



Foraging Behaviour and Habitat use by the European Free-Tailed Bat *Tadarida teniotis*

Authors: Marques, J. Tiago, Rainho, Ana, Carapuço, Mafalda, Oliveira, Paulo, and Palmeirim, Jorge M.

Source: *Acta Chiropterologica*, 6(1) : 99-110

Published By: Museum and Institute of Zoology, Polish Academy of Sciences

URL: <https://doi.org/10.3161/001.006.0108>

BioOne Complete (complete.BioOne.org) is a full-text database of 200 subscribed and open-access titles in the biological, ecological, and environmental sciences published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Complete website, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/terms-of-use.

Usage of BioOne Complete content is strictly limited to personal, educational, and non - commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

BioOne sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

Foraging behaviour and habitat use by the European free-tailed bat *Tadarida teniotis*

J. TIAGO MARQUES¹, ANA RAINHO², MAFALDA CARAPUÇO³, PAULO OLIVEIRA³,
and JORGE M. PALMEIRIM⁴

¹UMC — Unidade de Macroecologia e Conservação, Universidade de Évora, Antiga Fábrica dos Leões,
7000 Évora, Portugal; E-mail: jtsm@uevora.pt

²Instituto de Conservação da Natureza, Rua de Santa Marta, 55, 1150-294 Lisboa, Portugal

³Laboratório Marítimo da Guia — Instituto do Mar, Estrada do Guincho, 2750 Cascais, Portugal

⁴Centro de Biologia Ambiental e Departamento de Biologia Animal, Faculdade de Ciências da Universidade
de Lisboa, Campo Grande, 1749-016 Lisboa, Portugal

Autumnal foraging behaviour and habitat use by *Tadarida teniotis* were studied in Southern Portugal, using seventeen radio-marked individuals, followed over multiple nights from fixed and mobile stations. *Tadarida teniotis* proved to be a late emerger, leaving the roost about one hour after sunset and, in contrast to most insectivorous bat species, only had one foraging bout. These bouts were very long, lasting an average of 6 hours and 39 minutes. Bout duration was unrelated to climatic conditions and so probably determined by foraging success. In the early evening almost all bats were foraging, but this activity declined steadily through the night. They kept flying even during fairly cold nights, but did not leave the roost on the coldest nights, in which they probably remained in torpor. As predicted by its body mass and wing morphology, *T. teniotis* was found to be a strong flyer, reaching speeds of over 50 km/h, and flying for up to 10 hours without resting periods. The observed speeds were 2.5 times higher than the predicted maximum range speed, which may be possible due to peculiar adaptations to high-speed flight. On most nights bats flew straight to a previously identified feeding site, but on a few they made slower indirect flights, suggesting a search for profitable foraging areas. Upon arriving to a feeding site most bats remained there for the rest of the foraging trip. The median size of these sites was just over 100 ha. Several tracked bats used the same feeding area simultaneously. The range of the colony had a radius of over 30 km, but most feeding sites were concentrated in a mountainous region located about 5 km north of the roost. The studied bats foraged preferentially over forested areas, particularly pine and cork oak woodlands. They used both alluvial plains and the valleys of a mountainous area, but not its ridges. Our observations support the hypothesis that *T. teniotis* is an opportunistic forager, depending on temporary concentrations of prey, such as insect swarms.

Key words: *Tadarida teniotis*, Molossidae, foraging, flight-speed, habitat selection, radio-tracking

INTRODUCTION

The European free-tailed bat (*Tadarida teniotis*) is the only Palaearctic representative of a mostly tropical family, the Molossidae. It has an extensive geographic

range, from Europe and North Africa to China and Japan, but in Europe it is restricted to a broad band along the Mediterranean (Aellen, 1966; Hutson, 1999). It has a somewhat unusual thermal behaviour, as expected from a representative of a tropical

family living in a temperate zone (Arlettaz *et al.*, 2000). Although this peculiarity may strongly influence various aspects of the ecology and behaviour of the species, it remains one of the least known bats of the European fauna.

Tadarida teniotis is a large bat, which generally roosts in rock crevices, but can also be found in buildings when their structure is similar to the natural roosts (Arlettaz, 1990, 1995). Like other molossids, *T. teniotis* has particularly long and narrow wings and a very high wing loading, which are characteristics associated to fast hawking bat species (Norberg and Rayner, 1987). This species seems to be able to exploit a wide variety of habitat, such as scrublands, woodlands, lakes and urban areas (Carmel and Safriel, 1998; Russo and Jones, 2003). It searches for prey high above the ground, using long low-frequency pulses (Zbinden and Zingg, 1986). The use of low-frequency echolocation in this species appears to be an adaptation for predating large tympanate insects, mainly moths (Lepidoptera) and lacewings (Neuroptera; Rydell and Arlettaz, 1994).

Tadarida teniotis is protected by the European Habitats directive and by the Bern (www.nature.coe.int/english/cadres/bern.htm) and Bonn (www.wcmc.org.uk/cms/cms_conv.htm) conventions. The maintenance of its populations is dependent not only on the protection of roosts but also on the correct management of foraging areas. Due to social and economic changes and to financial incentives of the Common Agricultural Policy of the European Union, southern European landscapes are changing quickly, which is both a problem and an opportunity for species conservation. To protect and manage foraging habitat of a species it is crucial to know its habitat preferences, and have information about its use of space, such as the range around each colony that is utilized for foraging.

