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Food and feeding habits of insectivorous bats from Israel

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Abstract

Small numbers of fecal pellets were examined from nine of the 32 species of insectivorous bats from Israel. Based on these small samples, *Asellia tridens* and *Pipistrellus bodenheimeri* were lepidopteran/dipteran and lepidopteran/dipteran/coleopteran feeders, respectively; *Myotis nattereri* fed primarily on lygaeids and coleopterans; *Otonycteris hemprichi* fed exclusively on coleopterans; *Pipistrellus kuhlii* fed on hymenopterans and coleopterans; *Pipistrellus rueppelli* and *Tadarida teniotis* fed mostly on lepidopterans and coleopterans; *Plecotus austriacus* fed exclusively on lepidopterans, and *Rhinolophus clivosus* was a generalist feeder, taking several different kinds of insect prey. Information on dietary analysis is supplemented with direct observations on the foraging habits of these bats.

Introduction

Knowledge of an animal's diet is important for interpreting its ecological role as a predator and its impact on local environments. Such knowledge is especially important as natural habitats are being altered owing to increased urbanization, modern agricultural practices (intense irrigation and pesticide applications), and deforestation. In recent years, the use of pesticides in Israel was rated second in the world per capita (Makin 1989). Thus, knowledge of their insect prey is important for assessing the potential value of bats in controlling insect pests, especially in areas where urban and cultivated lands have replaced natural habitats.

There have been a limited number of observations on food habits and foraging behavior of bats in Israel (Makin 1987; Bates and Harrison 1989; Harrison and Bates 1991; Yom-Tov 1993; Yom-Tov et al. 1992a, b), and only one substantial report on foraging behavior (*Pipistrellus kuhlii,* Barak and Yom-Tov 1989). Yom-Tov's (1993) analysis of morphological characters of insectivorous bats in the Dead Sea area is the most comprehensive account of foraging characteristics of bats in Israel. The purpose of this study is to present preliminary information on food and feeding habits on selected insectivorous bats in Israel, based primarily on samples of fecal remains collected from bats captured at feeding sites. These results are supplemented by observations of foraging behaviour at sites where bats were captured.

Material and methods

Fecal pellets were collected from nine species of bats, eight of which were captured in mist nets set at feeding sites. These include *Asellia tridens, Myotis nattereri, Pipistrellus bodenheimeri, Pipistrellus kuhlii, P. rueppelli, Plecotus austriacus, Otonycteris hemprichi, Rhinolophus clivosus,* and *Tadarida teniotis* (feces from the latter species was collected at a roosting site). Following capture, individuals of each species were placed in holding bags allowing feces to be deposited before releasing the bats at the site of capture. Collection localities for each species are noted below. Most collection sites were located in the vicinity of the Dead Sea. A summary of the geography, climate, and vegetation in this region is given in Yom-Tov et al. (1992b).

We used fecal analysis to assess food habits so we could release the bats alive after collecting the feces for analysis. For insectivorous bats, this method is comparable to stomach content analysis (Kunz and Whitaker 1983). Contents of fecal samples were identified to family and analyzed using the methods described in Whitaker (1988). Each pellet was examined separately and the percent volume of each food item was estimated visually in each pellet. Most results are presented as overall percent volume (sum of individual volumes/total volume for the sample × 100) and percent frequency (number of pellets of occurrence/total number of pellets in sample × 100). Observations of feeding behavior were made at the time bats were captured and fortuitously at other times. These were supplemented by unpublished observations and those reported by Yom-Tov et al. (1992a, b). Unless otherwise noted, means and standard deviations for body masses of bats are from Yom-Tov et al. (1992b).

Results and discussion

Data on nine species of insectivorous bats known from Israel are summarized below.

Asellia tridens (12 pellets, 2–5 mm long, $\bar{x}$ = 4.9 mm, from Navit Pools). This bat ranges across northern Africa from Morocco and Senegal to Egypt and Ethiopia, Zanzibar, Arabian Peninsula to Pakistan. In Israel bats were captured over a fresh water pool surrounded by lush vegetation at an oasis south of the Dead Sea. All contained Lepidoptera (61,3 % volume, 100 % frequency) and all but one contained Diptera, mostly chironomids (38.8 % volume, 91.7 % frequency). Based on an analysis of 147 fecal pellets from this bat collected at an abandoned mine (North of Elat), the following prey items (expressed as percent frequency) were taken: Coleoptera (59), Hymenoptera (21), Orthoptera (14), Lepidoptera (3), Diptera (2), and Odonata (1).

