Local distribution and foraging behavior of the spotted bat (Euderma maculatum) in northwestern Colorado and adjacent Utah

Jay F. Storz

University of Colorado, Boulder
LOCAL DISTRIBUTION AND FORAGING BEHAVIOR OF THE SPOTTED BAT (EUDERMA MACULATUM) IN NORTHWESTERN COLORADO AND ADJACENT UTAH

Jay F. Storz

ABSTRACT.—This study investigated local distribution and foraging behavior of the spotted bat (Euderma maculatum) in Dinosaur National Monument, Colorado-Utah, by monitoring audible echolocation calls. The occurrence of this species was verified in a variety of habitat types in canyon bottoms and other relatively low elevation sites, indicating that the animals are widely distributed and locally common in the area. Foraging spotted bats concentrated flight activity in the open-air space above meadows and occasionally exploited near-canopy habitat (within 8 m of foliage). Bats began to forage shortly after dark, and activity levels were relatively constant throughout the night. Foraging spotted bats attacked airborne prey every 2.15 min on average. Consistent with published observations, spotted bats maintained exclusive foraging areas. Distinct vocalizations indicating agonistic encounters occurred when a bat encroached on the foraging area of a conspecific.

Key words: spotted bat, Euderma maculatum, Colorado, Utah, Dinosaur National Monument, foraging, habitat use, attack rates, echolocation.

The spotted bat (Euderma maculatum) is widely distributed across western North America and apparently exists in low population numbers throughout its range (Fenton et al. 1987). The species is rare in collections, and viable populations have been documented in only a few widely separated localities (Watkins 1977, O'Farrell 1981). Findings presented here and those of Navo et al. (1992) indicate that E. maculatum is locally common in canyon bottoms and other low-elevation sites in Dinosaur National Monument, Colorado-Utah, and occurs throughout a diverse range of habitat types.

Population studies (e.g., Leonard and Fenton 1983) in south central British Columbia have demonstrated that foraging spotted bats exhibit considerable habitat specificity; radiotracking in this same area (Wai-Ping and Fenton 1989) has demonstrated that individuals are faithful to specific sites over several consecutive nights. However, no clear association between foraging activity and any specific habitat conditions is apparent. In British Columbia, spotted bats forage over clearings in ponderosa pine (Pinus ponderosa) forests, open fields, and marshes (Leonard and Fenton 1983, Wai-Ping and Fenton 1989). There is little information about foraging habitat throughout the remainder of the geographic range of E. maculatum.

The purpose of this study was (1) to investigate local distribution of E. maculatum by monitoring echolocation calls, (2) to identify and describe foraging habitat, and (3) to make a preliminary examination of spatial and temporal patterns of habitat use by spotted bats in the study area.

METHODS

This study was conducted in the canyon bottoms and other relatively low elevation sites in Dinosaur National Monument (109°W, 40°31’N), northwestern Colorado and northeastern Utah, from 17 May to 9 June 1993. Navo et al. (1992) provided a description of the physiography and vegetation of Dinosaur National Monument. In each study site where spotted bats occurred, I monitored movement patterns and foraging behavior by listening to the low-frequency (15–9 kHz; Leonard and Fenton 1984) echo-location calls of this species, which are clearly audible to the unaided human ear (Woodsworth et al. 1981).

As reported previously (Navo et al. 1992), E. maculatum is readily identifiable because it has the lowest-frequency echolocation calls of...
any bat species in the study area. *Nyctinomops macrotis* and *Idionycteris phyllotis* also produce orientation sounds that are partly audible to humans, with frequencies of 25–17 kHz for *N. macrotis* (Fenton and Bell 1981) and 24–12 kHz for *I. phyllotis* (Simmons and O'Farrell 1977). These two species inhabit southern parts of the Colorado Plateau and the Great Basin (Milner et al. 1990, Tumlison 1993), but neither is known to occur as far north as Dinosaur National Monument, extralimital records of *N. macrotis* notwithstanding (Milner et al. 1990). To further ensure correct call identification, I referred to recordings of known *E. maculatum* calls. I also visually identified free-flying individuals (based on conspicuous white venter and large ears) at close range in the beam of a high-intensity flashlight after locating the animals by listening to orientation sounds. It should be noted that *I. phyllotis* is often buff-colored ventrally and therefore could be visually misidentified as *E. maculatum* in areas of sympathy.

