger insects that occur in its habitat; and apparently actively seeks out, visually, ground-inhabiting flightless insects, especially Jerusalem crickets.

Not to be confused with swarming is the periodic, or cyclic, eruption of most insects in which there is a tremendous increase in the population density of a species, over an extensive geographic area. Such outbreaks occur at more or less regular intervals from year to year. These high population densities of a given stage of an insect are usually of a long duration (that is, at least several days). Many insectivores with a wide feeding range take advantage of the sequence of these periodic increases of various forms (e.g., sphingid moths, long-horned beetles) during the summer months. As many of the winged raptors naturally take winged insects, the adult forms of prey, therefore, are more heavily victimized. Other arthropods apparently maintain a fairly uniform population density. Some of these (i.e., Jerusalem crickets, scorpions) are actively sought out as prey regardless of their abundance. Jerusalem crickets, for example, appear to be a food-item utilized in large numbers by many predators including bats, screech owls, and even skunks. Dixon's food table for Mephitis (1925) shows that some stomachs contained only these crickets.

The ability to prey upon a wide spectrum of arthropodous types and orders must be advantageous to animals with large distributional ranges, such as the Pallid bat, in that as various types of insects become scarce (smaller distributional range, or any other factors causing a population reduction) these predators are able to replace such prey with similar life-forms, or to utilize other available insects. Of course, even in a given area when the prey level may be reduced, they have an obvious advantage over other more restricted predators.

As has been noted by Dice (1952), "Each species of predator is especially adapted for capturing and devouring its prey which, in general, falls within a fairly well-circumscribed size class. In times of food shortage, however, prey of a size smaller or larger than usual may be utilized."

Moreover, it may be further stated, at least for the insectivorous forms, when unusual prey is utilized it is usually larger than, or else falls within, the upper limit of the prey selection range, with only exceptional feeding occurring below the lower limit.

It is noted by Powell and Stage (1962) that robberflies (predacious dipterans) will utilize larger prey when their more desirable prey is scarce, and that "At a lower limit visibility probably becomes a factor in conspicuousness and at upper limits ease of capture undoubtedly is of importance." Visibility is most likely an important factor for many nocturnal predators, especially owls.

Then there are examples of opportunistic feedings (on temporarily abundant prey not normally sought), particularly when animals such as ants and termites are swarming. Often the majority of the raptors (and even omnivores) will avail themselves of this immediate, but temporary, food supply regardless of the availability of their usual prey.

It seems that when raptors that ingest their prey feed outside of the upper limit of their prey size range, they can not handle the food in the normal manner. Their fragmentation of the insect is usually poor, resulting in large indigestible chunks, thus decreasing the efficiency of digestion. An isolated example of this is the case of a Flammulated Owl (Otus flammeolus) that apparently choked to death on a rather large long-horned grasshopper stuck in its throat (Kenyon, 1947).

Lack (1954), in an analysis of food as a limiting factor in the number of birds, lists four arguments in support of this assumption. Although this study was designed primarily for birds, many of those considered are insectivores. There are some far reaching conclusions that are worthy of consideration for raptors in general. His first argument is purely negative, as he admits, in which food is ranked over predation and disease as the likeliest cause of density-dependent loss. The second argument is that birds are usually more numerous where their food is more abundant. This needs no additional comment. A third argument for thinking that birds are limited in numbers by their food supply is that each species living in the same region depends on primarily different foods. As he states, "If food were not limiting numbers, it is hard to see why such differentiation in feeding habits should have been evolved, but its evolution is essential to survival if food is limiting, since . . ."

There is being practiced by some modern authors an undesirable tendency to synonymize competition and evolution. Hubbs, at the vertebrate speciation symposium (In Blair [ed.], 1961) stated, "the idea that the concept of competition can be extended to include all of natural selection or all of evolution is nonsense, because in the first place there are many relationships of animals and evolution besides tooth-and-death struggle."

Availability of food, of course, is one of the environmental factors operating on any biological organism; however, many other factors (e.g., climate, shelter) are also exerting pressure. It is possible to conceive that biological forms may be affected by ecological and genetic factors that will tend to alter their feeding habits regardless of the density of the food. In regard to natural selection without competition, Birch (1957) notes, "the frequency of a genotype in a sexual cross-fertilizing population may be altered by selection which does not involve any shortage of common resources."