This medium sized bat ($\bar{x}$ = 9.8 g ± 1.9 g) is known to take large insects (Tettigoniidae, Blattodea, and Lepidoptera) and transport them to underground shelters where they are consumed. The diet of *A. tridens*, as determined in the present study, is consistent with its habit of foraging over bodies of water and its use of Doppler-shift compensation (Gustafson and Schnitzler 1979), which may allow it to use information on the wing-beat frequency of certain insects to facilitate prey capture. The echolocating calls have the highest recorded frequency (around 121 kHz) among the bats in Israel. One of us (B. Shalmon) observed *A. tridens* flying around street lights in the settlements of Hazeva and En Gedi. This bat reportedly is nearly extinct in the Mediterranean zone in Israel, and is confined mostly to drier zones (Makin 1989). This bat is a highly desert-adapted species that reportedly roosts (and feeds) in the vicinity of oases (Gaisler et al. 1972). In Oman it has been observed flying near the ground and feeding in palm groves (Nowak 1991).

Myotis nattereri (2 pellets, both 4 mm long, from Zoarim Cave, Upper Galilee). This 9–11 g bat is a widespread species, ranging from northern Europe southward to Morocco, across central Asia to Japan. In Israel, individuals were captured in dense Mediterranean maquis, where it was also observed feeding. Four prey items were identified with percent volumes and frequencies as follows: Lygaeidae (42.5 %, 50 %), Coleoptera (42.5 %, 100 %), spider (10 %, 50 %) and Diptera (5 %, 50 %).

Compared with similar species of *Myotis* (e.g. *M. capaccinii*), the intensity of echolocation calls is very low. It has morphological adaptations for slow, maneuverable flight (Norberg and Rayner 1987); in Scandinavia this bat feeds along the contours of trees, often among the branches (Baagøe 1987). The relatively wide diversity of prey taken, including Diptera, suggests that it also feeds near water.

Otonycris hemprichi (11 pellets, 3–7 mm, $\bar{x}$ = 5.0, from Sapir). Bats were captured over a fresh water pool in arid habitat, surrounded by vegetation. All fecal pellets examined contained 100 % Scarabaeidae. This relatively large ($\bar{x}$ = 19.0 g ± 2.0 g) long-eared, desert-dwelling bat ranges from the arid regions of Morocco and northern Niger through Egypt and across the northern Arabian Peninsula to Kazakhastan and Pakistan (Nowak 1991; Harrison and Bates 1991). This bat flutters like a large butterfly over water and nearby vegetation (Yom-Tov 1993). In southern Kirghizia (central Asia) this bat has been

observed foraging close to rock surfaces (Rybin et al. 1989). Typical of gleaners, *O. hemprichi* is a low-intensity echolocating or whispering bat. At times it probably relies on vision and passive listening to locate its prey. Based on an analysis of its body mass and wing morphology (low aspect ratio and low wing loading), Fenton and Norberg (1988) postulated this bat should be carnivorous. In Israel it has been captured while foraging in a date palm grove and, in nearby Jordan, it has been captured over a small pool in an arid mountain gorge (Bates and Harrison 1989).

Pipistrellus bodenheimeri (14 pellets 2–4 mm long, $\bar{x}$ = 2.8). Fourteen pellets were examined from three different localities (Tab. 1). Overall, the most important food items included Lepidoptera, Coleoptera, and Diptera. Lepidopterans were the major food at two

Table 1. **Food as indicated by 14 fecal pellets from *Pipistrellus bodenheimeri* at three localities in Israel**