**Sampling Locations**

To investigate the ecological distribution of *E. maculatum*, I sampled 15 sites at 12 locations representative of common low-elevation habitat types in the area (Fig. 1). Riparian sites (Jenny Lind Rock, 1603 m; Echo Park, 1553 m; Split Mountain Gorge, riverbank and sandbar, 1439 m) are characterized by wide channels and reaches of calm water bounded by steep sandstone cliffs. Isolated stands of boxelder (*Acer negundo*) and cottonwood (*Populus fremontii*) line the riverbanks along with thickets of tamarisk (*Tamarix* sp.).

Orchid Draw (1484 m) and Red Wash (1537 m) are dry desert washes characterized by rabbitbrush (*Chrysothamnus nauseosus*), sagebrush (*Seriphidium tridentata*), greasewood (*Sarcobatus vermiculatus*), and shadscale (*Atriplex confertifolia*), with tamarisk dominating drainage bottoms.

Echo Park Meadow (1548 m) and Pool Creek (1635 m) are both open meadows with dominant ground cover of cheatgrass (*Anisantha tectorum*), various bunchgrasses, and isolated clumps of boxelder. Echo Park Meadow encompasses an area of ca 18 ha, bounded by the Green River to the west and high (150–230 m) sandstone cliffs on remaining sides. The meadow at Pool Creek (ca 8 ha) is situated at the mouth of a narrow canyon; boxelder and cottonwood form a dense, continuous canopy over much of the adjacent creek.

Remaining locations consist of a moist meadow (Hog Canyon, 1635 m), open sagebrush shrublands (Rainbow Park, 1488 m; Island Park, 1512 m), and a narrow canyon with thick riparian vegetation (Jones Hole, 1585 m).

**Sampling Methods**

At all locations I remained at a single site during each night of sampling. By pacing from a boxelder, which served as a focal point of bat foraging activity in Echo Park Meadow, I estimated that calls of *E. maculatum* were detectable at a distance of roughly 100 m. Therefore, the area sampled at each site is here defined as the air space within a hemisphere of radius 100 m. On several nights periods of high wind and/or rain reduced this range of detectability, with an attendant underestimation of bat activity. Furthermore, sites differed slightly in levels of background noise from nearby streams, the amount of obstructive vegetation, and various atmospheric conditions such as relative humidity, all of which affect the propagation of sound (Lawrence and Simmons 1982).

Study sites were situated either at the mouths of canyons or draws or in the middle of open areas where movement patterns of bats could best be assessed and the range of detectability was maximized. In locations characterized by expansive terrain (open meadows or shrublands), I monitored two different sites separated by >300 m on consecutive nights to assess uniformity of activity levels over large areas. All sites were monitored from 2000 to 0200 h with the exception of Echo Park Meadow, which was monitored from 2000 to 0400 h for seven consecutive nights (19–26 May) to assess temporal patterns of foraging activity.

At locations where I observed high levels of foraging activity (e.g., Echo Park Meadow and Pool Creek), bat activity was quantified by timing the duration of individual foraging sessions and recording the number of feeding buzzes (the increased rate of echolocation pulse repetition associated with attacks on airborne prey; Griffin et al. 1960). Following Leonard and Fenton (1983), the occurrence of feeding buzzes indicates foraging activity, and a foraging session is defined as the time during which a single spotted bat hunted continuously within the study site. To permit comparison
Fig. 1. Map showing sampling locations for monitoring activity of *Euderma maculatum* in Dinosaur National Monument in late spring 1993. Circles = locations at which transient occurrences of commuting or foraging bats were recorded; triangles = foraging areas (see text for details).

of relative levels of activity throughout the night, the time spent by spotted bats in the study site was totaled for every 15-min period sampled. Sampling periods during which heavy rain occurred were not considered.