However, because these bats tend to fly fast and to forage far from the roosts, their spatial foraging behaviour is difficult to study and even the most basic knowledge required for managing *T. teniotis* foraging ranges is still missing.

The objectives of this study were (i) to identify the patterns of activity of *T. teniotis* through the night and their relation to ambient conditions, (ii) to characterize its spatial foraging patterns, and (iii) to identify its autumn habitat preferences.

MATERIALS AND METHODS

Study Area

Our study took place in the Setúbal region, on the western coast of Portugal (38°30'N; 8°51'W). A mosaic of agricultural and forestry fields dominates the area, but it also includes the Sado estuary, the hilly region of the Natural Park of Arrábida (maximum elevation 500 m a.s.l.), and the city of Setúbal (113,000 inhabitants). It has a Mediterranean-type climate with cool humid winters and warm dry summers.

The studied *Tadarida teniotis* colony, which included a few hundred individuals, roosted in an abandoned 14-storey building. At the time of the study bats mostly occupied crevices in the balconies but were also found in hollow walls.

Capture and Radio-Tracking

We fitted 17 bats with 1.4 g radio transmitters (BD-2G, Holohil Systems, Ontario, Canada; Table 1), attaching them to the skin between shoulder blades using surgical cement (Skin-Bond Cement, Smith & Nephew, Inc., Largo, Florida). Bats were captured at the roost, under license issued by the Instituto da Conservação da Natureza. Animals were tracked by triangulation from three fixed telemetry stations positioned in strategic high points, and one mobile station installed on a car (see Fig. 4). Each precision direction finding station consisted of a 4-m high metal tower equipped with two parallel 6-element Yagi antennas and a precision null combiner (Telonics Tac-5, Telonics, Mesa, Arizona; Springer, 1979). Bearings, taken every five minutes if possible, were synchronised by continuous radio communication between operators. We determined bearing error by placing radio tags at known locations; accuracy was usually below 2°. Most fixes included in the habitat selection

TABLE 1. Individual data, tracking survey data, and emergence and return times of followed *T. teniotis*. (*) — median value (first quartile–third quartile). Individuals 512, 491, 481 and 140 flew off the tracking range and/or lost their transmitters in the first couple of days

Code	Sex	Body mass (g)	Capture	Days monitored	Fixes	Minutes in contact	Emergence time*	Return time
532	♂	38.75	22–09	4	5	25		
512	♂		23–09	2				
492	♀		23–09	1				
481	♂		23–09	2				
140	♂		30–09	1				
533	♂		04–10	4	5	330		
173	♂		04–10	16	102	1905	20:13 (19:54–20:21)	5:18 (1:44–6:11)
151	♀		10–10	4	10	325	21:09	5:50
187	♀		10–10	11	55	1235	20:03 (19:56–20:08)	4:39 (3:44–4:39)
360	♀		18–10	1		10	19:39	
278	♀	30.25	21–10	7	10	335		3:13
482	♂	22.50	21–10	1				
320	♂	34.25	22–10	6	29	720	20:05	
165	♂	31.75	30–10	9	113	1480	19:23 (19:11–19:34)	1:55 (1:33–2:34)
212	♀	34.25	30–10	6	178	1640	19:24 (19:16–20:44)	3:00 (23:55–5:49)
213	♂	38.50	05–11	10	3	20		
227	♀	40.00	05–11	10	35	440	20:00	4:55

analysis were within 1 km of the nearest tracking station. At this distance the 2° bearing error corresponds to a linear location error of about 35 m, although if the azimuths crossed at poor angles this error could be larger. At our request, the signal intensity of the transmitters was maximized in detriment of lifespan, and in optimal circumstances the detection range from the highest fixed station was over 35 km. Data were collected between 22nd of September and 14th of November 2001. Because most of the study period was in the summer time of the GMT results are presented in this format. Radio-tracking data were screened to eliminate potentially inaccurate locations (White and Garrot, 1990).

Nine individuals were captured to measure body mass and wingspan. Wing area was measured using digital pictures of the bats held against graph paper, with the elbow fully extended. Minimum power speed (V_{mp}) and maximum range speed (V_{mr}) were estimated with the equations indicated in Norberg and Rayner (1987).

Data Analysis

Mean speed of progress on the ground was measured using distances between successive radio-

locations and the time taken to travel them. In the case of commuting flights only sequences of radio-locations lined up with the roost were used. In these cases, speed of progress on the ground is equivalent to flying speed. Location error increases with the distance to the antennas, so we excluded distant locations from the analysis of habitat selection. Consequently, only a core area of 4180 ha, particularly well covered with our fixed antenna network, was used for that analysis.

Spatial dependency between successive locations was avoided using the method described by Swihart and Slade (1985). As a result, all locations obtained less than 10 minutes apart were removed from the data set. Bats that, after this process, had less than 17 locations inside the core area were excluded, leaving us with 10 individuals (4 ♀♀ and 6 ♂♂) for the habitat selection analysis. Locations were integrated in a GIS and plotted over digital land use maps. Feeding areas were delimited using 80% fixed kernel, and the amount of smoothing was defined by least squares cross validation (Seaman and Powell, 1996).

We identified nine land use types: cork oak woodlands (dominated by *Quercus suber* at various densities); other oak woodlands (dominated by other *Quercus*); stone pine woodlands (dominated by *Pinus pinea*); maritime pine woodlands (dominated by

Pinus pinaster); scrub (low and medium Mediterranean scrub); open fields (meadows, pasture, and cereal fields); annual crops (including irrigated areas); orchards (olive groves, vineyards and orchards); and others (including land use types with low representation in the area, like urban areas, bare rock, beaches, dunes, and stone quarries).

