Naturwissenschaften
DOI 10.1007/s00114-008-0496-3

ORIGINAL PAPER

Frequent summer nuptial flights of ants provide a primary food source for bats

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Received: 30 August 2008 / Revised: 22 November 2008 / Accepted: 26 November 2008

Abstract In many ant species, nuptial flight tends to be short in time and assumed to be synchronous across a large area. Here, we report that, in the upper Jordan Valley, northern Israel, massive nuptial flights of Carpenter ants (*Camponotus* sp.) occur frequently throughout the summer, and their alates form up to 90% of the diet of the greater mouse-tailed bat (*Rhinopoma microphyllum*) during this period. This fat and protein-rich diet enables female bats to lactate during summer, and the large amount of fat that both sexes accumulate may serve as an energy source for their following winter hibernation and posthibernation mating in early spring (March–April). We suggest that the annual movement of these bats to the Mediterranean region of Israel may have evolved in order to enable them to exploit the extremely nutritious forms of ant alates when the bats' energetic demands are highest.

Keywords Ants · *Camponotus* · Chiroptera · Diet · Nuptial flight · *Rhinopoma*

Introduction

Ants are widespread and abundant in almost every terrestrial ecosystem (Hölldobler and Wilson 1990; Folgarait 1998), yet surprisingly little is known about their reproductive ecology (Dunn et al. 2007). In many ant species, mating occurs in nuptial flights, in which males and females emerge from their maternal nest in order to mate and establish new colonies. Most ant species are exogamous and invest much energy and biomass in their reproductive castes, making the precise timing of nuptial flights also of paramount importance for their predators. Synchronization among colonies could serve as an anti-predator strategy by swamping the predator population. Such a reproductive strategy is known for many ant and termite species, as well as for tropical trees with mass flowering (e.g., Van Schaik et al. 1993; Kelly 1994).

In temperate latitudes, nuptial flights are brief, usually synchronized with meteorological events such as first rain of the season or an extremely hot day (Hölldobler and Wilson 1990) or concentrated at the beginning of summer or early fall (Dunn et al. 2007). There are two main types of ant mating syndromes (Hölldobler and Bartz 1985; Hölldobler and Wilson 1990; Boomsma et al. 2005): (1) male aggregation, in which large swarms of male alates gather in aggregations that function as leks, at which the females arrive to select males. These gatherings tend to be short in time and are assumed to be synchronous across a large area and (2) female "calling," in which females attract males. This latter syndrome can last for very long periods or even year-round, with occasional males flying out in search of calling females. The first strategy is known to occur in *Camponotus felah* and *Camponotus sanctus* in Israel. These species usually perform mass nuptial flights on spring afternoons, synchronized with a low-pressure system from North Africa that brings dry air and high temperatures ("sharav"), and is usually followed by a burst of rain (Kugler 1989).

Compared with other flying insects, ant alates are very high-quality food as their bodies contain high proportion of

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fat (sometimes >50% of dry mass) and protein (Redford and Dorea 1984). Thus, ant alates are common food items for many insectivores, including bats (Whitaker 2004). However, they have not been reported as a main food for bats, and no bat species is known to be specialized to feed on ants (Pine et al. 1975; Whitaker 2004). This is probably due to the fact that many ant species perform their nuptial flights during daytime or sporadically (Brigham 1990).