Mayr elaborates on competition (1963) as follows: "There has been a tendency in recent years to exaggerate food as the controlling factor in competitive situations.

As a matter of fact, many other controlling factors must be considered. In the tropics, for instance, food appears to be less important than in the temperate zone, and in all zones competition may occur even where food is superabundant. . . . No unanimity has yet been achieved concerning the precise definition of competition, yet it always means that two species seek simultaneously an essential resource of the environment (such as food, or a place to live, to hide, or to breed) that is in limited supply."

However, I prefer Elton and Miller's definition of competition (1954) in that they exclude active consideration of the various resources of the environment: "Interspecific competition, in the more limited and correct use of the notion, refers to the situations in which one species affects the population of another by a process of interference, i.e. by reducing the reproductive efficiency or increasing the mortality of its competitor."

I suspect that as far as insectivorous species of animals are concerned there is no competition for food because insects are rarely in limited supply. This would relegate competition for food, in insectivorous forms, to a minor role. Perhaps, in times of great stress (relative lack of insects), food competition might assume a greater role, but probably only to the more restricted insectivores.

The overcoming of reduced insect populations in the winter months (at least in the Southwest) by bats has taken many forms: many insectivorous bats apparently migrate away from the continental United States (Myotis velifer, Tadarida brasiliensis); others go into hibernation (Antrozous pallidus, Eptesicus fuscus), and at least one (Macrotus californicus) may be able to modify its diet to include a greater proportion of plant materials.

Lack (1954), in support of his third argument, mentions a situation where four similar birds (Great Tit, Blue Tit, Coal Tit, and Marsh Tit) will feed together during a period when food, such as leaf-eating caterpillars, is temporarily superabundant. From this and several other examples, he suggests that "In these and other cases, several species feed together only when a particular food is very abundant, thus confirming the view that normal differentiation in feeding stations has been evolved to avoid competition for food." I strongly suspect that the above situation does not indicate any long range competition for food. It really only represents opportunistic feeding. Furthermore, the mere fact that similar animals come together temporarily to feed is no proof that they fed commonly together in the past, and have since diverged because of food-competition displacement.

Davis and Mumford, in their paper on the ecological habits of the Eastern pipistrelle (Pipistrellus subflavus), note (1962) many examples of common feedings with other bats for this bat. They report that Pipistrelles commonly feed without conflicts with Red bats (Lasiurus borealis) and Big brown bats (Eptesicus fuscus). Other species noted occasionally to share common feeding grounds are Hoary bats (Lasiurus cinereus), Evening bats (Nycticeius humeralis), Indiana bats (Myotis sodalis), and Silver-haired bats (Lasionycteris noctivagans). However, it appears that all of these reports of common feedings are based on field observations and not on digestive tract analyses.

The general prey selection, both in regard to types and size range, is similar for both Brazilian free-tails and Pipistrelles. This is not surprising, for I have often observed these two kinds of bats feeding together in the same areas. Perhaps the Free-tailed bats are more tolerant of prey species. Their stomachs are often filled by a given prey (such as hemipterans), which, in the Pipistrelles' stomachs, may only amount to a few of these forms. Perhaps this indicates that the Pipistrelles had sampled this type of prey and found it wanting.

As noted above, some of the Brazilian bats start their foraging in the crepuscular periods, along with the Pipistrelles. These common feedings apparently involve selection of prey (e.g., leafhoopers) that are not of an opportunistic situation. Yet, in these forms which apparently overlap with regard to prey and size range selection, I have still to observe any antagonistic behavior on the feeding grounds.

With regard to the other important requirement, shelter, these bats do not compete. One is a colonial cave bat, while the other is a solitary crevice dweller. For these reasons, Tadarida brasiliensis and Pipistrellus do not appear to be competitors, in the sensu stricto definition of competition formulated by Elton and Miller (1954). It should be clearly understood that these are the only two insectivorous bats of different genera that I observed with similar feeding habits, and moreover, occurring together on the same feeding grounds. Although other species may share certain food-items (compare the California leaf-nosed and the Pallid bats' food habit listings), each have their own peculiar feeding stations.

Brazilian free-tailed bats feed on very small insects, as small as two millimeters. The overall size range of the prey is 2 to 10 mm (but they will take prey up to 25 mm long), with about 5 mm as average length. They chew their food quite finely. They have a wide range of prey selection as to orders of insects, taking any that occur as small flying forms, the smaller moths, beetles, and true bugs. They appear to be opportunistic with regard to the selection of flying ants.