The percentage of bat locations in each habitat was compared to habitat availability within the above described core area. Confidence intervals around these percentage values were used to establish statistical significance. Selectivity was measured with Ivlev's Index (Krebs, 1989).

Small samples and high individual variability preclude the use of meaningful statistical tests to compare the behaviour of males with that of females, but a visual inspection of the data suggests that there are no major differences between them. Consequently, males and females were pooled in all the analyses.

RESULTS

Patterns of Activity

Overall, radio-tracked bats left the roost well after sunset (median time after sunset = 59 minutes, \bar{x} = 65 minutes; Fig. 1). In our

study most individuals left the roost at about the same time, but their time of return was very variable (Fig. 1). They made only one foraging trip each night, which lasted an average of 6 hours and 39 minutes (Fig. 2). No noticeable resting periods were recorded during these foraging trips.

Low night temperatures during the study period ranged from 5.7 to 15.5°C, and maximum night wind-speed from 0.3 to 3.6 m/s. Neither temperature nor wind-speed seemed to influence the duration of the foraging trips (Spearman rank correlation, $r_s = 0.16$, $n = 14$, $P = 0.60$, and $r_s = -0.13$, $n = 14$, $P = 0.67$, respectively). Bats foraged in fairly cold nights and with strong winds, but in stormy weather they returned to the roost. However, on the two coldest nights (lows of 5.7 and 6.2°C), radio-tagged bats did not leave the roosts.

Between 20 and 24 hours almost all the bats were away foraging, and after that period the proportion of individuals foraging declined through the night (Fig. 2).

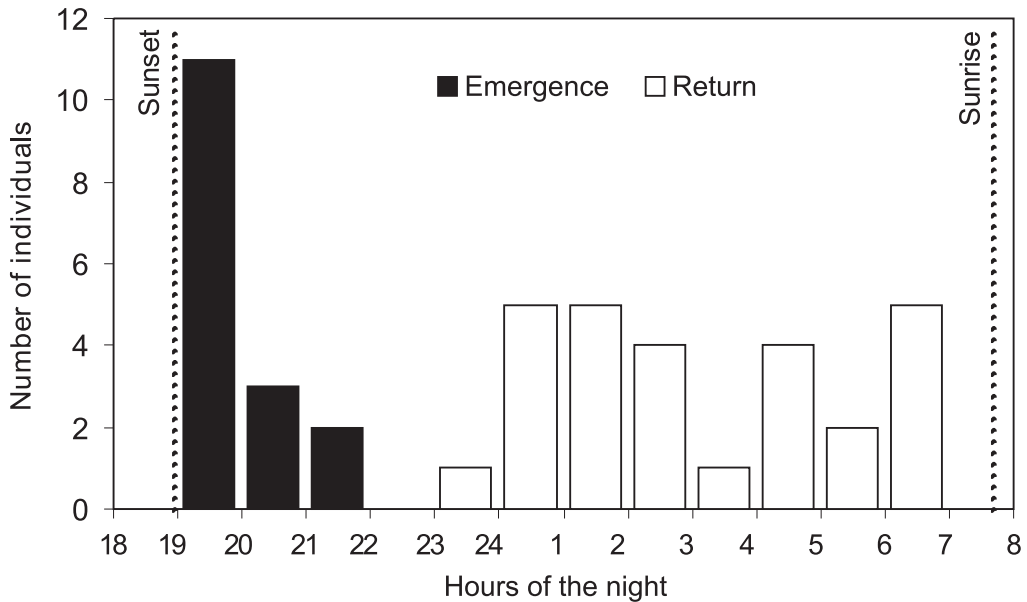


FIG. 1. Time of emergence and return to the roost. Due to the variation in night length during the study period, the times shown may have an error of up to 20 minutes

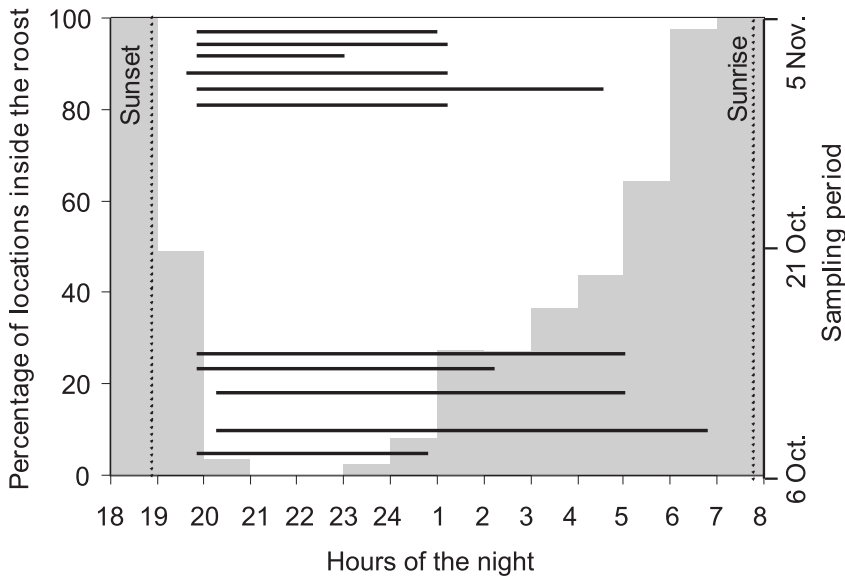


FIG. 2. Relationships between the percentage of bats inside the roost and duration of foraging flights. The sampling period is also shown. Grey bars represent the use of the roost by bats, which is very low between 20 and 24 hours. Horizontal lines show the duration of foraging flights, some of which lasted almost a full night. The shorter flights registered in November concern bats that flew directly to and from specific feeding areas. Due to the variation in night length during the study period, the times shown may have an error of up to 20 min.