The greater mouse-tailed bat (*Rhinopoma microphyllum*) is a medium-sized bat (average weight 25 g) that appears during summer in high numbers in the northern Jordan valley, Israel. It is an arid-zone or subtropical species, occurring from Sumatra and India through Arabia to northwestern Africa (Simmons 2005; Schlitter and Qumsiyeh 1996). In these areas, it is known to be either active all year-round (Gaur 1980; Advani 1981) or may undergo winter torpor (Anand-Kumar 1965). In Iran, this species is known to perform a seasonal migration, at least in high elevations (M. Sharifi, personal communication). In Israel, the greater mouse-tailed bat is found on the northernmost edge of its range (Schlitter and Qumsiyeh 1996). Based on the mitochondrial control region sequences, three clades were observed over the species' range: oriental, intermediate, and palaearctic. The Israeli population, which belongs to the Palaearctic clade, was found to be isolated from the Oriental and Intermediate clades. High level of sequence similarity was found within the Israeli population of greater mouse-tailed bats (Levin et al. 2008). The greater mouse-tailed bat is an open-space forager that takes its prey on the wing (Norberg and Rayner 1987) and forages at heights ranging from several to tens of meters above ground (Habersetzer 1981; Harrison and Bates 1991; Mendelssohn and Yom-Tov 1999). In the Rajasthan desert, India, greater mouse-tailed bats consume mainly Coleoptera but also small fractions of Lepidoptera, Orthoptera, and Hymenoptera. After the monsoon rains (July–September), termites (Isoptera) were found in high fraction (48.5%) in 48 *R. microphyllum* stomachs (Advani 1981). In Iran, this species preys mostly on beetles (75–85% volume), during summer (Sharifi and Hemmati 2002).

Here, we report that in northern Israel nuptial flights of *Camponotus* ants occur frequently throughout the summer and that their alates form the bulk of the diet of the greater mouse-tailed bats during their reproductive and prehibernation periods.

Materials and methods

Study site and study animals The study was conducted in the northern Jordan Valley, Israel. This area, which is part of the Great Rift Valley, is a 60-km-long and 7–15-km-wide strip and its elevation ranges between 210 m below sea level in the south (Lake Kineret) and 150 m above sea level in the origin of the Jordan River in the north. Due to its particular topography and climate, this area hosts a very rich and diverse flora and fauna and constitutes a very important migration route for many birds and flying insects (Leshem and Yom-Tov 1998; Podulka et al. 2004; Kravchenko et al. 2007). The climate of this area is Mediterranean, with hot dry summers and relatively cool and rainy winters. During summer (July–August), average temperatures range between 37°C maximum during the day and 23°C minimum during the night (Jaffe 1988).

Bat chronology In order to determine arrival time of mouse-tailed bats to their summer quarters, during 2003–2008, we visited their roosting sites every week from mid-May until the bats appeared in their colonies and later every week or two until they left their roosts in early autumn. All seven colonies were located on the foot of the mountains on both sides of the Valley but particularly on its eastern slopes (Fig. 1).

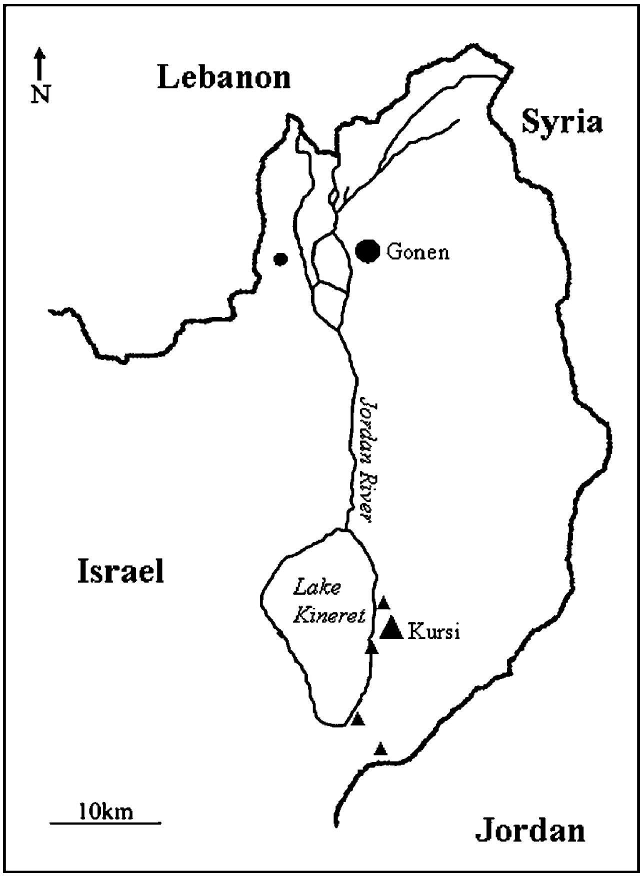

Fig. 1 The study area: male colonies (*circles*) and female colonies (*triangles*). The two largest colonies are represented by *larger symbols* (see "Results")