To assess spatial patterns of habitat use, I described the foraging flights of spotted bats into a minicassette recorder and noted flight patterns and use of available foraging space relative to a near-canopy habitat zone (within 8 m of tree canopies) and an open-area zone (the clutter-free air space over the open meadow). These habitats correspond to habitat zones 1 and 4, respectively, proposed by Aldridge and Rautenbach (1987). I recorded the duration of foraging activity occurring within each zone as well as the number of bats simultaneously present within the study site and interactions between them.

I recorded the number of feeding buzzes heard during each foraging session for each night of observation at Echo Park Meadow and Pool Creek for the purpose of calculating attack rates (feeding buzzes/min) of foraging spotted bats. I considered only those foraging sessions of duration >3 min during which all feeding buzzes produced by a single individual within the study site could be counted accurately.

At other locations where I observed only transient occurrences of foraging or commuting spotted bats, activity was quantified by recording the number of bat passes (sensu Fenton 1970) per 15-min sampling period.

**RESULTS AND DISCUSSION**

I observed spotted bats in 13 of 15 sites sampled (Table 1). At 8 of these locations I observed only commuting bats. Passes of commuting spotted bats occurred sporadically throughout the night. At locations where two separate sites were monitored on consecutive nights, the number of passes remained fairly constant (passes/night: Echo Park, 5, 4; Hog Canyon, 5, 6; Island Park, 6, 10), and directions of travel appeared similar for bats on both nights.

Availability of cliff roosting sites has been suggested as a limiting factor in the distribu-
Table 1. Number of passes of Euderma maculatum per 15-min sampling period between 2000 and 0200 h at Dinosaur National Monument (16 May–8 June 1993). See text for general description of habitat types.

<table>
<thead>
<tr>
<th>Sampling location</th>
<th>Number of nights</th>
<th>Number of sampling periods</th>
<th>( n )</th>
<th>( \bar{x} )</th>
<th>Range</th>
</tr>
</thead>
<tbody>
<tr>
<td>Jenny Lind Rock</td>
<td>1</td>
<td>24</td>
<td>0</td>
<td>0</td>
<td></td>
</tr>
<tr>
<td>Echo Park</td>
<td>2</td>
<td>48</td>
<td>9</td>
<td>.19</td>
<td>0–2</td>
</tr>
<tr>
<td>Hog Canyon</td>
<td>2</td>
<td>48</td>
<td>11</td>
<td>.23</td>
<td>0–3</td>
</tr>
<tr>
<td>Orchid Draw</td>
<td>1</td>
<td>24</td>
<td>18</td>
<td>.75</td>
<td>0–6</td>
</tr>
<tr>
<td>Red Wash</td>
<td>1</td>
<td>24</td>
<td>32</td>
<td>1.33</td>
<td>0–1</td>
</tr>
<tr>
<td>Split Mountain Gorge (sandbar)</td>
<td>1</td>
<td>24</td>
<td>1</td>
<td>.04</td>
<td>0–5</td>
</tr>
<tr>
<td>Split Mountain Gorge (riverbank)</td>
<td>1</td>
<td>24</td>
<td>8</td>
<td>.33</td>
<td>0–8</td>
</tr>
<tr>
<td>Rainbow Park</td>
<td>1</td>
<td>16</td>
<td>4</td>
<td>.25</td>
<td>0–1</td>
</tr>
<tr>
<td>Island Park</td>
<td>2</td>
<td>48</td>
<td>16</td>
<td>.33</td>
<td>0–2</td>
</tr>
<tr>
<td>Jones Hole</td>
<td>1</td>
<td>24</td>
<td>0</td>
<td>0</td>
<td>—</td>
</tr>
<tr>
<td>All sites</td>
<td>13</td>
<td>280</td>
<td>99</td>
<td>.35</td>
<td>0–8</td>
</tr>
</tbody>
</table>

The abundance of high cliffs in Dinosaur National Monument as well as transient occurrences of commuting bats throughout a variety of widely separated low-elevation sites (Navo et al. 1992, this study) suggests that suitable roosting habitat is widespread throughout the area. However, information about microclimate requirements of this species is needed to fully assess actual availability of suitable roost sites.

