The influence of a local temperature inversion on the foraging behaviour of big brown bats, *Eptesicus fuscus*

Devin Arbuthnott[1, 2] and R. Mark Brigham[1]

[1]*Department of Biology, University of Regina, Regina, Saskatchewan, Canada*
[2]*Corresponding author: E-mail: darbuthn@sfu.ca*

To maximise foraging efficiency, it is reasonable to expect animals to forage in the highest quality patches. Insectivorous bats should therefore travel to and forage at sites with the highest insect abundance. Since insects are ectothermic, their levels of activity should be higher in warmer areas, making these high quality patches for bats. A nightly temperature inversion occurring in the Cypress Hills (Saskatchewan, Canada) presented an opportunity to test our hypothesis that big brown bats (*Eptesicus fuscus*) select foraging sites based on temperature as a proxy for insect abundance. If temperature is an important determinant of the foraging behaviour of *E. fuscus*, we expect bats to forage in the warmest site closest to local night roosts. We tracked 18 bats for a total of 111 nights over two years and found that individuals often spent at least some of each foraging bout in an area where the temperature inversion was small or non-existent. Bats sometimes travelled up to 11 km to reach this site. Foraging in areas where the temperature inversion was small provides indirect evidence that local temperature fluctuations are not a major influence on the selection of foraging area by *E. fuscus*. Also, since there was little difference in the temperature between the nearby predicted foraging sites and actual foraging sites, we argue that the effect of temperature on insect activity cannot be used to predict foraging habitat selection by these bats. We found that the insect community of the foraging area was different than that of the roosting area, and that beetles were more abundant in the foraging site. Our data suggests that insect community composition is potentially a stronger direct influence on bat foraging behaviour than is temperature.

Key words: *Eptesicus fuscus*, foraging behaviour, foraging site selection, environmental variables, insect community, foraging range

Introduction

While foraging habitats are a key resource for bats (Kunz and Fenton, 2003), foraging behaviour with respect to habitat selection has received less attention than most other aspects of bat ecology, such as roosting behaviour (Brigham, 2007). The level of insect activity should be an indicator of where insectivorous bats forage, but insect activity and abundance are subject to a number of climatic variables. For example, because insects are ectotherms, both their abundance and activity are known to change in response to temperature (Mellanby, 1939; Taylor, 1963; Bale, 1991), precipitation (Wolda, 1988), and vegetation structure (Haddad *et al.*, 2001). As a result, the activity of insectivorous bats should likewise be influenced (albeit indirectly) by such environmental variability. As insect community composition (species present/

abundance) is often associated with environmental variables, the study of foraging behaviour in insectivorous animals should consider conditions beyond just prey distribution and abundance (Harrel *et al.*, 2001). Of these environmental variables, temperature may have the greatest effect on aerial insect abundance, as increasing temperature is correlated with increasing insect activity (Taylor, 1963). The influence of temperature on bat foraging behaviour has been evaluated in a number of studies, and the results vary with species and geographic location. Many studies suggest that bat activity is positively correlated with temperature (e.g., Vaughan *et al.*, 1997; Gaisler *et al.*, 1998; O'Donnell, 2000; Meyer *et al.*, 2004; Milne *et al.*, 2005; Christie and Simpson, 2006), while others show the opposite (e.g., Chruszcz and Barclay, 2003; O'Donnell and Christie, 2006). It is not surprising that different species exhibit diverse reactions to temperature, given that they have different diets and energetic constraints. However, even for *E. fuscus* alone there is disagreement: Hamilton and Barclay (1998) found that foraging time increased with increasing temperature, whereas Rogers *et al.* (2006) and Wilkinson and Barclay (1997) discovered that the activity pattern of *E. fuscus* was not influenced by ambient temperature. While temperature is likely to be an important indicator of the level of foraging behaviour by insect eating bats, little work has specifically addressed the issue of temperature effects on foraging site selection by bats. We asked whether bats would choose warmer foraging sites (which should have higher insect activity) if most other environmental variables are similar?