Diet analysis Bat feces were collected from the largest male colony (Gonen 33° 06′ N 35° 39′ E; occupied by 3,000–6,000 bats) and the largest female colony (Kursi 32° 49′ N 35° 39′ E; occupied by 5,000–10,000 bats) throughout the summer (June–September) of 2004 (Fig. 1). Paper sheets (90×70 cm) were positioned under the colonies and replaced after feces collection, every 7–14 days. In order to minimize interference during late pregnancy and lactation, Kursi colony was sampled less frequently (every 14–16 days) during 2004 and not sampled at all during 2005–2008. We analyzed a random sample of 50 feces from each date and site and identified insect remains, following protocols in Whitaker (1988). We used a photographed key of insect body parts that we had made using common insects collected by light traps and hand nets in the study area. Each pellet was examined for the volumetric proportion of each insect group present in it. Qualitative analyses (sampling at the beginning of July and August) were performed for the male colony during summers of 2003 and 2005–2008 in order to confirm the consistency of the findings.

Unlike many other insectivorous bats, *Rhinopoma* species do not severely crush the exoskeleton of their prey, and therefore many food items, especially ants and small beetles, were found with their empty shells in almost one piece, thus enabling reliable identification to family, genus, or even species level.

Capturing the bats During summer 2004, greater mouse-tailed bats were captured inside their roosts using a hand net. Captured bats were sexed and weighed using a Pesola spring balance to an accuracy of 0.1 g; their forearm was measured to an accuracy of 1 mm, and their reproductive status (pregnancy, large testes) was determined. The bats were then released. Bat numbers were estimated based on direct counting during evening emergence from their roosts. All captures were carried out under a license (number 2003/1732, 2004/18248) from the Israeli Nature and Parks Authority (NPA).

Results

Study site and animals

All known colonies of *R. microphyllum* in Israel are limited to the rift valley. During 2003–2004, we visited four known colonies of the greater mouse-tailed bat in the northern Jordan Valley, and during 2005–2007 three new maternity