In times of reduced availability of prey (i.e., winter months), the Brazilian free-tailed bats migrate southward from the continental United States, while the Pipistrelles remain, with greatly reduced foraging activity. However, this is not ipso facto a case of food-competition displacement, and, most likely, for the Free-tails is a cold tolerance displacement, or really a genetically based immigration.

Marshall, (1957) in categorizing his concept of "joint feeding" notes that "Some birds are versatile enough in their foraging behavior to take advantage of unusual concentrations of food." He cites numerous examples of joint feedings; on one occasion he observed such obviously different birds as Red-shafter Flickers, Acorn Woodpeckers, Cassin Kingbirds, and Western Wood Pewees in continuous high flight catching small hymenopterans, thus for the moment adopting the feeding method of swallows.

Surely the common feedings mentioned above, and all of the examples noted by Dr. Marshall, do not imply that these birds ever fed at the same feeding station and have since, in time, diverged, returning to a "former" similar feeding station only in times of superabundance of food.

I therefore would like to limit the concept of competition in regard to food to the "everyday staples" of their diet, and not include in this term the situations in which food is temporarily superabundant in nature, for it seems that no form can wholly adapt to food that is available to it only temporarily and is not essential to its food habits.

CONCLUSIONS

Although most bats catch their prey while both are in flight, there are two notable exceptions. The Pallid bat typically preys on large ground-dwelling insects and scorpions for a small portion of its diet and the California leaf-nosed bat occasionally preys on larval insects that occur on vegetation. The latter is more or less omnivorous and feeds on plants, at least on fruit.

The Pallid bat takes apparently all large flying insects (20 to 70 mm) that occur in its habitat. One can not help being impressed by the large amplitude of prey species utilized by this insectivore, allowing it to occupy many habitats. However, there appears to be selectiveness when it preys on large ground-dwelling forms. This species, like the California leaf-nosed bat, has the unusual behavior of using a feeding roost to which it brings large insects and there feeds on the abdomens of these prey species.

The Leaf-nosed bat, perhaps because of its omnivorous habits, appears to not have a definite size range of species on which it preys.

For various reason, but mainly lack of adequate material, no size range of prey was indicated for the following bats: Cave, Red, Yellow, Evening, Allen's big-eared, Pocketed free-tailed, Big free-tailed, and Underwood's mastiff. Yet, as much as could be discerned from analyses of their digestive tracts was reported (such as the species, the size of the insects).

Of all bats studied, the crepuscular Western pipistrelles and the more nocturnal Brazilian free-tailed bats appear to be the only species with similar feeding habits. Both select prey species with body lengths of 2 to 10 mm (up to 25) with about 5 mm as the average length (of the same orders of insects). According to the definition of competition offered by Elton and Miller (1954) in the sense of "reducing the reproduction efficiency or increasing the mortality of its competitors", no competition between these bats was observed.

The food preferences of the Eastern pipistrelle appear to be very similar to those noted for the Western pipistrelles.

The Hoary bat appeared to be more restrictive, as far as orders of insects selected. It actively selects only moths in a size range of 6 to 30 mm, with an average length of 20 mm suggested with hesitation.

Another restricted insectivore is Townsend's big-eared bat. It also feeds on moths, selecting those of a size range of 3 to 10 mm, with an average of possibly 6 mm. The reason for these indefinite averages is the finely masticated condition of the prey which precluded finer measurements.

Although the Spotted bat was noted to have fed only on moths (8 to 12 mm), this analysis was based on the contents of but 5 digestive tracts and the earlier analysis of guano.

I have now contributed two conflicting reports based on two separate food habit analyses of the Greater mastiff bat. The second analysis is probably the more reliable in that the diet included large flying forms such as sphingid moths (ca. 60 mm). This is the largest bat in the continental United States (with an extremely large gape) and one would expect it to feed on the larger insects.

As a result of these studies I have reached the following major conclusions.

Each species of strictly insectivorous bats selects types of prey species that are within a more or less wide but definite size range of body lengths. There appears to be a given size for the majority of insects selected and when the selections are outside this given size, the length of the prey species are usually in the upper limit of the size range.