The great majority of the time away from the roosts was spent flying in foraging areas (56%), but they spent 20% of this time commuting to and from the roost, 12%

apparently searching for foraging areas, and 13% flying around the roost (Fig. 3). Foraging peaked at 22 hours but there were individuals foraging at all times of the night.

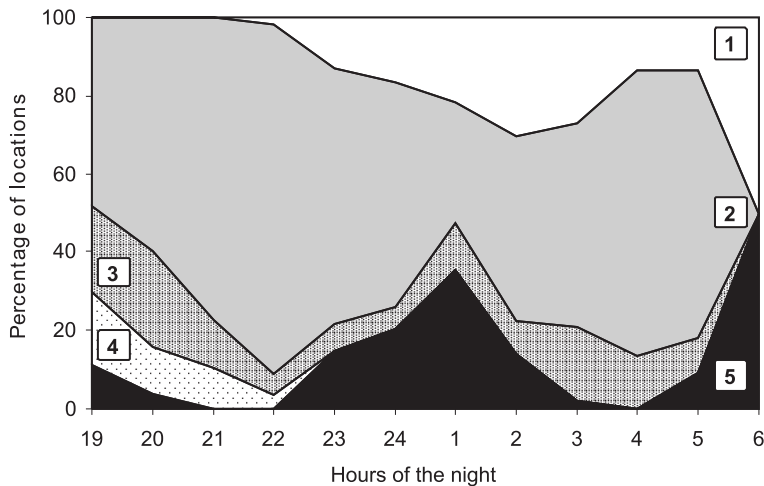


FIG. 3. Allocation of time in bats active outside the roost. 1) Return flights, 2) feeding, 3) searching, 4) outgoing flights, 5) flights around roost. Most of the active time is spent foraging, but there are important peaks of flying activity around the roost. Due to the variation in night length during the study period, the times shown may have an error of up to 20 minutes

Around one o'clock and just before sunrise a high proportion of the active bats were flying around the roost.

Spatial Foraging Patterns

Flight patterns varied much among individuals and nights. On some nights they used only one feeding area, to which they flew directly from the roost (e.g., Bat 212; Fig. 4), but they can also use several feeding areas, sometimes separated by large distances. Less frequently, they made very broad flights that did not lead the individuals directly to feeding areas (e.g., Bat 165; Fig. 4). In most cases (68%) they returned to the feeding area used in the previous night. Most of the feeding areas were within 5 km of the roost, but some areas were over 30 km away (Fig. 5). Feeding areas size was about 102 ha.

Average body mass of the nine individuals was 30 g, wing span 410 mm, wing

area 0.02 m², aspect ratio 9.82 and wing loading 19.2 N/m². These values resulted in a Vmp of 15.8 km/h, and a Vmr of 20.9 km/h.

The flights to the foraging areas were usually fast and direct (median speed 50 km/h; Fig. 6). The progress on the ground in other phases of the flight was usually much slower, but some return flights to the roosts were also very fast.

Habitat Preferences

Within the above defined core area, bats clearly preferred to forage over stone pine and cork oak woodlands (Fig. 7). Within the cork oak woodlands, they used most intensively areas where the stone pine was also present, intermixed with the oaks. This strongly supports a close association with stone pine. However, woodlands of another pine, the maritime pine, were underused. They foraged both on

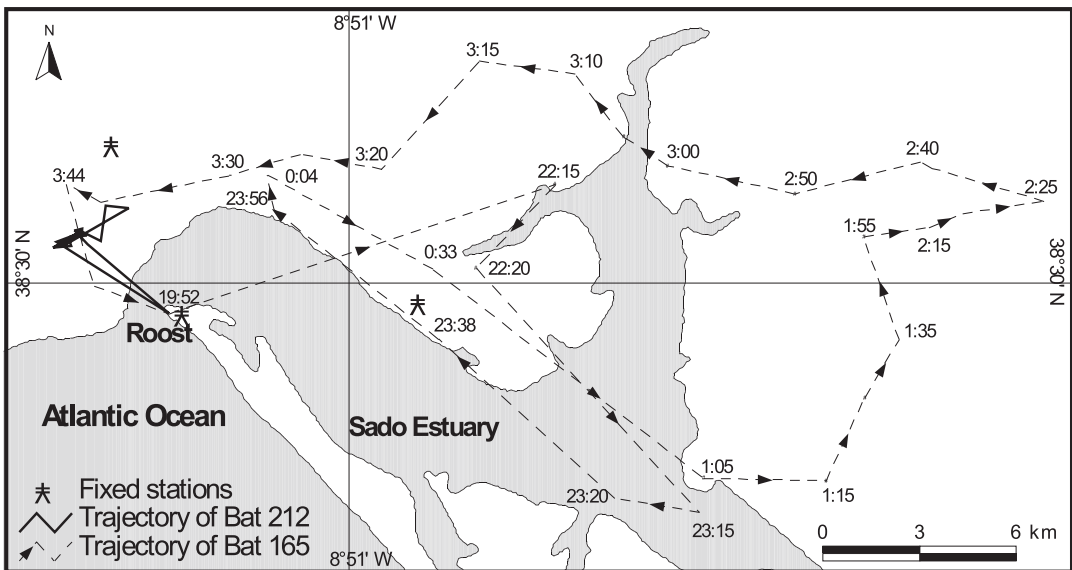


FIG. 4. Examples of the two types of foraging flights observed. Bat 212 flew directly to and from the feeding area, whereas bat 165 ranged over a very large area, probably searching for suitable feeding spots. The location of the fixed tracking stations is shown. The positions of the vehicle-mounted tracking station are not indicated, but they were usually outside the triangle formed by the fixed stations