A nightly temperature inversion which occurs in the Cypress Hills of southwestern Saskatchewan offers a unique system to evaluate the impact of temperature on bat foraging behaviour. Daytime heating and the resulting air currents cause a layer of cool air to flow into the Battle Creek valley during the evening such that the valley begins most nights as the warmest area in the region, but the upland plateau area becomes relatively warmer as the night progresses (K. A. Kolar, unpublished data). A colony of big brown bats that have been studied extensively (e.g., Kalcounis and Brigham, 1998, Willis *et al.*, 2003; Willis and Brigham, 2004) roost in trees in close proximity to both the plateau and valley, and therefore, in the context of temperature, two different habitats. As big brown bats are known to exhibit flexibility in foraging behaviour (Brigham, 1991), they are likely capable of taking advantage of patches of high insect abundance resulting from such a temperature inversion, and are therefore a good study species to evaluate the influence of temperature on foraging site selection. Also, because these two habitats are spatially close, they are subject to many of the same climatic conditions, such as precipitation. However, these habitats did differ in their proximity to water, as the valley contains a creek, which may be important, as it provides standing water for bats to drink (Adams and Simmons, 2002), and bats are typically more active in riparian areas (Grindal *et al.*, 1999; Holloway and Barclay, 2000; Fellers and Pierson, 2002; Mildenstein *et al.*, 2005; Almenar *et al.*, 2006).

Using temperature as a proxy for insect abundance, we expected that bats would use the closest, warmest location, given that they are central place foragers (Rosenberg and McKelvey, 1999), meaning they return to the same roosting area between foraging bouts (Willis and Brigham, 2004). Therefore, we predicted that the bats would begin foraging bouts in the valley, which provided them with an opportunity to drink, and as the temperature inversion occurred, they would move to the warmer plateau to forage. Since bats experience temperature and insect abundance simultaneously, we were

unable to discriminate between the influence of these two factors. We measured temperature and sampled flying insects to evaluate the differences between the two potential foraging habitats and monitored foraging movements using radio-telemetry to assess the importance of temperature on foraging site selection by big brown bats in Cypress Hills.

MATERIALS AND METHODS

Study Site

Our study was conducted in Cypress Hills Provincial Park, Saskatchewan, Canada (49°34'N, 109°53'W) between 1 June and 31 August of 2005 and between 1 June and 31 of July 2006. Female big brown bats form maternity colonies within this park throughout the summer, roosting exclusively in trembling aspen (*Populus tremuloides*) cavities (Kalcounis and Brigham, 1998; Willis *et al.*, 2003, 2006; Willis and Brigham, 2004). These bats form dynamic colonies, displaying fission-fusion sociality. Individuals switch between roost trees, and roost with different individuals from the same roosting group often (Willis and Brigham, 2004).

Radiotracking

We captured female big brown bats every 2–3 weeks during June–August 2005 and June–July 2006 in a modified harp trap (K. A. Kolar, unpublished data) as they emerged from roost trees. All captured bats were members of the same colony, though we trapped them exiting from different trees. During each trapping event, we attached radio-transmitters between the scapulae of 2–4 individuals using Skin Bond adhesive after clipping the fur. We ensured that the transmitter represented 5% or less of the bat's body mass (Aldridge and Brigham, 1988). To track bats to foraging areas, we stationed ourselves near the roosting area at the time of emergence and monitored the relative position/direction of each individual every five minutes for the duration of one foraging bout. We tracked 18 individuals (16 adult females and two juvenile males).

Temperature and Insect Measurements

For this paper, we define a temperature inversion as a relatively high altitude area being 5°C or more warmer than a nearby lower altitude area. We measured ambient temperature using iButton temperature loggers (Dallas Semiconductor). In 2005, we deployed nine loggers at a height of approximately 1.5 m under shaded tree branches within the roost area (Area 1, which includes valley, upland plateau, and roost trees), three in each habitat type: valley, upland plateau, and roost (at an intermediate elevation) separated by at least 20 m. In 2006, we assessed the presence and extent of the temperature inversion between the roosting and foraging areas by deploying iButtons in both the roosting area (Area 1) and the foraging area (Area 2, which also contained a valley and plateau — see Results): two in the valley and two in the plateau for each area (8 total). We synchronized the loggers to record temperature every ten minutes. We report temperature as the average of iButton records within each habitat for each recording time. Descriptive statistics (mean and standard deviation) were used to describe the mean duration of temperature inversions and the differences in temperature between plateau and valley.

In 2005, we sampled insects within the three habitats of the roost area (Area 1), by counting the number of flying insects observed within the beam of a flashlight held approximately 1.5 m high, while making a slow (approximately 30 s duration) circle (Woods, 2002). This method may overestimate actual insect abundance, as many night-flying insects are phototactic. However, because we were more concerned with relative abundance, the method is valid given that all counts were performed in a similar fashion. We conducted a total of 63 counts in each of the three locations between 1 June and 31 August 2005. Sampling sites in the valley and plateau were each within 4 km of roost trees. Counts in the valley and plateau were often conducted on the same nights, but on 14 occasions, counts were made on separate nights. We present mean values for all counts at each location. We tested for differences in insect abundance between the three sites using a Kruskal-Wallis nonparametric ANOVA.