	Sapir 18. 5. 1988		En Gedi 3. 3. 1988 25. 4. 1988		Neot Hakikar 3. 7. 1989	
Number of Pellets	5		7		2	
	% vol.	% freq.	% vol.	% freq.	% vol.	% freq.
Lepidoptera	71.0	100	68.6	100	—	—
Chrysomelidae	19.0	100	—	—	—	—
Scarabaeidae	4.0	40	—	—	—	—
Insect	3.0	40	—	—	—	—
Coleoptera	1.6	20	—	—	37.5	50.0
Chironomidae	1.4	40	—	—	—	—
Diptera	—	—	30	100	62.5	100
Spider	—	—	1.4	14.2	—	—

localities followed by chrysomelid beetles at one and dipterans at the other. Dipterans were the principal food item followed by coleopterans at the third locality. This small bat ($\bar{x}$ = 2.7 g ± 0.2 g) is restricted to extreme desert areas in Israel, the Sinai Peninsula and the southwestern Arabian Peninsula (Nowak 1991; Yom-Tov 1993). It appears to be an opportunistic predator, although lepidopterans comprised most of its diet in our sample. It was collected in open desert habitats, around street lamps in the settlements of Elat, En Gedi, and over freshwater pools in nearby arid regions. Although this bat may hibernate from October through April in Israel, it has been observed feeding in all months of the year (Yom-Tov et al. 1992a). In winter, the number of bats feeding near street lights is considerably smaller than during the summer months. In the Arabian peninsula, this bat has been observed flying (foraging?) along rows of tamarisk and eucalyptus trees that were planted around a cultivated area surrounded by desert and acacia trees (Harrison and Bates 1991).

Pipistrellus kuhlii (5 pellets 2–5 mm, $\bar{x}$ = 3.4, from Upper Galilee). Parts of winged ants (alates) were the most important items collected from individuals captured near street lamps at Sasa (56 % volume, 100 % frequency), followed by Coleoptera (24 %, 60 %), Chrysomelidae (8 %, 20 %) Lepidoptera (6 %, 60 %), Cerambycidae (4 %, 20 %) and unidentified insect remains (2 %, 20 %). One of the most common bats in Israel, this small, $\bar{x}$ = 7.0 g ± 0.5 g, species is known from southern Europe, southwestern Asia, northern, eastern, and southern Africa, and the Canary Islands (Kingdon 1974; Nowak 1991). Its feeding activity occurs mostly within the first three hours following sunset and is characterized by low, fast feeding flights in open areas. In urban areas it feeds on flying insects attracted to street lights (Haffner and Stutz 1985–86) and over water (Vernier 1989). In east Africa, Kingdon (1974) noted that this bat was attracted to insects swarming around ripe fruits on a peach tree. Schnitzler et al. (1987) indicated that it relies on low

frequency echolocation calls (35–40 kHz), which is typical of bats feeding in open areas (NEUWEILER 1983).

BARAK and YOM-TOV (1989) suggested that the echolocation calls produced by *P. kuhlii* caused some of the flying insects attracted to street lights (none were identified) to disperse and thus improve an individual bat's ability to capture prey. Evidence for this hypothesis was based on the observation that feeding rates were highest at those sites whee foraging group size increased from one to five individuals. Feeding rates of individual bats were lower when fewer bats were present, suggesting that prey capture in *P. kuhlii* is enhanced by feeding in small groups.

Pipistrellus rueppelli (7 pellets 2–7 mm, $\bar{x}$ = 3.3, from Navit Pools). Six of seven pellets examined contained 100 % lepidopterans. The seventh contained 65 % Lepidoptera and 35 % (volume) unidentified material. This 7.0 g ± 0.5 g Afrotropical species ranges from Egypt to Senegal and south to Angola and Botswana (HARRISON and BATES 1991), and southern Iraq (YOM-TOV et al. 1992b). In Israel this bat was captured while flying over small freshwater pools. In East Africa, it is known from savannah and arid regions, where it has been observed flying (feeding?) along rivers at dusk (KINGDON 1974; SKINNER and SMITHERS 1990). LANG and CHAPIN (1917) reported *P. rueppelli* flying (feeding?) adjacent to oil palms in riparian habitat. SKINNER and SMITHERS (1990) noted that *P. rueppelli* is also associated with rivers and swamps.

Plecotus austriacus (5 pellets 3–6 mm, $\bar{x}$ = 4.0, from Sapir). Bats with long ears (e.g., *Plecotus* and some other genera) are often lepidopteran specialists (FENTON and NORBERG 1988). Judging from our findings, *P. austriacus* is indeed a lepidopteran specialist, as all pellets examined contained 100 % Lepidoptera. This low-intensity echolocating bat ($\bar{x}$ = 6.7 ± 1.1 g) is known from southern Europe and Northern Africa, westward to Mongolia and western China, Cape Verde Islands and Senegal (NOWAK 1991). As with other members of its genus, *P. austriacus* is known to hover and glean insects from vegetation and other surfaces (ROBERTS 1977). Its short, broad wings, and low flight speed (NORBERG and RAYNER 1987) presumably facilitate captures of resting insects in these situations. Judging from its small size and weak dentition, ROBERTS (1977) suggested that this bat probably feeds "mainly on smaller moths, spiders and lacewings (*Planipennia* sp.)".