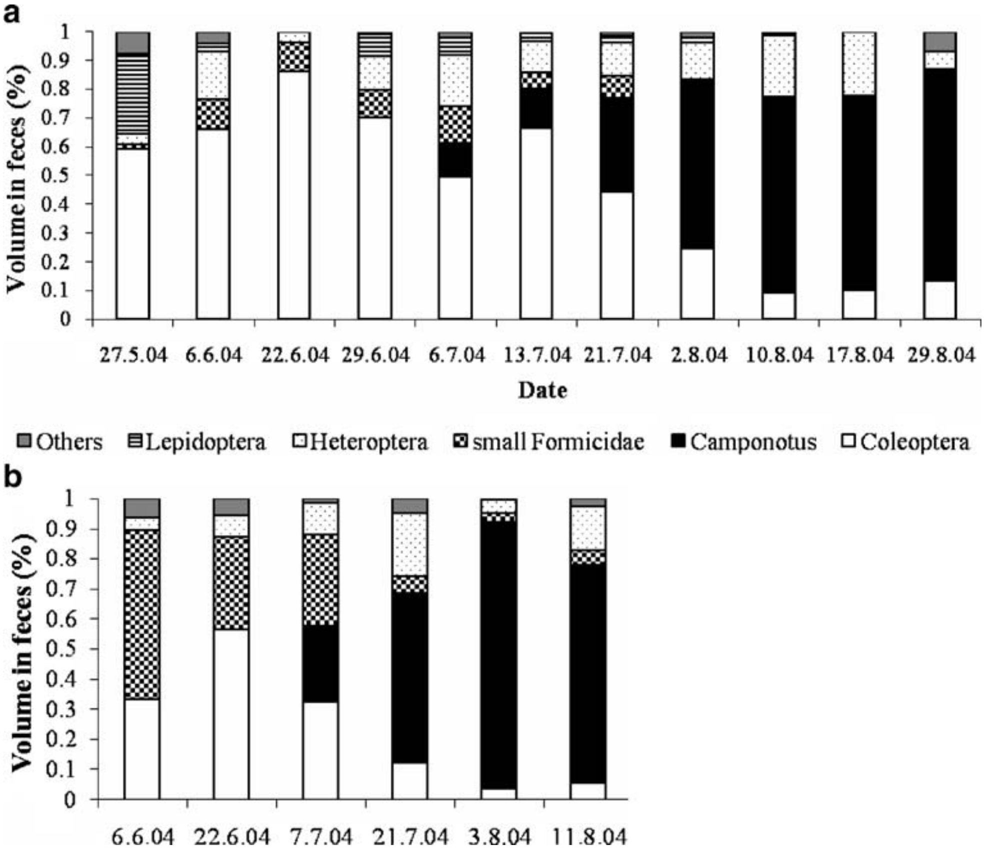

Fig. 2 Changes in diet composition of *R. microphyllum* during summer of 2004: **a** males, **b** females

Table 1 The frequency (%) of *Camponotus* alates in feces of *R. microphyllum* males (from Gonen cave) at the beginning and middle of summers 2003–2008

Year	2003		2004		2005		2006		2007		2008	
Sampling date	9.6	7.8	22.6–7.7	21.7–3.8	11.6–29.6	2.8–19.8	25.6–11.7	30.7–11.8	18.6–2.7	3.8–5.8	23.6–26.6	22.7–31.7
Camponotus frequency (%)	0	81.2	17	81	0	91	12.4	100	11	86.1	3.9	75

colonies were found in field surveys and following radio-tagged bats (Fig. 1). Based on direct counting of the bats during evening emergence, we estimate the total number of these bats in the study area as no less than 20,000 individuals.

Our observations indicate that the greater mouse-tailed bats arrive at the northern Jordan valley from their still-unknown winter quarters during the last week of May–beginning of June, the arrival dates during the 6-year study were identical. Some bats remain there until October, but most leave the roosts in late August. During the summer months, they inhabit shallow, dry, and warm caves and deserted military bunkers in this area. The bottom of these roosts is covered with a thick layer of shiny ant exoskeletons. Complete sexual segregation occurs during summer, where males inhabit the northern and higher part of the Jordan valley and females the southern lower part. One spring mating colony was found in the Judea desert 120 km south of the summer roosts (Wadi Darga 31° 40′ N 35° 26′ E). During April, males with developed testis and females were found in this cave. The bats left this colony during May, a few days before members of this species appeared in the summer roosts.

Females were observed with pups from early July and by mid-August all the young bats were seen leaving the roost during the evening foraging bouts. No reproductive males (with developed testes) were observed during summer (May–October).

Fecal analysis Analysis of the feces of the greater mouse-tailed bats revealed that they contained the remains of alates of several ant species almost continuously from June to September (Fig. 2). Two ant genera were identified in the bat feces: small (5 mm) *Paratrechina* sp. were found in high fraction in females feces in early summer (June and beginning of July) but were almost absent in male feces (56% in females vs. 30% in males; nested analysis of variance, $F_{10,\ 624}=12.7$, $P<0.001$). Large (15 mm, 0.2 g) carpenter ants (*Camponotus* spp.) appeared in the feces of both sexes from early July onwards, and their proportion increased up to 90% of the volume until the bats left their roosts in late August (Fig. 2 and Table 1). The majority of ants found in the feces were queen ants. These *Camponotus* belong to two species: *C. felah* and *C. sanctus*, both very common species in Mediterranean parts in Israel (Kugler 1989).

Before the bats left their summer roosts during August–September, *Camponotus* were found in more than 95% of the examined feces and accounted for up to 90% of their total volume throughout the study period (2003–2008; Table 1). *Camponotus* appeared in the bat feces from late June, until the bats left their summer roosts (as late as late September in 2007). This suggests that ants constitute the major food source consumed every summer by mouse-tailed bats. *Camponotus* heads were found attached by their mandibles to the lips of the bats (in at least nine cases during summer 2004), causing injury (Fig. 3). In a few cases, it was hard to remove the ant's head without injuring the bat. Many bats had scars on the lips that may indicate similar injuries.

Insects belonging to six other orders were also found in the feces but only three of those in amounts >5% of total volume (Fig. 2): coleopterans (mainly tenebrionids, carabids, scarabids, and curculionids), heteropterans (cydnids, pentatomids, lygaeids), and lepidopterans.

