

Prolonged foraging bouts of a solitary gleaning/hawking bat, *Myotis evotis*

Bryan J. Chruszcz and Robert M.R. Barclay

Abstract: We investigated the foraging behaviour of reproductive female long-eared bats, *Myotis evotis*, roosting solitarily in natural habitat in the badlands of the South Saskatchewan River valley, Alberta, Canada. *Myotis evotis* behaved differently than other temperate-zone insectivorous species studied previously. Individuals foraged all night, every night, regardless of ambient temperature or reproductive condition, and only spent a small proportion of the night roosting (less than 10% of the time spent out of the roost). A high daily energy demand and an energetically costly mode of flight may necessitate this behaviour. The ability to both aerial-hawk and glean prey from surfaces may make night-long foraging profitable for *M. evotis*, and for other flying nocturnal insectivores that can glean.

Résumé : Nous avons étudié le comportement de quête de nourriture chez des femelles reproductrices du vespertilion à longues oreilles, *Myotis evotis*, un percheur solitaire, dans son habitat naturel dans les badlands de la vallée de la Saskatchewan du Sud, en Alberta, Canada. Cette chauve-souris a un comportement différent de celui des autres chauves-souris insectivores de la zone tempérée étudiées précédemment. Les individus cherchent leur nourriture la nuit entière, toutes les nuits, quelle que soit la température ou leur condition reproductive, et ne se perchent que pour une courte période de la nuit (moins de 10 % de leur temps loin du perchoir). La demande énergétique quotidienne élevée et le mode de vol exigeant du point de vue énergétique peuvent nécessiter ce comportement. La capacité de chasser au vol et d'écumer les surfaces pour ramasser des proies font en sorte que la quête de nourriture pendant toute la nuit peut être une stratégie avantageuse pour *M. evotis* et pour d'autres insectivores nocturnes qui volent et qui sont capables d'écumer les surfaces.

[Traduit par la Rédaction]

Introduction

The foraging behaviour of temperate-zone insectivorous bats varies greatly (reviewed by Fenton 1990). In many species, individuals forage for one or two relatively short bouts per night, at dusk and (or) dawn, for a total of 1–4 h (Racey and Swift 1985; Brigham and Fenton 1991; Rydell 1993; Swift 1997; Wilkinson and Barclay 1997; Shiel et al. 1999). These foraging bouts correspond to peaks in insect abundance at dusk and dawn (Kunz 1974; Racey 1982; Racey and Swift 1985; Rydell 1993; Swift 1997) that are related to thresholds of ambient temperature (T_a) and light intensity (Taylor 1963). In particular, at low T_a (often around 10°C), the density of flying insects is low, foraging for aerially foraging insectivorous species is not profitable, and bats often return to their roosts or fail to emerge at all (e.g., Rydell 1989; Catto et al. 1995; Hamilton and Barclay 1998).

The influence of ambient conditions on the foraging behaviour of flying insectivores may be less pronounced in species that are not solely dependent on aerial prey. For example, owlet-nightjars (*Aegotheles cristatus*), nocturnal insectivorous birds that can forage on the ground as well as

aerially, forage all night regardless of ambient conditions (Brigham et al. 2000). Bats that can take prey in the air (hawking) as well as from surfaces (gleaning; Faure and Barclay 1994), such as the long-eared bat, *Myotis evotis*, are able to reproduce in climates that are inhospitable to strictly aerial hawkers, possibly because gleaners have access to another source of prey (Barclay 1991). While the ability to glean may offer advantages, the required slow, maneuverable flight is energetically expensive (Norberg and Rayner 1987), potentially increasing the energy demand on gleaners compared with aerial hawkers.

The purpose of this study was to examine the foraging behaviour of *M. evotis*, and in particular to determine what factors influence their foraging activity and whether gleaning potentially alters their response to changes in ambient conditions and energy demand.

