Opportunistic[1] feeding by desert bats (*Myotis* spp.)

M. B. FENTON

Department of Biology, Carleton University, Ottawa, Ontario K1S 5B6 and Department of Mammalogy,
Royal Ontario Museum, Toronto, Ontario

AND

G. K. MORRIS

Erindale College and Department of Zoology, University of Toronto, Mississauga, Ontario L5M 1C6
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By using a 'black light' and playback of sounds made by foraging insectivorous bats, we
examined opportunistic feeding behavior of bats near Camp Verde, Arizona, between 1 and 10
June 1975. Bats were significantly most active during 15-min periods when the light was on and
insects were aggregated over it. Bats feeding over the light selectively pursued and captured
larger insects, apparently ignoring the smaller ones. Bats did not respond to sounds simulating
feeding buzzes of bats, but showed a slight response to the foraging sounds of other bats.
Opportunistic feeding by insectivorous bats allows effective exploitation of patchily distributed
food resources and can lead to selective feeding when 'hatches' of insects are involved. Oppor-
tunistic feeding is not incompatible with selective feeding, and may eventually be established as a
strategy common to most insectivorous bats.

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Au moyen d'une lumière noire et d'enregistrements de sons produits par des chauves-souris
insectivores en train de se nourrir, on a étudié le comportement alimentaire opportuniste de
chauves-souris près de Camp Verde, Arizona, entre le 1er et le 10 juin 1975. Les chauves-souris
sont beaucoup plus actives durant les périodes de 15 min où la lumière est allumée et où les
insectes s'assemblent au-dessus. Les chauves-souris qui se nourrissent à la lumière pourchassent
et capturent de façon sélective les insectes les plus gros, ignorant, semble-t-il, les plus petits. Les
chauves-souris ne réagissent pas aux bourdonnements alimentaires simulés de chauves-souris,
mais manifestent une légère réaction aux sons d'autres chauves-souris en train de fourrager.
L'alimentation opportuniste des chauves-souris insectivores permet une exploitation très
efficace des ressources alimentaires dispersées selon une répartition contagieuse et permet
également une alimentation sélective lors des 'éclosions' d'insectes. L'alimentation opportuniste
n'est pas incompatible avec l'alimentation sélective et peut en fait servir de stratégie chez la
plupart des chauves-souris insectivores.

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Introduction

Bats are quick to exploit new roosting sites
(Brosset 1966; Fenton 1970a; Humphrey 1975)
and at least some species may be opportunistic
in their feeding. Barbour and Davis (1969) have
summarized several reports of *Lasiurus borealis*
feeding at concentrations of insects around light
traps, and many entomologists who use these
lights (in areas beyond the range of *L. borealis*)
have had to compete with bats for specimens
(H. F. Howden, personal communication).
Furthermore, Kunz (1974) has shown that

Myotis velifer adjusts its foraging patterns to
weather conditions, and T. A. Vaughan (personal
communication) has observed that several *M.
velifer* will converge on localized concentrations
of insects.

In spite of these observations, there appear to
be no published quantitative data concerning
opportunistic feeding by bats. We examined the
responses of bats to aggregations of insects in
a semiarid habitat where we suspected that
foraging bats might search for food over a
large area to avail themselves of patchily dis-
tributed insects. We also tested the responses of
bats to recorded bat foraging sounds and to

[1]Opportunism sensu Oxford.

artificial sounds simulating the feeding buzzes of hunting bats. The work was conducted on the floodplain of the Verde River, within 50 m of the river, and about 10 km south of Camp Verde, Arizona (ca. 34°25′ N; 111°30′ W), between 1 and 10 June 1975.

Materials and Methods

We used 15-min observation periods between 2030 and about 0100 hours Mountain Standard Time to study the responses of the bats. A typical schedule covering the period 2030 to 0115 hours on the night of 8–9 June was as follows: light, control, artificial bat sounds, control, light, control, playback of foraging sounds, control, light, control, artificial bat sounds, control, and light. 'Control' periods (no playback, no artificial bat sounds, no light) were always interspersed between 'experimental sessions.' We used t-tests to compare the results.