Diet and fattening pattern The proportion of *Camponotus* alates in the diet of the female bats increased during the

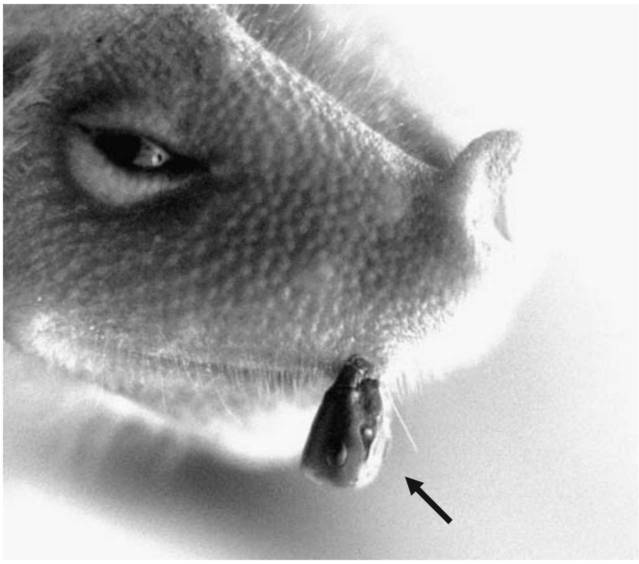

Fig. 3 A head of *Camponotus sp.* (indicated by an *arrow*) attached to the upper lip of a male *R. microphyllum*

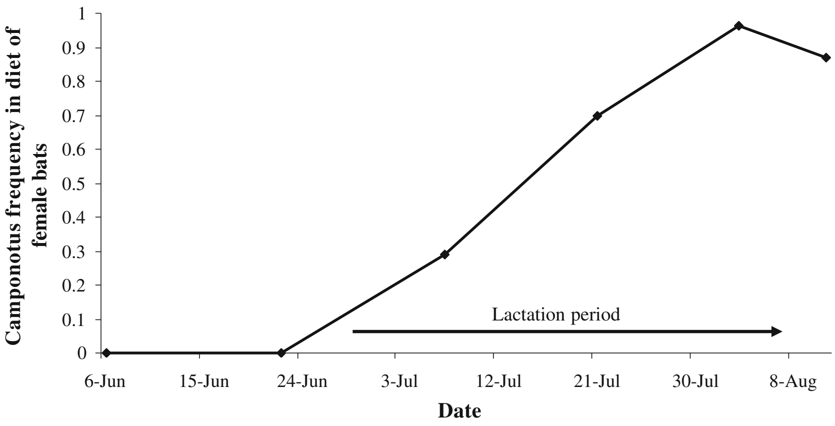

Fig. 4 The proportion of *Camponotus* in the diet of *R. microphyllum* females during summer 2004 in Kursi colony. The lactation period is marked at the *bottom* of the figure

summer, coinciding with the period of lactation (Fig. 4). Mean pregnant female mass was 22.3±1.4 g (mean±SD; n=39) in June 2004. In late August, before leaving the roost, the average female body mass was 27.3±3.5 g (n=51), a 22% increase. The proportion of *Camponotus* alates in the diet of males increased during the summer, coinciding with an increase in male body mass (Fig. 5). When arriving at the summer roosts, males had a very low-fat storage and average body mass was 20.2±3.6 g (n=37, 15 from Gonen colony and the rest from Avazim roost), but, before they left their summer roosts in mid-August, their body mass had reached a mean of 37.9±4.5 g (n=36, five from Gonen colony), a 88% increase, and they had visible (through the skin) fat storage.

Discussion

Our finding of alates of (mainly female) *Camponotus* in the feces of the greater mouse-tailed bat continuously for the three summer months is novel. Furthermore, unlike the known spring nuptial flights, summer flights of the alates found in the bats feces in our study were apparently not triggered by a meteorological event and occurred at night. It seems that these frequent summer nuptial flights of *Camponotus* spp. in the upper Jordan Valley occur on a massive scale, as can be deduced from the quantity of ants consumed. Food consumption by active insectivorous bats may be as high as half of their lean body mass during one night (Kurta et al. 1989). Assuming that each of the 20,000 mouse-tailed bats which inhabit the study area consumes only 7 g day^{-1} (20–33% of its mean body mass) of alates for a period of 50 days, the total amount of *Camponotus* consumed in the northern Jordan valley during summer is estimated to be about 7 tons.