In 2006, to assess differences in insect abundance and community composition between the hypothesized foraging areas near the roost (Area 1) and the observed foraging areas (Area 2), we set sticky traps and flight intercept traps (Kunz, 1988) in each location. We placed three sticky traps and two flight intercept traps in each area for four weeks. Due to logistic constraints, the traps remained in the same location for the duration of the study, collecting insects both day and night. We emptied samples from each trap weekly and identified insects to the level of order. Differences in insect composition between sites were tested using a Pearson's chi-square test. Differences

in mean abundance were evaluated using a *t*-test based on each trap's weekly insect abundance.

RESULTS

Radiotracking

We tracked 18 individuals (body mass, $\bar{x} \pm SE = 20.4 \pm 2.6$ g, range: 16.2–26.6 g) for a total of 111 tracking nights. Individuals did not remain in close proximity to the roost area (Area 1, which includes the valley, plateau, and roost trees) as expected. Instead, 17 of the 18 individuals consistently travelled 3–5 km southeast to forage over pastureland (Area 2: foraging area, which also includes a valley and a plateau), the distance to which depended on the day roost location. On one occasion, an individual travelled approximately 11 km to reach this area from its roost. Of 89 tracking nights for 17 individuals (those nights where we tracked from a stationary location), on 76, at least a portion of the night was spent within Area 2 (pasture foraging area). On average, 50% of each foraging bout (during the 89 tracking nights) was spent in Area 2, where a bout was defined as the time spent presumably foraging between the time of leaving the roost and returning.

Area 2 was primarily grassland, with less tree cover than Area 1, where we expected bats would forage. Bats exhibited no discernable preference for valley or plateau within Area 2. While bats spent a portion of most foraging bouts at this foraging site, there was no predictable temporal pattern. That is, when one bat was tracked over a number of nights, it did not leave the roost area or stay in the foraging area for a consistent amount of time each night. Also, when more than one bat was tracked on the same night, individuals often behaved differently in that they travelled to the foraging sites at separate times and remained for different durations.

Temperature

A temperature inversion (meeting the 5°C or more definition) occurred on 51 of the 75 nights that we recorded temperature for Area 1 (2005 and 2006 data), while an inversion occurred on 10 of 27 nights for which we have data from Area 2 (2006 data). In Area 1, differences in temperature between valley and plateau were as much as 12°C on any given night. The mean maximum difference of 7.2 ± 2.9°C between the two sites occurred just before sunrise. The average length of time that the inversion persisted was 158 ± 141 (SD) min. Within Area 2, the mean maximum temperature difference between plateau and valley was 4.6 ± 1.6°C and the average inversion duration was 71 ± 60 min.

The nightly temperature at Area 2 was significantly warmer than that of Area 1 (paired *t*-test: $t = -73.60$, *d.f.* $= 4591$, $P < 0.001$). While this difference was statistically significant, the actual difference in temperature was small, approximately 2°C (95% CI: -2.16 to -2.05). Furthermore, there was little difference between valley and plateau temperatures in Area 2, while there were noticeable differences between valley and plateau in Area 1 (Fig. 1).