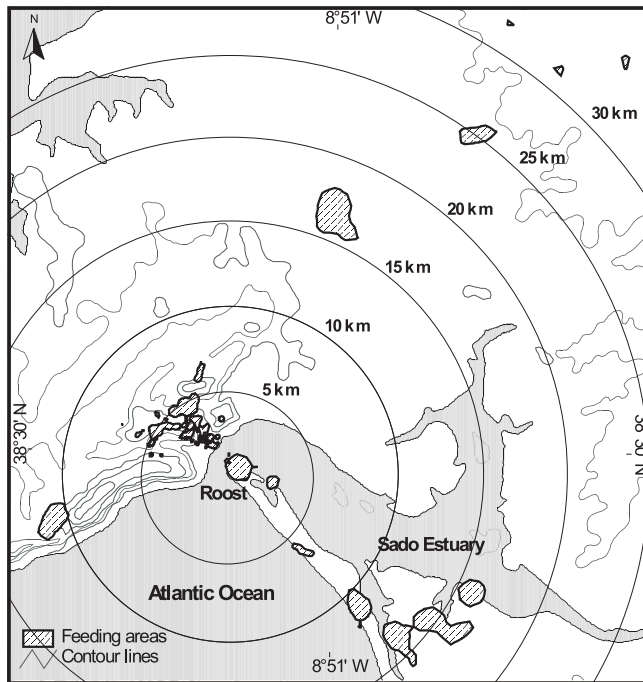


FIG. 5. Location of the feeding areas in relation to the roost. While most of these areas were close to the roost a few were surprisingly distant

alluvial plains and in mountainous areas, but in the latter their foraging activity was concentrated in valleys; peaks (above 300 m) were avoided.

DISCUSSION

Patterns of Activity

In Portugal, *T. teniotis* emerged from the roost later than in the Central European colonies (\bar{x} = 65 min vs. 39 min) studied by Arlettaz (1990), during the same season. However, in both regions this species emerges somewhat later than other European bat species of similar size, such as *Eptesicus serotinus* (19.2 and 14.2 minutes in two study areas; Catto *et al.*, 1996) or *Nyctalus noctula* (between 3 minutes before and 30 minutes after sunset; Jones, 1995).

Time of emergence in bats is likely to be partly determined by a trade-off between predation risk, which goes down with

darkness, and prey availability, which tends to be higher at dusk (Erkert, 1982; Rydell *et al.*, 1996). *Tadarida teniotis* is a large and fast-flying species and therefore less prone

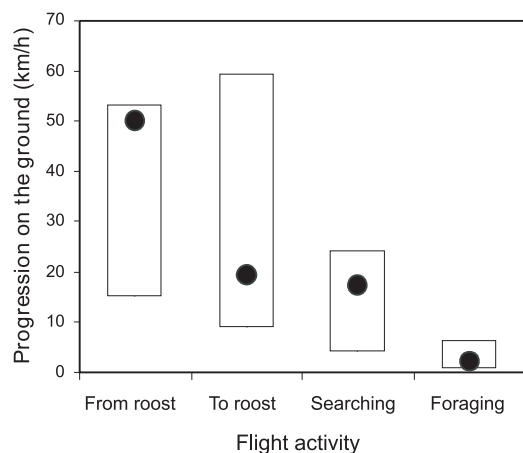


FIG. 6. Speed of progress on the ground of bats in various activities. Dots represent median values. In some direct flights to and from the roosts this value is likely to approximate flying speed

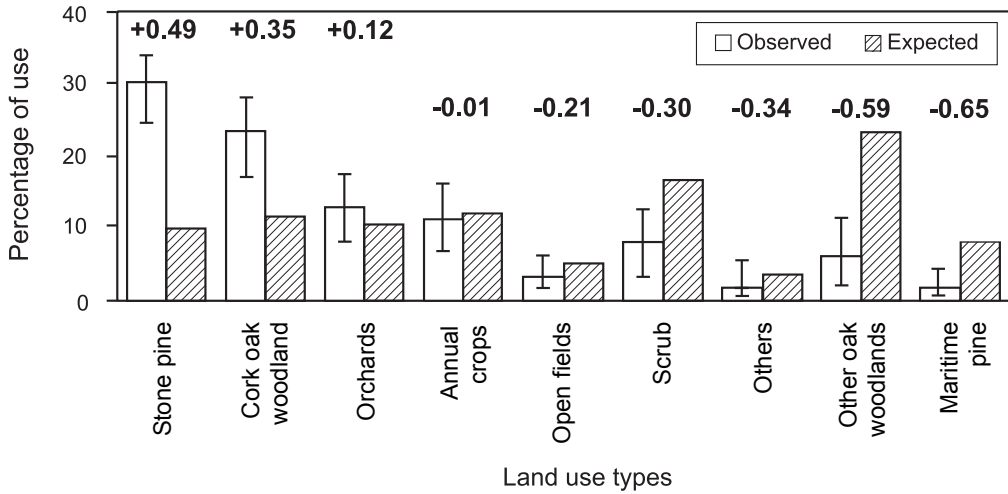


FIG. 7. Habitat selection in the core of the study area. Lines represent 95% confidence limits, and the numbers above columns Ivlev's selection index values. Comparing the availability of each habitat to the corresponding confidence intervals of the percentage of use, it is apparent that the only habitats that were clearly selected for are cork oak and stone pine woodlands