Rhinolophus clivosus (5 pellets 2–7 mm, $\bar{x}$ = 4.2, from En Gedi). Even though the available fecal sample was extremely small, six separate prey items were taken: Coleoptera, probably Chrysomelidae (53 %, 80 %); Hymenoptera (31 %, 20 %); Lepidoptera (11 %, 80 %); Insect (2 %, 40 %); Scarabaeidae (2 %, 20 %) and Lygaeidae (1 %, 20 %). This medium size bat ($\bar{x}$ = 11.0 g ± 2.0 g) is known from central and southwestern Asia, and in Africa from Liberia and Algeria eastward to Cameroon (NOWAK 1991), and southward to Southern Africa (HARRISON and BATES 1991; SKINNER and SMITHERS 1990). When foraging it flies below tree-top level (RAUTENBACH 1982) and low around trees and shrubs. In Israel, individuals were captured as they flew low between trees in the desert oasis of En Gedi. Elsewhere, the food items taken by this bat includes moths and small beetles (SKINNER and *Smithers* 1990), although it sometimes eats large beetles (KINGDON 1990). This bat establishes feeding roosts on branches of trees and beneath verandahs of houses where individuals cull hard parts of insects before eating them (RAUTENBACH 1982).

Tadarida teniotis. Nine samples were available, all from Karmiel (Lower Galilee). Fifty pellets were selected from each of these samples. Pellets were selected in order to include all sizes, from largest to smallest. Pellets ranged from 3 to 10 mm long, but averaged about 6 to 7 mm. Prey items as indicated by these nine samples are shown in table 2. Lepidopterans were the most important food, ranging from 65.4 % to 87.6 % by volume of the total material examined. Of the 450 pellets examined, 442 or 98.2 % of them contained moths, whereas 215 of these pellets or 47.8 % contained 100 % of this material. Coleopterans, especially ground beetles (Carabidae) and June beetles (Scarabaeidae), were the second most important food items. The amount of beetles eaten ranged from 6.8 % to 27.3 %

Table 2. **Food of *Tadarida teniotis* (% volume) on Karmiel, Israel, as indicated by nine samples of 50 pellets each on 9 different dates**

Dates	17. 8. 1991	3. 9. 1991	15. 3. 1992	15.–16. 3. 1992	16.–17. 3. 1992	18. 3. 1992	23. 6. 1992	25. 7. 1992	25.–26. 7. 1992
LEPIDOPTERA	75.5	76.3	82.4	69.6	65.4	87.0	75.3	85.4	87.6
COLEOPTERA[1]	(21.5)	(17.6)	(15.6)	(27.3)	(22.9)	(6.8)	(12.1)	(11.2)	(7.2)
Scarabaeidae	8.7	8.0	2.0	15.4	11.6	4.9	2.4	3.8	1.8
Carabidae	7.5	5.9	9.7	8.3	9.0	0.2	7.8	2.7	0.8
Tenebrionidae	—	1.7	—	—	—	—	—	—	—
Chrysomelidae	4.2	0.5	3.2	0.3	0.2	—	—	0.1	1.7
Curculionidae	—	0.2	—	—	—	—	0.4	0.6	0.3
Unid. Coleoptera	1.1	1.3	0.7	3.3	2.1	1.7	1.5	4.0	2.6
HEMIPTERA/HOMOPTERA									
Lygaiedae	1.4	1.1	2.0	1.4	4.6	1.8	4.2	0.9	1.4
Cicadellidae	—	0.3	—	—	—	—	1.1	—	—
Green Pentatomid	—	—	—	—	0.3	—	—	0.5	—
Unid. Hemiptera	—	—	—	1.5	—	—	—	—	—
ORTHOPTERA									
Gyllidae	1.2	1.5	—	0.2	6.8	4.3	7.3	1.8	3.8
HYMENOPTERA									
FORMICIDAE	—	0.3	—	—	—	—	—	—	—
DIPTERA	0.3	0.2	—	—	—	—	—	0.1	—
NEUROPTERA									
Hemerobiidae	—	0.1	—	—	—	—	—	—	—
EPHEMERIDA	—	1.3	—	—	—	—	—	—	—
Unidentified Insect	—	1.4	—	0.1	—	—	—	—	—
ACARINA (mites)	0.02	—	—	—	—	—	—	—	—

[1]Total Coleoptera volumes are given in parentheses.

volume. Crickets (Orthoptera: Gryllidae) also were regularly eaten, with consumption ranging upwards to 7.3 % volume.