Insects

The average number of insects sampled in 2005 for the valley, roost, and plateau within Area 1 were not significantly different [valley: 17 ($n = 21$ samples), roost: 9 ($n = 7$), and plateau: 13 ($n = 35$); Kruskal-Wallis ANOVA: $\chi^2 = 4.49$, *d.f.* $= 2$, $P = 0.11$ — Fig. 2]. Insect orders present included Diptera, Coleoptera, Lepidoptera, Hymenoptera, Trichoptera (Caddisflies), Hemiptera, Homoptera (Cicadas), and Ephemoptera (Mayflies). Insect order composition varied significantly between Area 1 and Area 2 in 2006 ($\chi^2 = 12.62$, *d.f.* $= 2$,
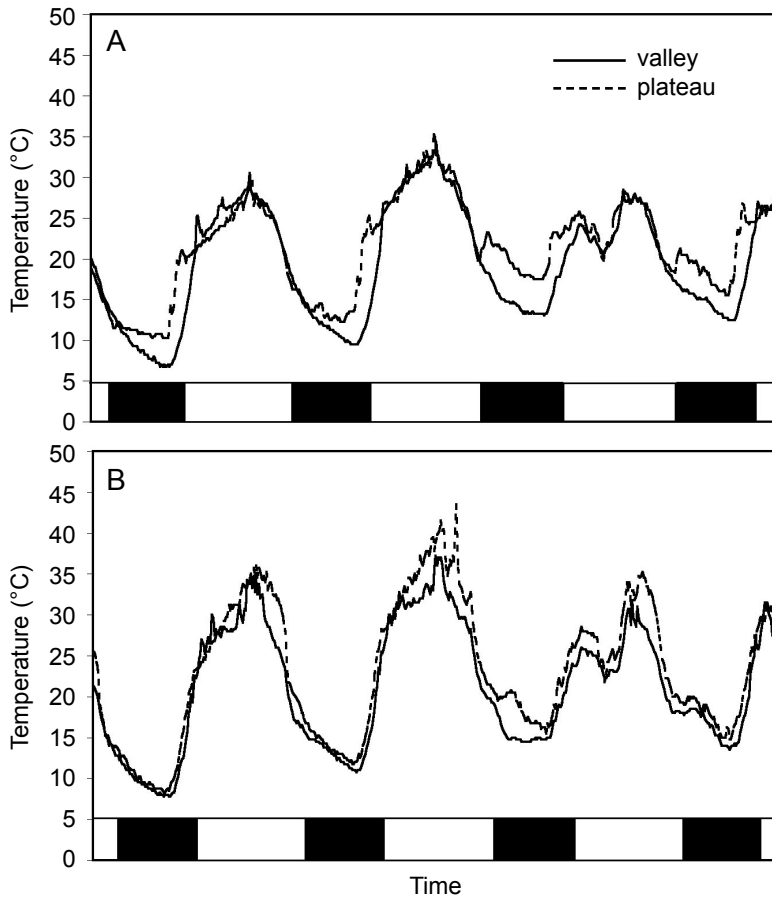
FIG. 1. Temperature profiles of roosting area (A) and foraging area (B) over four nights, illustrating the temperature inversion (when valley temperature is below plateau temperature). White bars represent daylight hours while black bars represent night

$P < 0.01$ — Fig. 3). Of the insects sampled in Area 1, 76% were Diptera, 15% Coleoptera, and 9% consisted of other orders, while at Area 2, 57% were Diptera, 27% Coleoptera, and 16% other orders. However, overall abundance was not significantly different between the two areas ($t = -1.46$, $d.f. = 33$, $P = 0.15$).

DISCUSSION

Eptesicus fuscus in the Cypress Hills did not simply forage in the valley or above the plateau within Area 1 on the basis of temperature as we expected. Instead, they travelled well outside of the roost area to forage,

substantially farther than the average 1.8 km linear distance reported by Brigham (1991) for the same species. Foraging occurred over a nearby cattle pasture, where there was little difference between plateau and valley in nightly temperature (Fig. 1), and therefore a large amount of foraging time occurred away from Area 1 where there was the greatest temperature inversion. This leads us to conclude that the local temperature inversion had little effect on bat foraging. Furthermore, we take the fact that there was little difference in temperature between the roosting and foraging sites as indirect evidence that these bats do not select sites based primarily on temperature. It is
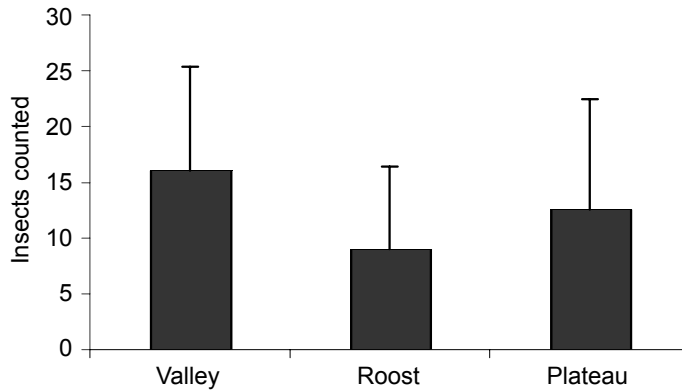
FIG. 2. Mean number ± SD of aerial insects counted between sites in the roosting area (Area 1) in 2005. Means were 17 for valley ($n = 21$ samples), 7 for roost ($n = 9$; at an intermediate elevation), and 13 for plateau ($n = 35$). Insect counts are not significantly different between sites

unlikely that individuals traveled 3–5 km nightly (and up to 11 km on some occasions) in order to reach a foraging site only 2°C warmer than the roost area. Evidence that temperature is not the only determining factor is also derived from our insect sampling data in Area 1 in that we found no significant difference in insect abundance between valley and plateau during the temperature inversion.

The variation we documented in foraging behaviour between individuals on the same night suggests that environmental variables are not the only factors influencing foraging. We conclude that there must be factors influencing individual behaviour which have more influence on foraging than temperature.