Generally, larger species of bats take larger insects. The only apparent exception is the Greater mastiff bat, Eumops perotis, a large species. In the only two detailed studies of this species I have detected two opposing food preferences. I suggest that possibly my original study which involved, together with digestive tracts, an analysis of guano, may have contained contaminative materials. It is strongly indicated that analyses of the contents of digestive tracts are preferable to analyses of guano because of the more direct and reliable association of the material and the bats.

There appear to be three basic methods of obtaining prey species utilized by insectivorous bats. Pallid and Leaf-nosed bats apparently use vision for detecting prey, especially insects that are found on the ground and vegetation. Other species (e.g., Pipistrelles and Brazilian free-tails) utilize the dense flights of crepuscular insects and appear to filter feed, without individual pursuit. Lastly, there are bats (e.g., Hoary and Big-eared) that echolocate in pursuit of individual prey.

Insectivorous bats are found to have two feeding periods. The post meridiem period is the more productive of the two. In many instances the more successful hunters of a given species obtain their fill rather quickly within the early minutes of this period (e.g., stomach filled in approximately 30 minutes). The ante meridiem feeding period, when utilized, offers less opportunity for successful hunting. The evening feeding period begins at twilight or shortly afterwards in complete darkness (zero solar radiation). Depending on the species of bat, this period may last to 12 A. M. The second feeding period begins at 3 A. M., and may last into the twilight of the morning.

The orders of insects most frequently preyed upon are moths (Lepidoptera), beetles (Coleoptera), grasshoppers (Orthoptera), true bugs (Hemiptera and Homoptera), and flying ants (Hymenoptera). Moths and beetles, both very large groups, have so many diverse types of so many sizes (from one mm up) that they may be available as universal food items for insectivores. At least the flying Orthopterans are, for the greater part, large forms (i.e., 15 mm or over). True bugs have many small flying types, and especially have dense flights, particularly in the twilight period, when most predation upon them occurs.

Flying ants are utilized by raptors as an opportunistic food item. They must be considered opportunistic food because of their irregular swarming. Being weak fliers, flying ants are easy to capture and are taken for food regardless of the typical feeding limits of the predator. Yet even ants, when taken in opportunistic feeding, are usually only utilized when they are in the upper limit of size range of food items.

Many orders of insects are not used for food by winged predators because their members are mostly small and flightless, or solitary fliers, or dirunal in habits. For example, two-winged flies (Diptera) are not taken in great numbers, although many of them are in the right size range. As a rule they do not make dense crepuscular or nocturnal flights, although the nematoceran Diptera are an exception.

These flies, however, are usually so small or such agile fliers that they seem to escape predation.

Unfortunately for the identifier of the insect remains, bats that pursue individual prey appear to approach their intended target (presumably of the acceptable length) from the rear and in a single snap engulf their victim. The closing of the bat's mouth usually shears off the head capsule and wings, which are lost. These parts for many forms (e.g., moths and flies) are the critical taxonomic structures.

Competition for food between bats or with other nocturnal insectivores was not observed in this study, probably because insects are usually very abundant.

LITERATURE CITED

Allard, H. A.

1937. Activity of the screech owl. Auk, 54:300-3.

Allen, G. M.

1939. Bats. Harvard Univ. Press, Cambridge, x + 368 pp.

McAtee, W. L.

1912. Methods of estimating the contents of bird stomachs. Auk, 29:449-64.

Bailey, V.

1905. Biological survey of Texas. N. Am. Fauna, 25:1-222.

Bailey, V.

1931. Mammals of New Mexico. N. Am. Fauna, 53:1-412.

Bailey, V.

1936. The mammals and life-zones of Oregon. N. Am. Fauna, 55:1-416.

Birch, L. C.

1957. The meaning of competition. Am. Nat., 91:5-18.

Bishop, S. C.

1947. Curious behavior of a hoary bat. J. Mamm., 28:293-4.

Blair, W. F. [ed.]

1961. Vertebrate Speciation. Univ. Texas Press, Austin, xvi + 642 p.

Borell, A. E.

1942. Feeding habits of the pallid bat. J. Mamm., 23:337.

Bradshaw, G. VR., and A. Ross

1961. Ectoparasites of Arizona Bats. J. Ariz. Acad. Sci., 1:109-12.

Burt, W. H.

1934. The mammals of southern Nevada. Trans. San Diego Soc. Nat. Hist., 7:375-428.

Burt, H. W.