to predation than most bats, which should allow it to emerge early (Jones and Rydell, 1994; Rydell *et al.*, 1996). Consequently, the fact that it left the roost late suggests that its emergence time is determined by the timing of prey availability. In fact, in contrast to many other flying insects, moths, the main prey of *T. teniotis* (Rydell and Arlettaz, 1994), do not have a peak of activity at dusk. Their availability only peaks after dusk and remains fairly high through the night (Taylor and Carter, 1961), making it unnecessary to start foraging early.

The great majority of insectivorous bats have a bimodal activity pattern, with a peak of foraging activity at dusk and a second peak towards the end of the night (Erkert, 1982). In contrast, the studied *T. teniotis* had a clearly unimodal activity pattern that peaked about 3 hours after sunset and tapered off through the night. However, on the average, the duration of the single bout of activity (\bar{x} = 6 hours and 39 minutes) was considerable longer than the sum of the multiple bouts observed in other species (e.g., about 2 hours for *M. myotis*, Audet, 1990; 2 hours and 38 minutes for *N. leisleri*,

Waters *et al.*, 1999; and about 1 hour for *E. serotinus*, Kervyn, 2001). A late and long foraging period may make a second feeding bout unnecessary for *T. teniotis*. In fact, on many nights the studied bats simply would not have sufficient night time to make a second foraging trip.

The duration of the single nightly foraging bout varied considerably, from 3 to 10 hours (Fig. 2). Since this period was found to be unrelated to climatic conditions it was probably determined by foraging success, as suggested by Aldridge and Brigham (1991) for *Eptesicus fuscus*. Consequently, foraging success appears to vary substantially from night to night, which is consistent with a strategy of search and exploitation of temporary concentrations of prey. Shorter foraging bouts would occur when the bats quickly locate high concentrations of prey. The long duration of the foraging flights recorded demonstrates a great capacity for sustained flight by *T. teniotis*, as far as we know unsurpassed by other reports of bat flight duration in the literature.

On the two coldest nights (minimum temperatures below 6.2°C), the studied bats

did not forage and remained inside the roost. They had probably entered torpor, since Arlettaz *et al.* (2000) demonstrated that the ideal range of ambient temperatures for torpor in this species is 7.5–10°C, unusually high for crevice roosting temperate bats. Although most of the night active period was used for foraging, a considerable amount of time was spent flying in the immediate vicinity of the roost. Since it is unlikely that the availability of prey there can support a large number of foraging individuals, foraging is probably not the main purpose of this behaviour. Social interactions related to mating are also an unlikely justification for it if *T. teniotis* only mates in the spring, as reported for other temperate molossid, (Novak, 1994; Krutzsch *et al.* 2002). Activity around the roost could be related to information transfer about profitable food patches. In fact, it has been speculated that colonial animals that are dependent on difficult to locate and unpredictable resources may observe successful returning individuals to obtain information about the location of food (Barta and Giraldeau, 2001).

Spatial Foraging Patterns

Our data support the hypothesis put forward by Arlettaz (1995) that *T. teniotis* is an opportunistic forager that mostly exploits prey swarms. As expected from a species with such a strategy, the tracked animals often changed foraging area from night to night, probably abandoning sites when resources became scarce. In addition, a few bats were observed making broad flights, apparently in search of unpredictable prey swarms, which in the case of one individual was followed by repeated visits to a specific feeding site on subsequent nights. They apparently spend much of the time searching for unpredictable prey swarms, but return to the same feeding area when prey

swarms persist there for several nights. Several bats were tracked while foraging at these sites, and visual observations there confirmed the presence of concentrations of *T. teniotis*. The observed size of the feeding area, remarkably small for a fast flying bat that forages well above the canopy, is also compatible with the exploitation of concentrated prey swarms.

Prey swarms may be located either during the broad search flights that we observed and/or, as suggested by Wilkinson (1995), by information transfer. This could take place near the roosts, as mentioned above, or by eavesdropping on other foraging individuals. High flight and strong low frequency calls (thus propagating long distances; Zbinden and Zingg, 1986) should facilitate eavesdropping in this species. Also the large number of social buzzes produced when several *T. teniotis* forage in the same airspace (Fenton, 2003) may advertise the discovery of a concentrated patch of food to conspecifics (Wilkinson and Boughman, 1998).

The speed of commuting flights from the roosts to the foraging area was in general higher than that of the return flights, although a few of these were also very fast. The median outgoing commuting flight speed (50.1 km/h), was about 2.5 times higher than the predicted V_{mr} (20.9 km/h). In fact it has been predicted that bat commuting flight speeds should exceed V_{mr} (Norberg, 1981), and this has been observed with other species, such as *Pipistrellus pipistrellus* (Jones and Rayner, 1989) and *Nyctalus leisleri* (Shiel *et al.*, 1999). However, the observed discrepancy is particularly high, and this may be due to peculiar adaptations of molossids for high-speed flight (Vaughan and Bateman, 1980). Very fast flight and the capacity of flying during particularly long periods, may allow these bats to take advantage of unpredictable resources of a very large area, which is

reflected in the large foraging range of the studied colony.