To foster local concentrations of insects, we placed an F15T8/BL 18-in. 'black light' on the ground. Within 1 min of turning on the light, flying insects began converging near it, and depending upon the wind conditions, there was usually a concentrated cone of small flying insects (mainly Trichoptera, Diptera, and Coleoptera) extending to about 2 m above the ground. Larger insects (mainly Lepidoptera and Coleoptera) flew around over the light and through the swarm of smaller insects. When ambient temperatures dropped below 20 °C, the numbers of insects declined markedly.

The sounds of bats were recorded on a Lockheed 417 instrumentation tape recorder at 76 cm/s as the animals foraged over the light. The microphone (Bruel and Kjaer $\frac{1}{2}$-in. 4133) was mounted on a mast 3 m above the ground. The base of the mast was 4.75 m from the black light, while the microphone was aligned parallel to the ground and directed toward the insect aggregation above the light. Artificial bat sounds (10- to 20-s bursts of frequency-modulated pulses, each pulse 10 ms in duration sweeping down from 60 kHz to 10 kHz) were produced with an Exact (model 126) sweep generator. The recorded feeding sounds and the artificial sounds were broadcast using a power amplifier and speaker built to the specifications outlined by McCue (1961). The speaker was mounted on the mast alongside the microphone and facing in the same direction.

Bat foraging sounds played back through this system showed increasing intensities through the trains of pulses. Individual pulses within a train often reached intensities of 80–90 dB at 10 cm from the speaker, and sometimes exceeded 90 dB. Sounds produced artificially had intensities of 101 dB at 10 cm from the speaker. We measured these sound levels using the linear scale of a B and K 2204 sound-level meter on impulse setting, and a B and K 4133 microphone.

Bat activity was monitored using a Holgate Ultrasonic Detector tuned to 40 kHz, and during playback of the bat foraging sounds, the B and K 4133 microphone and a Tektronix 5103N oscilloscope. Bat activity was measured as 'bat passes' (sensu Fenton 1970b). We also observed bats active in the area over the light and in front of the speaker and microphones through a Zoomar Night Vision Scope.

The observers were positioned at a vantage point 3 m from the base of the mast (7.75 m from the light), and the tape recorder, oscilloscope, power amplifier, and signal generator were 10 m behind the observers (17.75 m from the light). Power for the apparatus was provided by a Pincor GRF 1800 generator located 100 m from the study site. A Hammond 174H autotransformer was interposed between the end of the extension cord and the aforementioned equipment.

The Bats

We trapped (Tuttle 1974) seven species of bats at various locations along the river and the cliffs at the edge of the floodplain, including 63 Myotis yumanensis, 22 M. velifer, 12 Antrozous pallidus, 8 Pipistrellus hesperus, 8 Tadarida brasiliensis, 1 Myotis leibii, and 1 Plecotus townsendii. Vaughan (personal communication) has also found Eptesicus fuscus in the vicinity. Based on capture frequencies in the trap within 50 m of our study site, and on the distinctive sizes, flight patterns, and foraging habits of M. leibii, P. hesperus, and A. pallidus, we feel confident that the bats whose activity we monitored over the light and around the speaker were mostly Myotis, and probably M. yumanensis. None of the M. velifer was caught within 500 m of our study site.

However, analysis of the tape that we used for playback indicated that at least two species of bats foraged over the light: the Myotis which was detected by the Holgate (tuned to 40 kHz), and an unidentified bat whose primary echolocation sounds (20–35 kHz) were not detected by the Holgate tuned to 40 kHz. Therefore, although at least two species of bats fed over the light, the data reported below pertain only to one, presumably Myotis yumanensis.

Results

During this study we made observations over ninety 15-min periods including 47 controls, 26 light, and 17 playback situations (12 of foraging sounds and 5 of artificial bat sounds). Bat activity averaged significantly higher ($p < 0.001$) during the periods when the black light was turned on, but there were no significant differences between average activity levels during control or either of the playback situations (Table 1). However, activity levels were quite variable, as indicated by the very large standard deviation values (Table 1), and this warrants consideration of the observations in more detail.