Methods

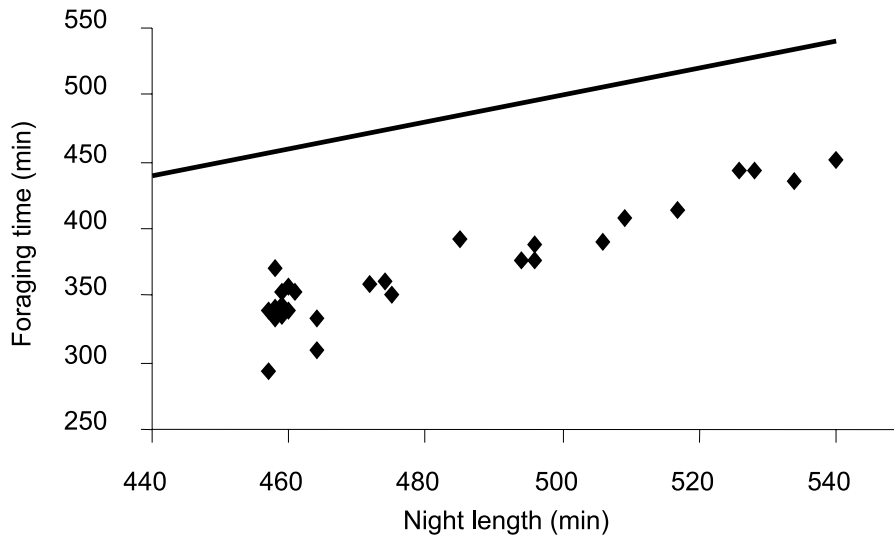
We conducted our study from May through August 1997 and 1998 in the badlands of the South Saskatchewan River valley about 20 km south of the town of Bindloss, Alberta, Canada (50°73'N, 110°56'W, elevation 700 m). The river valley is bordered by steep sandstone cliffs cut by drainage gullies (or coulees) eroded into the sandstone (Chruszcz and Barclay 2002). Reproductive female *M. evotis* roost in the coulees in sandstone boulders lying above the more permeable surrounding sandstone. Individuals forage in and around clusters of cottonwoods (*Populus deltoides*) at the edge of the river (Holloway and Barclay 2000).

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Fig. 1. Effect of night length on time spent foraging by reproductive female long-eared bats, *Myotis evotis*. The longer the night, the longer females spent foraging. Ten females were used in this analysis ($n = 29$ bat-nights). The solid line indicates foraging time = night length (regression line for the relationship: foraging time = 0.99 night length $- 108.5$).



We captured bats in mist nets and determined the reproductive condition of all captured females (i.e., pregnant, lactating, postlactating; Racey 1988), as well as body mass (Sartorius PT600 balance, ± 0.1 g) and age (subadult or adult; Anthony 1988). Animals were cared for in accordance with the guidelines of the Canadian Council on Animal Care.

To find roosts, track foraging bats, and monitor body temperatures, we attached temperature-sensitive radio transmitters (Holohil Systems Ltd., Carp, Ont.) weighing either 0.54 g (1997) or 0.56 g (1998) to reproductive females. We trimmed the fur between the shoulder blades and glued the transmitters to the skin using Skinbond[®] surgical adhesive (Canadian Howmedica, Guelph, Ont.; e.g., Hamilton and Barclay 1994). Such transmitters accurately reflect body temperature (Barclay et al. 1996).

We monitored tagged bats every 10–20 min from the time they emerged from their roosts until they finished foraging, using a Merlin-12 telemetry receiver (Custom Electronics, Nokomis, Fla.). We defined foraging time as the period between emergence from the roost at dusk and return to the roost at dawn because bats did not spend long periods of time roosting during the night (see Results). We used a HOBO[®]-TEMP data logger (Model HTEA-37+46, Onset Computer Corporation) positioned 1.5 m above the ground to continuously record T_a . We monitored the body temperature of radio-tagged bats from the time they returned to their roost after foraging until they emerged again the following evening (see Chruszcz and Barclay 2002). Using the definitions of torpor and deep torpor proposed by Grinevitch et al. (1995) and Hamilton and Barclay (1994), we determined the amount of time individuals spent in torpor each day.

We analysed foraging time using analysis of covariance (ANCOVA) with night length (defined as the time between sunset and sunrise), time spent in torpor the day before, and T_a at the time of return to the roost as covariates. Reproductive condition and individual were included as class variables and values are presented as means \pm SE.

Results

We captured 23 adult female *M. evotis* over two field seasons, some more than once. We used data from various subsets of these bats depending on whether or not we had attached a transmitter to the bat in question, the reproductive condition of the individual, and the analysis being performed.

Aldridge and Brigham (1988) suggested that for flying animals, transmitters should be $<5\%$ of an individual's body mass. In this study, involving the smallest transmitters available, transmitter mass ranged from 5.9 to 8.9% of bat mass ($7.3 \pm 0.1\%$, $n = 34$). Nonetheless, the timing of activity and the behaviour were no different in radio-tagged bats than in other individuals, and there was no evidence of negative effects on reproduction or change in body mass (Chruszcz 1999). For example, we caught female *M. evotis* during every hour of the night ($n = 44$) and capture rates did not vary during the first, second, and third 2-h periods ($\chi^2 = 1.92$, $df = 2$, $P > 0.05$). This suggests that, as the radiotelemetry data revealed, female *M. evotis* were active all night (see below).