This relatively large insectivorous bat ($\bar{x}$ = 18.5 ± 2.0 g) has a wide distribution, ranging from Madeira, the Canary Islands, Morocco and the Iberian peninsula, eastwards through North Africa and southern Europe to southern China, Tiawan and Japan (Harrison and Bates 1991). *Tadarida teniotis* is a fast, high flying bat (Gaisler and Kowalski 1986) often observed 20–50 m above the ground where it feeds largely on moths. In Israel it is commonly observed flying above settlements and cities, feeding on such insects attracted to street lights. The high intensity, low frequency (12–14 kHz) echolocation calls of this bat are audible to humans. It is one of the most beneficial bats to farmers, which suffer heavy damage to crops from noctuid moths (e.g., *Spodoptera litoralis, Argotis ipsilon*, and *Earias insulana*). Other reports indicated that members of the genus *Tadarida* are often generalist feeders, but consume large numbers of moths (e.g., Ross 1967; Kunz et al. 1994).

Based on our preliminary dietary analysis of nine species of insectivorous bats from Israel, some appear to specialize either on coleopterans (beetles) or on lepidopterans (moths), whereas others are generalist predators. As in other species of insectivorous bats, food habits can be expeced to vary depending on the locality, season, and ability of the bat to detect (visually or accoustically) certain types of insects, and morphological characteristics. Using an analysis of morphological characteristics, Yom-Tov (1993) placed 15 species of bats known from the Dead Sea area into three feeding guilds as follows: Guild 1 included species with long wing tips, third digits and articulating metacarpals 1.3 times, or more, longer than the forearm, and normal-size ears (forearm/ear ratio was 2.5 or larger). Species in the present study that were included in Yom-Tov's guild 1 include *Asellia tridens, Rhinolophus clivosus, Pipistrellus bodenheimeri, P. rueppelli, P. kuhlii*, and *Tadarida teniotis*. These bats feed in a variety of habitats, including high altitudes (*Tadarida*) at medium to low heights (*Pipistrellus*), or forage amongst vegetation (*Asellia, Rhinolophus*). Yom-Tov's guild 2 included species with wing tips that are similar to species listed in Guild 1, but each have exceptionally large ears (exceeding 30 mm), which are twice the size of other bats included in his analysis. The two species which Yom-Tov included in Guild 2, and that we also examined, include *Otonyceris hemprichi* and *Plecotus austriacus*. Both species fly low and slowly and produce low-intensity echolocation calls (i.e., whispering bats). None of the species listed in Yom-Tov's guild 3 were included in our study. Although morphological data may offer general insights into the feeding ecology of an animal (e.g., Freeman 1988; Fenton and Norberg 1988; Yom-Tov 1993), it cannot be used to predict the behavioral or dietary variability such as we observed in the present study.

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Zusammenfassung

Nahrung und Ernährungsverhalten einiger insektivorer Fledermäuse aus Israel

Kleine Proben von Kotpillen von 9 der 32 in Israel vorkommenden insektivoren Fledermausarten wurden analysiert. Nach diesen Proben fraß *Asellia tridens* (n = 12) überwiegend Lepidoptera, Diptera und Coleoptera. *Myotis nattereri* ernährte sich vorwiegend von Lygaeidae und Coleoptera; *Otonycteris hemprichi* ausschließlich von Coleoptera; *Pipistrellus kuhlii* von Hymenoptera und Coleoptera; *Pipistrellus rueppelli* und *Tadarida teniotis* überwiegend von Lepidoptera und Coleoptera; *Plecotus austriacus* ausschließlich von Lepidoptera, und *Rhinolophus clivosus* erwies sich als Generalist

und nahm viele verschiedene Insekten als Nahrung. Ergänzend werden Direktbeobachtungen über das Suchverhalten dieser Fledermäuse mitgeteilt.

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