The sometimes long commuting distance and predictable foraging area also suggests that temperature alone does not determine foraging site selection by big brown bats in Cypress Hills. If temperature was being used as a cue for foraging site selection, then we would expect bats to travel to the plateau within Area 1, as it is often the same temperature as the foraging site, as well as being significantly closer to the roosting site. During foraging bouts, it seems that bats forage at a preferred site,
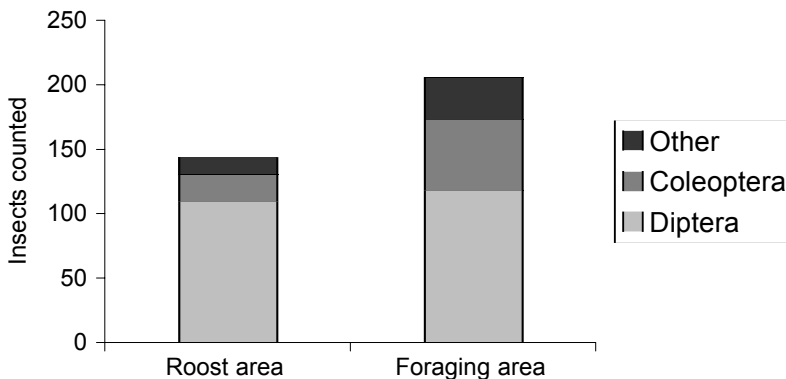

FIG. 3. Insect abundance by order between roost (Area 1) and foraging (Area 2) areas in 2006. 144 insects were captured in the roost area and 206 were captured in the foraging area using sticky and flight intercept traps. Insect compositions between sites are significantly different ($P < 0.01$)

rather than selecting locations close to the roost with the warmest temperatures. Fidelity to foraging site has also been documented by Brigham (1991).

The apparent unimportance of temperature (via its proxy effects on insect abundance) leads to the larger and more difficult task of determining what factors influence overall insect abundance, community composition, and therefore bat foraging behaviour. Bats are known to be more active in certain habitats relative to others (Brigham, 2007), but what are the proximate causes being used by bats to select foraging sites? One possibility may be the reduction in structural clutter (lack of trees) within the foraging site, as big brown bats tend to be more active in open habitats (Brigham and Fenton, 1991; Menzel *et al.*, 2005). The low risk of predation on foraging bats in the Cypress Hills likely contributes to their use of open areas while foraging. However, it seems unlikely that this is the principal explanation for site selection since there are available open areas much closer to roost sites that were not used by these bats.

A more likely explanation for foraging site selection of big brown bats is the opportunity for a selective diet. Our insect sampling found that the pasture had a greater proportion of beetles, relative to other insect orders, likely a result of the abundance of cattle. Beetles are often a common prey item for *E. fuscus* (Brigham and Saunders, 1990; Agosta and Morton, 2003; Agosta *et al.*, 2003). Similar to these bats, Greater horseshoe bats (*Rhinolophus ferrumequinum*) in the United Kingdom (Duvergé and Jones, 1994; Jones *et al.*, 1995) flew from roost areas to feeding sites 1.5–3 km away to forage primarily on beetles; while there was some flexibility in foraging sites, there was an observable preference for grazed pasture over other habitat types. Like *E. fuscus*, *R. ferrumequinum* bats consumed Coleoptera in higher

proportions than their relative abundance within the insect community (Jones *et al.*, 1995). Insect sampling showed that cattle pastures had a higher abundance of Coleoptera, specifically dung beetles resulting from the presence of cow feces. These foraging sites were also colder than nearby available woodlands, suggesting that temperature is also unimportant for site selection of *R. ferrumequinum*. Since beetles are large, relative to other aerial insects, they may provide energetically advantageous prey items for foraging bats. Furthermore, beetles are typically high in poly-unsaturated fatty acids, which likely facilitate torpor use (Schalk and Brigham, 1995), a strategy that is commonly used by bats in the Cypress Hills (Willis, 2003; Willis *et al.*, 2006).

In conclusion, we took advantage of a nightly temperature inversion in the Cypress Hills uplands to assess the importance of temperature on bat foraging behaviour. Big brown bats consistently travelled large distances to forage at a single site with temperature characteristics similar to sites much closer to roosts. While our data do not provide as direct a test of the importance of temperature in foraging site selection as we had hoped, they do show that *E. fuscus* does not take advantage of high temperature patches or use these patches as a proxy for insect abundance. In fact, it appears that temperature alone has little effect on the decision-making behaviour of bats with respect to foraging. Furthermore, our data indicate how far individuals are willing to travel, presumably to reach high quality foraging patches. Since bats travelled to nearby cattle pastures, which contains a higher proportion of beetles, we hypothesize that these bats select sites based, at least in part, on the local insect community composition.

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