Habitat Preferences

In a study based on data collected with ultrasound detectors in southern Italy Russo and Jones (2003) did not find significant differences in the use of various foraging habitats by *T. teniotis*. In contrast, in our study it was highly selective, foraging mostly over stone pine and cork oak woodlands, and a mixture of both. Since this species forages well above the canopy, food abundance, rather than habitat structure, is the likely direct reason for this preference. However, habitat structure may have an indirect effect by influencing food abundance. We do not have measures of food abundance over the various habitats, but migrating moths tend to prefer to rest in dense woodlands (Waring, 1989). Resident moths that live on pines, often in large numbers (e.g. pine processionary moth *Thaumetopoea pityocampa*), could also be important prey for *T. teniotis* in the region. Russo and Jones (2003) also reported a comparatively high activity over Mediterranean woodlands (although not statistically higher than over other habitats), but did not notice a particularly high use of pine woodlands. At the time of this study the preference for stone pine and cork oak was marked, but since *T. teniotis* seems to concentrate on prey swarms it is quite likely that its habitat preferences will shift seasonally in response to changes in prey abundance.

Tadarida teniotis has been observed exploiting prey concentrations over illuminated areas (Arlettaz, 1990), and a study in Israel showed that its activity was significantly higher over settlements (Carmel and Safriel, 1998). However, a large urban area close to the roost of our colony (the city of Setúbal) was used very little by the tracked

bats. In the mountainous sector of our study area the tracked animals clearly avoided the peaks and concentrated their activity in the valleys. Since they are powerful flyers, known to forage in high mountains (Arlettaz, 1995) and the peaks were not high, the most likely explanation for this pattern is that the terrain influenced the distribution of the prey. The vegetation on the peaks may be less suitable habitat for the prey, and stronger winds may constrain insect flight.

The results of our study suggest that, although *T. teniotis* appears to be an opportunistic forager, at least during part of the year it is dependent on specific habitats. In our region these selected habitats are under great pressure from expansion of urban areas and frequent forest fires. The dependency on patches of temporary high food abundance may justify the use of very large home ranges by the colonies, which implies that the management of their habitat should encompass large areas.

ACKNOWLEDGEMENTS

A project funded by Imoarea and managed by Margarida Santos Reis and Francisco Andrade partially covered the cost of this study. Thanks are due to Carla Marques, Helena Oliveira, Hugo Rebelo, and Sofia Lourenço for help during data collection. We also thank the forestry association AFLOPS and the company SAPEC for allowing the installation of receiving stations in areas under their management.

LITERATURE CITED

- AELLEN, V. 1966. Notes sur *Tadarida teniotis* (Raf.) (Mammalia, Chiroptera) — I. Systématique, paléontologie et peuplement, répartition géographique. *Revue Suisse de Zoologie*, 73: 119–159.
- ALDRIDGE, H. D. J. N., and R. M. BRIGHAM. 1991. Factors influencing foraging time in two aerial insectivores: the bird *Chordeiles minor* and the bat *Eptesicus fuscus*. *Canadian Journal of Zoology*, 69: 62–69.
- ARLETTAZ, R. 1990. Contribution à l'éco-éthologie du