1938. Faunal relationships and geographic distribution of mammals in Sonora, Mexico. Univ. Michigan Press, Misc. Publ. No. 39:7-77.

Campbell, C. A. R.

1925. Bats, Mosquitoes, and Dollars. Stratford Co., Boston, Mass., viii + 262 p.

Constatine, D. G.

1952. A program for maintaining the free-tailed bat in captivity. J. Mamm., 33:395-7.

Davis, W. B.

1939. The Recent Mammals of Idaho. Caxton Printers, Ltd., Caldwell, Idaho, vii + 400 p.

Davis, W. B.

1960. The mammals of Texas. Texas Game and Fish Comm., Bull. No. 47:1-252.

Dice, L. R.

1952. Natural Communities. Univ. Michigan Press, Ann Arbor, x + 547 pp.

Dixon, J.

1925. Food predilections of predatory and fur-bearing mammals. J. Mamm., 6:34-46.

Durrant, S. D.

1935. Occurrence of the spotted bat in Utah. J. Mamm., 16:226.

Elton, C. S., and R. S. Miller

1954. The ecological survey of animal communities: with a practical system of classifying habitats by structural characters. J. Ecol., 42:460-96.

Engler, C. H.

1943. Carnivorus activities of big brown and pallid bats. J. Mamm., 24:96-7.

Frost, S. W.

1959. Insect Life and Insect Natural History. Dover Publ., Inc., New York, viii + 526 p.

Gates, W. H.

1936. Keeping bats in captivity. J. Mamm., 17:268-73.

Van Gelder, R. G., and W. W. Goodpaster

1952. Bats and birds competing for food. J. Mamm., 33:491.

Goldman, E. A.

1926. [Review] Bats, mosquitoes, and dollars. J. Mamm., 7:136-8.

Gould, E.

1955. The feeding efficiency of insectivorous bats. J. Mamm., 36:399-407.

Gould, E.

1959. Further studies on the feeding efficiency of bats. J. Mamm., 40:149-50.

Griffin, D. R.

1958. Listening in the Dark. Yale Univ. Press, New Haven, xviii + 413 p.

Griffin, D. R.

1959. Echoes of Bats and Man. Doubleday and Co., Inc., Garden City, NY, 156 p.

Griffin, D. R., F. A. Webster, and C. R. Michael

1960. The echolocation of flying insects by bats. Animal Behav., 8:141-54.

Grinnell, H. W.

1918. A synopsis of bats of California. Univ. Calif. Publ., Zool., 17:223-404.

Grinnell, J.

1914. An account of the mammals and birds of the lower Colorado Valley. Univ. Calif. Publ., Zool., 12:51-294.

Gudger, E. W.

1925. Stitching wounds with the mandibles of ants and beetles. A minor contribution to the history of surgery. J. Am. Med. Assoc., 84:1861-4.

Hall, E. R.

1939. The spotted bat in Kern County, California. J. Mamm., 20:103.

Hall, R. E.

1946. Mammals of Nevada. Univ. Calif. Press, Berkeley, 710 p.

Hamilton, W. J., Jr.

1930. Notes on the mammals of Breathitt County, Kentucky. J. Mamm., 11:306-11.

Hamilton, W. J., Jr.

1933. The insect food of the big brown bat. J. Mamm., 14:155-6.

Hatt, R. T.

1923. Food habits of the pacific pallid. J. Mamm. 4:260-1.

Howell, A. B.

1920. Contribution to the life-history of the California Mastiff bat. J. Mamm., 1:111-7.

Howell, A. B.

1920. Some California experiences with bat roosts. J. Mamm., 1:169-76.

Huey, L. M.

1925. Food of the California leaf-nosed bat. J. Mamm., 6:196-7.

Huey, L. M.

1936. Desert pallid bats caught in mouse traps. J. Mamm., 17:285-6.

Keyon, K. W.

1947. Cause of death of a flammulated owl. Condor, 49:88.

Klopfer, P. H.

1962. Behavioral Aspects of Ecology. Prentice-Hall, Inc., New Jersey, 166 p.

Klugh, A. B.

1924. Notes on Eptesicus fuscus. J. Mamm., 5:42-3.

Koersueld, E. Van

1950. Difficulties in stomach analysis. Proc. Xth Intern. Ornith. Cong., p. 592.

Krutzsch, P. H.