We examined foraging time using data from five pregnant ($n = 20$ bat-nights) and five lactating females ($n = 17$ bat-nights). T_a ranged from 7°C to over 20°C on those nights. Individuals spent only a small proportion of the night roosting. Females stopped flying 5.1 ± 0.8 times per night, for a total of 32.3 ± 4.8 min ($n = 37$ bat-nights). This was less than 10% of the total time spent out of the roost. As these short breaks may have been used to consume large prey (Faure and Barclay 1994), we considered them to be part of the foraging bout and calculated foraging time as the time between a female's emergence from her roost at dusk and her return at dawn.

Female *M. evotis* foraged every night. Variation in foraging time was significant (ANCOVA, $F_{[12,16]} = 18.1$, $r^2 = 0.93$, $P < 0.001$) but was primarily due to variation in night length ($F_{[1,16]} = 8.85$, $P < 0.009$; Fig. 1). The longer the night, the longer a bat spent foraging. Pregnant females foraged for 341.2 ± 4.9 min and lactating females for $397.7 \pm$

8.4 min per night, but this difference was not significant when night length was accounted for. T_a and time spent in torpor did not have a significant effect on foraging time.

Discussion

Female *M. evotis* foraged every night for long periods (6–7 h), regardless of reproductive condition or T_a , whereas periods of roosting between foraging bouts are common in other species, and a low T_a curtails foraging (e.g., Kunz 1974; Racey 1982; Barclay 1982, 1989; Racey and Swift 1985; Rydell 1989; Catto et al. 1995; Wilkinson and Barclay 1997). The amount of time *M. evotis* spent foraging was determined primarily by the amount of time available for them to do so (i.e., night length). We suggest that the long foraging bouts of *M. evotis* reflect a combination of a flexible foraging style that is profitable under a wide range of environmental conditions, high energy demand, and relatively low prey availability.

While the abundance of flying insects declines in the middle of the night in our study area (Holloway and Barclay 2000) and elsewhere (e.g., Barclay 1985), the availability of nonvolant prey fluctuates less than that of aerial prey (Barclay 1991). Aerially foraging insectivorous bats forage during the peaks in insect abundance at dusk and dawn (e.g., Rydell 1993; Swift 1997; Holloway and Barclay 2000), but the ability to glean prey may allow *M. evotis* to forage profitably all night. Likewise, *M. evotis* may be able to forage profitably even when a low T_a reduces the abundance of flying insects and aerial-hawking bats do not forage.

The foraging behaviour of *M. evotis* is similar to that of some other gleaning insectivorous animals. Female *Myotis myotis*, a relatively large gleaning bat in Europe, spend over 6 h foraging per night (Audet 1990), and owl-nightjars have a continuous nocturnal activity pattern (Brigham et al. 2000). These studies suggest that prolonged foraging may be more common in gleaning species than in strictly aerial insectivores.

Even if the flexible foraging behaviour of reproductive female *M. evotis* enables them to forage profitably all night, why do they need to, especially given their regular use of torpor (Chruszcz and Barclay 2002), which should reduce energy demand? Aerially foraging insectivorous species typically forage for considerably shorter periods (e.g., Rydell 1993; Shiel et al. 1999). In the same habitat as that used in our study, even the larger (15–20 g) big brown bat (*Eptesicus fuscus*) forages for only 160–200 min per night (Wilkinson and Barclay 1997).

The slow, maneuverable flight of *M. evotis* is energetically expensive (Norberg and Rayner 1987), and combined with low-intensity echolocation calls (Faure and Barclay 1994), means that their rate of encounter with aerial prey is likely less than that of faster, louder aerial-hawking species in the area. *Myotis evotis* may thus have a lower net rate of energy intake than other species.

For female mammals, daily energy demand is typically highest during lactation, and lactating bats often forage for longer than do pregnant ones (e.g., Kunz 1974; Racey and Swift 1985; Barclay 1989; Rydell 1993; Wilkinson and Barclay 1997). Although pregnant and lactating females foraged for similar proportions of the night, night length starts to increase near the end of pregnancy, and thus more foraging time is available to lactating than to pregnant *M. evotis*. In addition, insect abun-

dance may be higher during the lactation period and foraging efficiency may increase after parturition, owing to lower flight costs and increased maneuverability resulting from decreased mass.

The combination of regular torpor use, solitary roosting (Chruszcz and Barclay 2002), and prolonged foraging is unusual for a temperate-zone insectivorous bat. It suggests that reproductive female *M. evotis* in our study area, near the northern limit of the species' geographic range (van Zyll de Jong 1985), are on a particularly tight energy budget.

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