Summer nuptial flights of *Camponotus* species seem to occur in other parts of Israel too, possibly on smaller scales than those in the Jordan Valley area. During July–September of 2007–2008, we monitored several wild *C. fellah* nests (located at the Tel Aviv University Zoological Gardens 32° 06′ N 34° 48′ E) that are known for their spring nuptial flights. From mid-July, we documented nuptial flights of five to 20 queens each, which left the same particular nests every evening. These flights lasted 2–5 min and always started in the short period after sunset and before complete darkness. We suggest that they were triggered by sunset.

The possible reason for the occurrence of two strategies of nuptial flights in *Camponotus* (once diurnal flight in

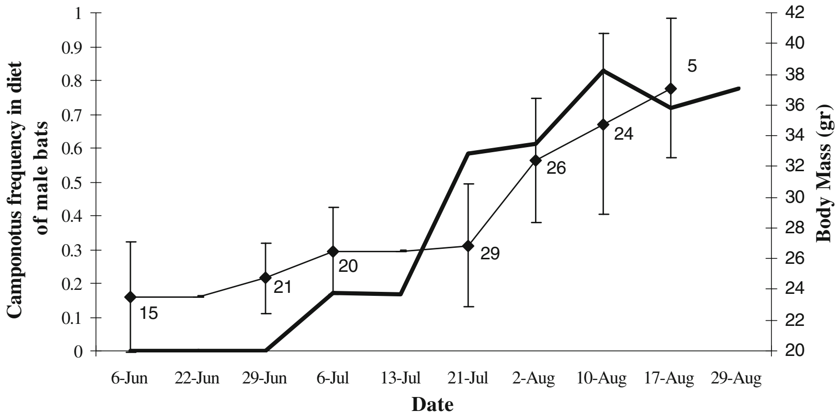

Fig. 5 The increase in male body mass of *R. microphyllum* during summer 2004 (mean± SD; sample sizes are given in the figure) and the change in *Camponotus* frequency in their diet during this summer (in Gonen colony)

spring and frequent nocturnal flights in late summer) is enigmatic: the short nuptial flight, well synchronized with all the nests in the area, may serve as an anti-predator defense strategy and ensure exogamous pairing. In contrast, a prolonged nuptial flight could increase the risk that predators will synchronize with it. It seems that the latter is the case here: greater mouse-tailed bats in the upper Jordan Valley take advantage of and synchronized with this rich food source that is available for the entire summer. We found that during late July and August these bats feed almost exclusively on *Camponotus* alates. The female bats give birth and lactate from the beginning of July until mid-August, coinciding with an increase in the proportion of ants in their diet (Fig. 4). This is also the period when these bats (including lactating females) increase their body mass considerably (Fig. 5). We found that body mass of males before they left their summer roosts increased on average by 88% in comparison at their mass when they arrived to the study area. Female mass increased by 22% during this period, but this is in relation to the mass of pregnant females. Hence, the actual body mass increase of females is larger since a newborn pup weighs about 5 g (E. Levin, unpublished observation). Taking this factor into consideration, the actual increase in female body mass is around 58% (an increase from 17.3 g (22.3–5) to 27.3 g, see above). The large amount of fat accumulated may serve as an energy source for the following winter hibernation and posthibernation mating in early spring (greater mouse-tailed bats mate in late March after winter dormancy; Anand-Kumar 1965). In addition to the high energetic value of ant alates, fat intake (alates may contain up to 50% fat; Redford and Dorea 1984) can function as an important source of metabolic water (1.04 g H_2O per gram of metabolized fat) for the bats. This water source may be important during lactation, when demands for water and milk production are maximal (Kunz et al. 1995), especially as mouse-tailed bats were never observed drinking water. We suggest that the annual movement of these bats to the Mediterranean region of Israel may have evolved in order to enable them to exploit the extremely nutritious forms of ant alates when the bats' energetic demands are highest.