- Molosse de Cestoni, *Tadarida teniotis* (Chiroptera), dans les Alpes valaisannes (sud-ouest de la Suisse). *Zeitschrift für Säugetierkunde*, 55: 28–42.
- ARLETTAZ, R. 1995. *Tadarida teniotis*. Pp. 198–202, in *Säugetiere der Schweiz. Verbreitung, Biologie, Ökologie* (J. HAUSSE, ed.). Birkhäuser Verlag, Basel, 501 pp.
- ARLETTAZ, R., C. RUCHET, J. AESCHIMANN, E. BRUN, M. GENOUD, and P. VOGEL. 2000. Physiological traits affecting the distribution and wintering strategy of the bat *Tadarida teniotis*. *Ecology*, 81: 1004–1014.
- AUDET, D. 1990. Foraging behavior and habitat use by a gleaner bat, *Myotis myotis* (Chiroptera: Vespertilionidae). *Journal of Mammalogy*, 71: 420–427.
- BARTA, Z., and L.-C. GIRALDEAU. 2001. Breeding colonies as information centers: a reappraisal of information-based hypotheses using the producer-scrounger game. *Behavioral Ecology*, 12: 121–127.
- CARMEL, Y., and U. SAFRIEL. 1998. Habitat use by bats in a Mediterranean ecosystem in Israel — conservation implications. *Biological Conservation*, 84: 245–250.
- CATTO, C. M. C., A. M. HUTSON, P. A. RACEY, and P. J. STEPHENSON. 1996. Foraging behaviour and habitat use of serotine bat (*Eptesicus serotinus*) in southern England. *Journal of Zoology (London)*, 238: 623–633.
- ERKERT, H. G. 1982. Ecological aspects of bat activity rhythms. Pp. 201–242, in *Ecology of bats* (T. H. KUNZ, ed.). Plenum Publishing Corporation, New York, 425 pp.
- FENTON, M. B. 2003. Eavesdropping on the echolocation and social calls of bats. *Mammal Revue*, 33: 193–204.
- HUTSON, A. M. 1999. *Tadarida teniotis* (Rafinesque, 1814). Pp. 156–157, in *The atlas of European mammals* (A. J. MITCHELL-JONES, G. AMORI, W. BOGDANOWICZ, B. KRYŠTUFEK, P. J. H. REIJNDERS, F. SPITZENBERGER, M. STUBBE, J. B. M. THISSEN, V. VOHRÁLIK, and J. ZIMA, eds.). Academic Press, London, 484 pp.
- JONES, G. 1995. Flight performance, echolocation and foraging behaviour in noctule bats *Nyctalus noctula*. *Journal of Zoology (London)*, 237: 303–312.
- JONES, G., and J. M. V. RAYNER. 1989. Optimal flight speed in Pipistrelle bats, *Pipistrellus pipistrellus*. Pp. 247–253 in *European Bat Research 1987* (V. HANÁK, I. HORÁČEK, and J. GAISLER, eds.). Charles University Press, Praha, 718 pp.
- JONES, G., and J. RYDELL. 1994. Foraging strategy and predation risk as factors influencing emergence time in echolocating bats. *Philosophical Transactions of the Royal Society of London B*, 346: 445–455.
- KERVYN, T. 2001. *Écologie et éthologie de la serotine commune, Eptesicus serotinus* (Chiroptera, Vespertilionidae): perspectives en vue de la conservation des chiroptères. PhD Thesis, Université de Liège, Liège, 164 pp.
- KREBS, C. J. 1989. *Ecological methodology*. Harper Collins Publications, New York, 654 pp.
- KRUTZSCH, P. H., T. H. FLEMING, and E. G. CRICHTON. 2002. Reproductive biology of male Mexican free-tailed bats (*Tadarida brasiliensis mexicana*). *Journal of Mammalogy*, 83: 489–500.
- NORBERG, R. Å. 1981. Optimal flight speeds in birds when feeding young. *Journal of Animal Ecology*, 50: 473–477.
- NORBERG, U. M., and J. M. V. RAYNER. 1987. Ecological morphology and flight in bats (Mammalia: Chiroptera): wing adaptations, flight performance, foraging strategy and echolocation. *Philosophical Transactions of the Royal Society of London B*, 316: 335–427.
- NOWAK, R. M. 1994. *Walker's bats of the world*. The Johns Hopkins University Press, Baltimore, 287 pp.
- RUSSO, D., and G. JONES. 2003. Use of foraging habitats by bats in a Mediterranean area determined by acoustic surveys: conservation implications. *Ecography*, 26: 197–209.
- RYDELL, J., and R. ARLETTAZ. 1994. Low-frequency echolocation enables the bat *Tadarida teniotis* to feed on tympanate insects. *Proceedings of the Royal Society of London B*, 257: 175–178.
- RYDELL, J., A. ENTWISTLE, and P. A. RACEY. 1996. Timing of foraging flights of three species of bats in relation to insect activity and predation risk. *Oikos*, 76: 243–252.
- SEAMAN, D. E., and R. A. POWELL. 1996. An evaluation of the accuracy of the Kernel density estimators for the home range analysis. *Ecology*, 77: 2075–2085.
- SHIEL, C. B., R. E. SHIEL, and J. S. FAIRLEY. 1999. Seasonal changes in the foraging behaviour of Leisler's bats (*Nyctalus leisleri*) in Ireland as revealed by radio-telemetry. *Journal of Zoology (London)*, 249: 347–358.
- SPRINGER, J. T. 1979. Some sources of bias and sampling error in radio triangulation. *Journal of Wildlife Management*, 43: 926–935.
- SWIHART, R. K., and N. A. SLADE. 1985. Testing for independence of observations in animal movements. *Ecology*, 66: 1176–1184.

- TAYLOR, L. R., and C. I. CARTER. 1961. The analysis of numbers and distribution in an aerial population of macrolepidoptera. *Philosophical Transactions of the Royal Society of London*, 113: 396–386.
- VAUGHAN, T. A., and M. M. BATEMAN. 1980. The molossid wing: some adaptations for rapid flight. Pp. 69–78, *in* Proceedings of the Fifth International Bat Research Conference (D. E. WILSON and A. L. GARDNER, eds.). Texas Tech Press, Lubbock, 434 pp.
- WARING, P. A. 1989. Comparison of light-trap catches in deciduous and coniferous woodland habitats. *Entomologist's Record*, 101: 1–10.
- WATERS, D., G. JONES, and M. FURLONG. 1999. Foraging ecology of Leisler's bat (*Nyctalus leisleri*) at two sites in southern Britain. *Journal of Zoology (London)*, 249: 173–180.
- WHITE, G. C., and R. A. GARROT. 1990. Analysis of wildlife radio-tracking data. Academic Press, London, 383 pp.
- WILKINSON, G. S. 1995. Information transfer in bats. Pp. 345–360, *in* Ecology, evolution and behaviour of bats (P. A. RACEY and S. M. SWIFT, eds.). Clarendon Press, Oxford, 421 pp.
- WILKINSON, G. S., and J. W. BOUGHMAN. 1998. Social calls coordinate foraging in greater spear-nosed bats. *Animal Behaviour*, 55: 337–350.
- ZBINDEN, K., and P. ZINGG. 1986. Search and hunting signals of echolocating European free-tailed bats, *Tadarida teniotis*, in southern Switzerland. *Mammalia*, 50: 9–25.

Received 20 August 2003, accepted 10 January 2004