During 20 of the 26 periods when the light was operated, the levels of bat activity were sharply different from adjacent controls (e.g. 57 vs. 3 or 7 bat passes; 10 vs. 0 or 1; 131 vs. 2 or 69), and on 37 of the 47 control periods, the number of bat passes was less than 10 ($\bar{x} = 2.65 \pm 2.45$). These data indicate that during some light periods (6 of 26) there was relatively

TABLE 1. Activity of bats during control and experimental periods

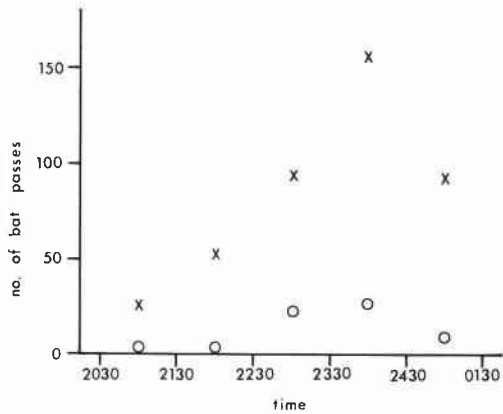| | Control | Light | Sound | |
			Bat foraging	Artificial bat noises
Sample size*	47	26	12	5
Mean no. bat passes	10.96	63.19	14.42	21.00
Standard deviation	20.37	50.33	15.67	33.69

*Number of 15-min observation periods.

FIG. 1. The average number of bat passes during control (○) and light (×) periods between 2030 and 0130 hours Mountain Standard Time. Sample sizes for controls from 2030 hours: 13, 14, 12, 6, and 3 fifteen-minute periods. The comparable numbers of the light periods are 7, 9, 6, 2, and 2 fifteen-minute periods.

little bat activity, and during some control periods (10 of 47), the levels of bat activity were high.

In general, insects around the light elicited little response from the bats for the first hour after dark (2000 to 2100 hours), while by 2300 hours, more bats were active and feeding (Fig. 1). Therefore, both light and control periods before 2100 hours had relatively low levels of bat activity, and both conditions had higher activity between 2230 and 2430 hours (Fig. 1). The absence of bats from the light before 2100 hours did not correspond to a paucity of insects around the light, but to high levels of bat activity along the Verde River (documented by observation and listening to the bats). This gave the impression that the bats went initially to the river (perhaps to drink and forage), and subsequently spread out over the floodplain (2100 hours). From 2430 or 0100 hours on, there

was an overall decline in bat activity corresponding to temperatures below 20 °C and to fewer insects.

Evidence that the bats were feeding during periods of high activity is provided by the numbers of feeding buzzes recorded during periods of observation. We counted feeding buzzes during nine light periods when they averaged $29 \pm 13\%$ of the bat passes recorded. The comparable average for 23 control periods was $11 \pm 17\%$. However, although we heard feeding buzzes during all of the nine light periods, they only occurred during 8 of the 23 controls, when they averaged $32 \pm 10\%$ of the bat passes. This figure is not significantly different from that recorded during the light periods, indicating that the feeding behavior pattern was not disrupted by the light.

During periods when there was a marked response (20 of 26) to the light, the bats apparently reacted very quickly. We measured the time between when the light was turned on and the appearance of the first bat for 18 of the light periods, and this averaged 2.22 ± 1.48 min. It is possible that the bats used the light as a landmark and responded to it, rather than to the insects around it. However, the lack of significant change in response times between the start and completion of the study suggests no learned response. There were no other electric lights within 2 km of the study site, but the area was used extensively by campers and the response to light may represent an established learned response.