I observed foraging spotted bats by sight and sound at five locations, three of which (Echo Park, Orchid Draw, Red Wash) involved only transient occurrences of bats that were observed executing steep dives and other abrupt flight maneuvers coincident with feeding buzzes as they passed through the area. I observed a single spotted bat foraging over a sand-and-gravel bar at Echo Park, but activity levels at this location were lower than those reported by Navo et al. (1992), who sampled this same site previously. Fairly high levels of activity occurred at Orchid Draw and Red Wash (Table 1), and I heard three feeding buzzes at each site. However, because spotted bats apparently capture prey opportunistically while commuting to specific foraging sites (Wai-Ping and Fenton 1989), observations of foraging bats passing through an area cannot be considered indicative of habitat preferences.

At Echo Park Meadow, spotted bats first arrived at the study site at 2123 h ± 11 min Mountain Daylight Time (\( n = 6 \) rain-free evenings), always after dark, and remained active throughout the night (Fig. 2). Spotted bats foraged within the study site for 6.22 ± 2.40 min out of every 15-min sampling period between 2100 and 0400 h (\( n = 2490 \) min; Fig. 2), and foraging sessions lasted 5.48 ± 2.74 min (\( n = 187 \)). At Pool Creek, spotted bats hunted within the study site for 6.82 ± 5.03 min out of every 15-min sampling period between 2100 and 0200 h (\( n = 525 \) min), and foraging sessions lasted 8.97 ± 8.78 min (\( n = 30 \)). These activity levels offer strong evidence that open meadows represent important foraging habitat for E. maculatum in this area.

Comparatively low levels of activity were recorded at riparian sites adjacent to Echo Park Meadow (Echo Park, Jenny Lind Rock). Because no physiographic barriers are present that might restrict accessibility to the bats, it appears that open water courses do not represent foraging areas of choice. These observations agree with those of Leonard and Fenton (1983), who reported that in British Columbia spotted bats foraged in forest clearings and open fields to the exclusion of a nearby river.

The temporal pattern of foraging activity in Dinosaur National Monument is similar to that reported from British Columbia (Leonard and Fenton 1983), where spotted bats were active throughout the night. Because radiotracking (Wai-Ping and Fenton 1989) has demonstrated that individual spotted bats hunt on the wing >300 min per night, reports of apparent peaks in nightly activity (which have been especially pronounced in mistnetting studies, e.g., Easterla 1973) are likely artifacts related to the proximity of sampling sites to diurnal roosts and/or drinking sites.

At Echo Park Meadow and Pool Creek, foraging spotted bats typically flew in large circular or elliptical orbits at heights of 10–30 m above the ground. In 1088.8 min of observation of foraging spotted bats at Echo Park
Fig. 2. Foraging activity patterns of Euderma maculatum at Echo Park Meadow (19–26 May 1993). Bars represent mean time (+ SD) spent by bats in the study site per 15-min sampling period from 2000 to 0400 h (n = 6 for each 15-min period in the interval 2000–0345 h, n = 4 for 0345–0400 h).

Meadow, 81.5% of activity occurred over the open meadow, which constituted roughly 85% of the site, while 18.5% of activity occurred within 8 m of the foliage of fully leaved box elders at mid- to upper-canopy level. Such activity consisted of bats circling closely above and around individual trees or isolated clumps of trees. I rarely observed bats within 0.5 m of the canopy, and I never observed hovering flight or other evidence of foliage gleaning. In 290.8 min of observation of foraging spotted bats at Pool Creek, all activity occurred over the open meadow, although a much larger percentage of the study site area comprised canopies of boxelder and cottonwood than at Echo Park Meadow.