There are two contrasting views regarding feeding strategies of insectivorous bats: they may be opportunistic feeders and exploit patchy insect aggregations (Gould 1978; Fenton and Morris 1976) or may be non-opportunistic and select from among available insects (Whitaker 2004; Brigham 1990). The greater mouse-tailed bat seems to belong to the first group: in Iran and India, it is known to feed on beetles and other agricultural pests such as moths and young stages of the locust *Schistocerca gregaria* (Advani 1981; Sharifi 2002). However, we show here that, in northern Israel, it is capable of exploiting ant nuptial flights to such a degree that they form the main part of its diet. In contrast, the other two open-space forager bats that co-exist in northern Israel (*Nyctalus noctula* and *Tadarida teniotis*) had, during the same season, only a low fraction of ant alates in their feces (0–40% volume; Whitaker et al. 1994, E. Levin *unpublished observation*). It seems that foraging on ant alates requires specialized foraging skills, possessed by the greater mouse-tailed bat and lacking in the other two species. These "skills" may be related to the unique wing form of the Rhinopomatidae family, characterized by a very long forearm and short phalanges, and typical "gliding" form of flight (Norberg and Rayner 1987). We suggest that the high sociality of this bat species may be beneficial in locating and consuming swarming prey like ant alates. Although ant alates were occasionally reported in the diet of many other bat species (e.g., Whitaker and Rodriguez-Duran 1999; Sparks and Valdez 2003; Gloor et al. 1995; Whitaker 2004), we are not aware of any other bat species for which ant alates comprise the majority of its diet.

Acknowledgements We thank Abraham Hefetz, John O. Whitaker, and Robert B. Suter for reading and commenting on an early draft, Naomi Paz for editing the manuscript, Tamar Katzav-Gozansky and Shai Meiri for fruitful discussions, and Armin Ionescu-Hirsch for identifying the ants. We thank two anonymous reviewers for their helpful comments. This work was supported by The Open University of Israel Research Fund to AB and by the Israel Cohen Chair for Environmental Zoology to YYT.

References

Advani R (1981) Food and feeding ecology of the rat tailed bat in the Rajasthan Desert. Act Theriol 26:269–272

Anand-Kumar TCA (1965) Reproduction in the rat-tailed bat *Rhinopoma kinneari*. J Zool 65:147–155

Boomsma JJ, Baer BC, Heinze J (2005) The evolution of male traits in social insects. Annu Rev Entomol 50:395–420

Brigham M (1990) Prey selection by big brown bats (*Eptesicus fuscus*) and common nighthawks (*Chordeiles minor*). Am Mid Nat 124:73–80

Dunn RR, Parker C, Geraghty M, Sanders NJ (2007) Reproductive phenologies in a diverse temperature ant fauna. Ecol Entomol 32:135–142

Fenton MB, Morris GK (1976) Opportunistic feeding by desert bats, *Myotis* spp. Can J Zool 54:526–530

Folgarait PJ (1998) Ant biodiversity and its relationship to ecosystem functioning: a review. Bio Conserv 7:1221–1244

Gaur BS (1980) Roosting ecology of the Indian desert rat-tailed bat, *Rhinopoma kinneari* Wroughton. In: Wilson DE, Gardner AL (eds) International bat research conference (5, 1978, Albuquerque). Texas Tech Press, Lubbock, pp 125–128

Gloor S, Stutz H-PB, Ziswiler V (1995) Nutritional habits of the noctule bat *Nyctalus noctula* (Schreber, 1774) in Switzerland. Myotis 32:231–242

Gould E (1978) Opportunistic feeding by tropical bats. Biotropica 10:75–76

Habersetzer J (1981) Adaptive echolocation sounds in the bat *Rhinopoma hardwickei*: a field study. J Comp Physiol 116:63–76

Harrison DL, Bates PJJ (1991) The mammals of Arabia, 2nd edn. Harrison Zoological Museum, Sevenoaks, p xvi + 354

Hölldobler B, Bartz SH (1985) Sociobiology of reproduction in ants. In: Hölldobler B, Lindauer M (eds) Experimental behavioral ecology and sociobiology. Gustav Fischer Verlag, Stuttgart, pp 237–257