By watching through the Night Vision Scope, we were able to count the numbers of bats active over the experimental site. On 19 occasions when the light was on and we attempted to count the numbers of bats, the breakdown was as follows: two bats, seven times; three bats, four times; four bats, five times; and one, six,

and eight bats, one time each. Pairs of bats feeding together over the light often flew in formation, but we observed no obvious attempts on the parts of some bats to drive others away from the vicinity of the light. The bats feeding around the light appeared to concentrate on the larger insects, rarely venturing into the cone of smaller flying insects immediately above the light.

The differences between the average numbers of bat passes recorded during the control periods and the times when the foraging or artificial bat sounds were played back are not significant. On none of the five occasions when the simulated feeding sounds were broadcast did the level of bat activity exceed adjacent controls. However, on 3 of the 12 periods when bat-foraging sounds were played back, the levels of bat activity were much higher than adjacent controls (6 June—16 vs. 6 and 0 bat passes, and 17 vs. 3 and 1; and 7 June—13 vs. 5 and 1). Comparison of these values indicates significantly ($p < 0.005$) higher activity during the periods of playback of the foraging sounds of the bats.

Therefore, in spite of the general lack of significant differences, there is some evidence of response by bats to the foraging sounds of other bats. The lack of consistency in this regard may be due to several equipment factors. The signal produced by the speaker was very directional, and we did not rotate or otherwise move the speaker around during playback. Furthermore, as a result of the characteristics of the B and K $\frac{1}{2}$-in. microphone, substantial components of the bat vocalizations above 50 kHz were missing from the recordings.

Observation during the playback periods revealed that some bats flew directly towards the speaker, veering away just before colliding with it. During the three periods of playback when there were strong responses (increases in the levels of bat activity relative to adjacent controls), only one bat seemed to be involved.

Discussion

The results of this study clearly indicate that the bats we observed were opportunistic feeders, quick to locate and exploit local concentrations of insects, from which they appeared to take the largest appropriate individuals. Bryant (1973) has made similar observations of house martins (*Delichon urbica*) that probably fed in shelter belts, selecting the largest suitable insects from natural heterogeneous (by species) concentrations.

Opportunistic feeding is not incompatible with selective feeding as reported for some species of bats (Buchler 1973; Fenton 1975). In fact, when bats exploit 'hatches' of insects, which often represent large numbers of one or two species, selectivity is the result of opportunistic feeding. However, opportunistic feeding as demonstrated in this study did not involve random feeding (cf. 'filter feeding' of Ross 1967), for the bats we observed invariably pursued and caught the larger insects attracted to the light, apparently ignoring the highly abundant smaller ones.

Therefore, an insectivorous bat feeding on local concentrations of one or two insect species will appear to be highly selective in its diet, while one selecting some insects from a concentration which includes a variety of prey species is being both selective and opportunistic. The actual selection of prey will be influenced by characteristics of predator and prey. For example, Vaughan (1976) observed that the direct flight of sphingid moths made them more vulnerable to *Cardioderma cor* than moths with erratic flight paths. This situation may also explain the relatively large proportion of sphingids taken by *Nycteris thebaica* (Fenton 1975).

Both bats which establish and use foraging territories, and other species which do not, may be opportunistic feeders. Vaughan (1976) found that individual *C. cor* set up feeding territories and moved throughout them hunting from suitable perches, a strategy which allowed the exploitation of localized concentrations of prey within the territory. Refuging species such as *Myotis velifer* (Kunz 1974) probably do not establish individual feeding territories, but move over large areas to locate insects. The *Myotis* we studied appeared to behave like lesser nighthawks (*Chordeiles acutipennis*), which converge on localized concentrations of food to permit efficient harvesting of the resource (Caccamise 1974).

When animals are spread out over an area searching for food, the use of noises associated with feeding (Fish 1954; Moulton 1960; Kruuk 1972; Schaller 1972) or specific behavior patterns (Frisch 1950; Gould 1974) that allow

others to locate the food would be adaptive. Although our data are not conclusive, they suggest that bats may use the foraging sounds of other bats to locate concentrations of food.

We suspect that most insectivorous bats will eventually be shown to be opportunistic feeders, a strategy compatible with their size and physiological requirements with respect to body temperature (McNab 1970).

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