1944. Notes on the little known pocketed bat. J. Mamm., 25:201.

Krutzsch, P. H.

1950. Carnivorous behavior in the big brown bat. J. Mamm., 31:91.

Krutzsch, P. H.

1955. Observations on the California mastiff bat. J. Mamm., 36:407-14.

Lack, D.

1954. The Natural Regulation of Animal Numbers. Oxford Univ. Press, London, viii + 343 p.

Lewis, J. B.

1940. Mammals of Amelita County, Virginia. J. Mamm., 21:422-8.

Marshall, Jr., J. T.

1957. Birds of pine-oak woodland in southern Arizona and adjacent Mexico. Pac. Coast Avif., 32:1-125.

Mathias, P., and J. Seguela

1940. Contribution à la connaissance de la biologie des chauves-souris. Mamm., 4:15-19.

Mayr, E.

1963. Animal species and evolution. Harvard Univ. Press, Cambridge, xiv + 797 p.

Nelson, E. W.

1918. Smaller mammals of North America. Nat. Geog. Mag., 33:493.

Nelson, E. W.

1926. Bats in relation to the production of guano and the destruction of insects. USDA Dept. Bull., No. 1395:1-12.

Orr, R. T.

1954. Natural history of the pallid bat, Antrozous pallidus (Le Conte). Proc. Calif. Acad. Sci., 28:165-246.

Pittman, H. H.

1924. Notes on the feeding habits of the little brown bat. J. Mamm., 5:231-2.

Poole, E. L.

1932. Breeding of the hoary bat in Pennsylvania. J. Mamm., 13:365-7.

Poulson, E. B.

1929. British insectivorous bats and their prey. Proc. Zool. Soc. London, I:277-303.

Powell, J. A., and G. I. Stage

1962. Prey selection by robberflies of the genus Stenopogon, with particular observations on S. engelhardti Bromley (Diptera: Asilidae). Wasmann J. Biol., 20:139-57.

Pye, J. D.

1961. Echolocation by bats. Endeavour, 20:101-11.

Ramage, M. C.

1947. Notes on keeping bats in captivity. J. Mamm., 28:60-2.

Roeder, K. D., and A. E. Treat

1961. The detection and evasion of bats by moths. Am. Sci., 49:135-48.

Ross, A.

1960a. Distribution records for Trichobius sphaeronotus Jobling, with a first report for Arizona (Diptera: Streblidae). Pan-Pac. Ent., 36:81-2.

Ross, A.

1960b. Notes on Trichobius corynorhini on hibernating bats (Diptera: Streblidae). Wasmann J. Biol., 18:271-2.

Ross, A.

1961a. Biological studies on bat ectoparasites of the genus Trichobius (Diptera: Streblidae) in North America, North of Mexico. Wasmann J. Biol., 19:229-246.

Ross, A.

1961b. Notes on food habits of bats. J. Mamm., 42:66-71.

Sherman, H. B.

1930. Birth of the young of Myotis austroriparius. J. Mamm., 11:495-503.

Sherman, H. B.

1935. Food habits of the Seminole bat. J. Mamm., 16:224.

Sherman, H. B.

1940. Notes on the food of some Florida bats. J. Mamm., 20:103-4.

Snodgrass, R. E.

1935. Principles of Insect Morphology. McGraw-Hill Book Co., Inc., New York, ix + 667 p.

Sprague, J. M.

1938. Notes on hibernating bats. J. Mamm., 19:500.

Stager, K. E.

1939. Status of _Myotis_ _velifer_ in California, with notes on its life history. J. Mamm., 20:225-8.

Stager, K. E.

1943. California leaf-nosed bat trapped by desert shrub. J. Mamm., 24:396.

Storer, T. I.

1926. Bats, bat towers and mosquitoes. J. Mamm., 7:85-90.

Townsend, C. H.

1887. Field notes on the mammals, birds and reptiles of northern California. Proc. U. S. Nat. Mus., 10:159-241.

Vaughan, T. A.

1959. Functional morphology of three bats: _Eumops_, _Myotis_, _Macrotus_. Univ. Kansas Publ., Mus. Nat. Hist., 12:1-153.

Vorhies, C. T.

1935. The Arizona specimen of _Euderma_ _maculatum_. J. Mamm., 16:224-6.