Hölldobler B, Wilson EO (1990) The ants. Belknap, Cambridge

Jaffe S (1988) Climate of Israel. In: Yom-Tov Y, Tchernov E (eds) The zoogeography of Israel. Dr. W. Junk, Dordrecht, pp 79–74

Kelly D (1994) The evolutionary ecology of mast seeding. Trends Ecol Evol 9:465–470

Kravchenko VD, Fibiger M, Hausmann A, Müller GC (2007) The lepidoptera of Israel. In: Müller GC, Kravchenko VD, Hausmann A, Speidel W, Mooser J, Witt T (eds) Pensoft series faunistica vol. 2, Noctuidae 63. Pensoft, Sofia

Kugler J (ed) (1989) Plants and animals of the Land of Israel—insects. Ministry of Defense, Tel Aviv

Kunz TH, Whitaker JO Jr, Wadanoli MD (1995) Dietary energetics of the Mexican free-tailed bat (*Tadarida brasiliensis*) during pregnancy and lactation. Oecologia 101:107–115

Kurta A, Bell GP, Nagy KA, Kunz TH (1989) Energetics of pregnancy and lactation in free-ranging little brown bats—*Myotis lucifugus*. Physiol Zool 62:804–818

Leshem Y, Yom-Tov Y (1998) Routes of migrating soaring birds. Ibis 140:41–52

Levin E, Yom-Tov Y, Barnea A, Huchon D (2008) Genetic diversity and phylogeography of the greater mouse-tailed bat *Rhinopoma microphyllum* (Brünnich, 1782) in the Levant. Act Chirop (in press)

Mendelssohn H, Yom-Tov Y (1999) Mammalia of Israel. The Israel Academy of Sciences and Humanities, Jerusalem

Norberg UM, Rayner JMV (1987) Ecological morphology and flight in bats (Mammalia; Chiroptera) wing adaptations, flight performance, foraging strategy and echolocation. Phil Trans Royal Soc London 87:335–427

Pine RH, Clark DR, Lufriu T (1975) Yet another instance of bat versus ant. Mammalia 39:509–510

Podulka S, Rohrbaugh RW, Bonney R (2004) Handbook of bird biology. Cornell Laboratory of Ornithology, Ithaca

Redford KH, Dorea JG (1984) The nutritional-value of invertebrates with emphasis on ants and termites as food for mammals. J Zool 203:385–395

Schlitter DA, Qumsiyeh MB (1996) *Rhinopoma microphyllum*. Mamm Spec 542:1–5

Sharifi M, Hemmati Z (2002) Variation in the diet of the Greater mouse-tailed bat, *Rhinopoma microphyllum* (Chiroptera: Rhinopomatidae) in south-western Iran. Zool Middle East 26:65–70

Simmons NB (2005) Order Chiroptera. In: Wilson DE, Reeder DM (eds) Mammal species of the world: a taxonomic and geographic reference, 3rd edn. vol. 1. Johns Hopkins University Press, Baltimore, pp 312–529

Sparks WD, Valdez EW (2003) Food habits of *Nyctinomops macrotis* at maternity roost in Mexico, as indicated by analysis of guano. South Nat 48:132–135

Van Schaik CP, Terborgh JW, Wright SJ (1993) The phenology of tropical forests: adaptive significance and consequences for primary consumers. Annu Rev Ecol Syst 24:353–377

Whitaker JO Jr (1988) Food habit analysis of insectivorous bats diet. In: Kunz TH (ed) Ecological and behavioral methods for the study of bats. Smithsonian Institution Press, Washington D.C., pp 171–189

Whitaker JO Jr (2004) Prey selection in a temperate zone insectivorous bat community. J Mamm 85:460–469

Whitaker JO Jr, Rodriguez-Duran A (1999) Seasonal variation in the diet of Mexican free-tailed bat, *Tadarida brasiliensis antillarum* (Miller) from a colony in Puerto Rico. Caribbean J Sci 35:23–28

Whitaker JO Jr, Shalmon B, Kunz TH (1994) Food and feeding habits of insectivores bats from Israel. Mamm Biol 59:74–81