The predilection of E. maculatum for foraging over open terrain in Dinosaur National Monument agrees with the pattern observed in previous studies (e.g., Woodsworth et al. 1981, Leonard and Fenton 1983). Low-frequency echolocation calls and long intercall intervals suggest that spotted bats use a foraging strategy based on long-range prey detection and high-level flight (Simmons and Stein 1980, Woodsworth et al. 1981, Barclay 1986). This strategy likely is best suited to open areas (Neuweiler 1984). Although I never directly observed these bats gleaning prey from foliage during this study, observations of near-canopy foraging contrast with those of some other workers (e.g., Wai-Ping and Fenton 1989) who have reported that this species never attacked insects near foliage or any other type of surface. Information about individual variability in foraging behavior is needed before drawing conclusions about variability between populations related to different ecological conditions.

At both Echo Park Meadow and Pool Creek, there were 118 instances in which two or three E. maculatum were present within the study site simultaneously. Leonard and Fenton (1983, 1984) estimated that spotted bats in British Columbia maintain a distance of at least 50 m between adjoining foraging areas and suggested that this spacing is accomplished through a combination of mutual avoidance and active monitoring of encroachments by conspecifics. This same system appears to be operating at foraging areas in Dinosaur National Monument. Consistent with observations of Leonard and Fenton (1983), foraging spotted bats often produced agonistic vocalizations when the 50-m buffer zone was breached by an intruding bat. Such vocalizations sounded qualitatively different from feeding buzzes and occurred only during close-range encounters between conspecifics. Information about known individuals and resource availability is needed to elucidate the role of agonistic interactions in the foraging ecology of E. maculatum.

During this study I heard a total of 247 feeding buzzes, and never more than one per min from the same individual. In a sample of 37 foraging sessions, spotted bats attacked an insect every 2.15 min on average (0.466 ± 0.294 attacks/min, range 0.16–0.94; n = 152 feeding buzzes). These rates generally agree with values reported in previous studies (Leonard and Fenton 1983, Wai-Ping and Fenton 1989), further confirmation that this species attacks prey at a rate much lower than is typical of bats that forage from continuous flight (Barclay 1985, Hickey and Fenton 1990).

Density of clutter in an environment imposes differential constraints on the maneuverability and perceptual capacities of bats, thereby determining the accessibility of different habitats by influencing foraging efficiency (Neuweiler 1984, Aldridge and Rautenbach 1987, Fenton 1990). Spotted bats appear to forage preferentially in open areas, which may be
related to the use of a long-range foraging strategy (Barclay 1986), and the ability to exploit edge situations may reflect a measure of behavioral flexibility in this regard. Because spotted bats are obviously not greatly restricted in foraging habitat with regard to vegetation associations (Wai-Ping and Fenton 1989, Navo et al. 1992), structural features of the environment related to density of clutter may be more predictive of habitat suitability and the use of available foraging space. However, information on individual variability is needed before drawing conclusions about the foraging strategy of this species.

ACKNOWLEDGMENTS

I am grateful to D. M. Armstrong, K. W. Navo, M. B. Fenton, M. L. Leonard, M. A. Bogan, C. E. Bock, J. A. Gore, and G. T. Skiba for advice regarding study site locations and sampling methods. I thank the personnel of Dinosaur National Monument, and especially S. J. Petersburg, for cooperation and for sharing knowledge of the area. Critical comment on the manuscript from D. M. Armstrong, M. B. Fenton, R. M. Timm, M. J. O'Farrell, and two anonymous reviewers was much appreciated. Funding was provided by the Undergraduate Research Opportunities Program, University of Colorado at Boulder.

LITERATURE CITED


Received 7 February 1994
Accepted 20 June 1994