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SITE FIDELITY IN THE NORTHERN BAT (*EPTESICUS NILSSONI*) DURING PREGNANCY AND LACTATION

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A maternity colony of northern bats (*Eptesicus nilssonii*) in southern Sweden (57°47'N, 13°25'E) was studied from May to August 1982–1986. The northern bat, a medium-sized (8–15 g) insectivorous (Rydell, 1986a) vespertilionid, is the most common bat in Sweden. Maternity colonies roost in buildings and usually are composed of 10–70 females (Lehmann, 1983; Ryberg, 1947).

The study area consisted of a 5-ha park, characterized by rows of old deciduous trees and small openings, and a surrounding open farmland (fields and pastures) with some large isolated trees and patches of woodland. Several buildings occur within the park, among them four heated houses that provided roosts for the bat colony.

Bats were observed as they emerged from their roost several times per week and counted at irregular intervals. Most adults were caught every year in mist nets or a Tuttle-trap erected in front of exit holes two or three times per summer. All adult colony members were marked individually with metal bands covered by reflecting tape. Females were examined for signs of current reproduction (Kunz, 1974). Full-grown unmarked females with apparently unsuckled nipples were assumed to be yearlings. Many juveniles escaped capture, but those caught were recognized easily by size and color. The bats were released within 0.5 min after capture.

The search for foraging bats, aided by binoculars and a bat detector (QMC S-100), was conducted on foot during 20 nights in 1982 and 1983; subsequently, feeding sites were revisited irregularly throughout the study. The detector permitted instantaneous species identification (Ahlén, 1981). Color codes of marked bats were identified with a halogen headlight. To examine site fidelity and social interactions among foraging bats, I observed one feeding site continuously for 27 nights and another for 15 nights in 1983–1985. These sites were barns (near which insects accumulated) situated on open farmland 100 m from each other and 200 and 300 m from the main roost. Observations started when the first bats emerged from the roost and lasted at least until midnight, usually covering an entire foraging period. All arrivals and departures and social interactions were recorded to the nearest 10 s. Statistics were performed according to Sokal and Rohlf (1981).

Four occupied houses, but none of several unheated buildings, within the park were used as roosts by the bats. Shifts between these roosts, 50–100 m apart, were observed 14 times (one–four per summer). Except for two instances which followed my initial trapping efforts in 1982, the reasons for the shifts are unknown. The main roost, used for 71% of the study period, was situated near the chimney in the roof of an old wooden house. The secondary roost, used for 24% of the study period, was located in the south-facing wall of a modern brick house. Each of the other houses in the park was used once in spring. All roosts were inaccessible to humans.

Roosts usually were occupied by females from late May (range, 18 May–8 June), and the number of bats increased until mid-June (range, 4–24 June), when the last individuals arrived. The first isolation calls, which indicated that births had occurred, were usually heard in early July (range, 29 June–11 July), and the first juveniles appeared outside the roost 15–17 days later (range, 15–26 July). The bats abandoned the area in late July or early August, when the young became independent.

The colony initially (1982–1984) consisted of 27–30 females. It remained stable in number and composition except for a reduction to 17 parous females in 1985, after an exceptionally prolonged winter. About 20% (range, 17–21%) of the females were yearlings except in 1985, when no yearlings appeared. Adult males never were found in the colony.

Annual recapture frequencies of adult (≥ 2 years old) females ranged from 54 to 85% (total 70.9%, $n = 103$). Female yearlings were recaptured at significantly lower frequencies (total 40.0%, $n = 15$; $G = 4.1$, $P < 0.05$). Three (20%) females marked as juveniles reproduced in their natal colony when 2 years old. Ninety-seven percent ($n = 68$) of the adult females examined, but none of the yearlings, were either pregnant or lactating. Males ($n = 17$) were not recaptured after their first winter. The difference between recapture frequencies for males and females is significant ($G = 6.7$, $P < 0.01$).

Exchange of individuals between adjacent colonies appeared to be rare. Only one unmarked adult was

TABLE 1.—Use (in min; n = number of nights) of two feeding sites by female *Eptesicus nilssonii* near the roost in southern Sweden, June–July, 1983–1985. Dash indicates that individual was present in the colony and reproducing; blank indicates that individual was not present or not reproducing.

Individual	Site A						Site B					
	1983		1984		1985		1983		1984		1985	
	Min	n	Min	n	Min	n	Min	n	Min	n	Min	n
Total nights observed		3		15		9		5		3		7
RW	50.6	3	111.2	13			2.0	1	2.4	1		
BR			218.0	9	25.6	3			0.1	1		—
GB	10.1	1	78.0	8	31.6	7	4.1	1			13.9	6
RY					62.3	5					14.5	5
OW	0.2	1	47.6	9	20.0	6						—
B	5.0	2					33.8	5				
YG							19.5	5	14.3	3		
YR	1.3	2									2.7	2
BW	0.1	1	1.4	1					0.3	2		
WG	0.1	1	1.4	1	0.1	1						—
OG					0.5	1						—
OO							4.1	2	0.2	1		
WR									0.1	1		—

caught in the colony after the initial capture of all individuals in 1982. Two other maternity colonies, which occupied houses 800 and 1,100 m from the study site, were inspected each year, but no marked individuals were found there. Inspection of houses ($n = 30$) located between these roosts and those used by the marked bats revealed no additional colonies.

After evening emergence, the bats foraged near the roost and in the park, but spread subsequently toward the open farmland, where they established individual foraging paths around trees and buildings and along edges of woodlands. They normally stayed a few minutes in each area before moving directly to another feeding site. Several individuals often foraged sequentially at each site (Rydell, 1986b). Approximately 700 observations of marked, foraging bats were distributed among 25 more-or-less-distinct sites, 80% within a range of 400 m, and none >1,200 m from the main roost. In addition to the marked bats, unmarked individuals were observed throughout the area. Feeding sites were used on similar seasonal schedules but with slightly different intensities in each year of the study.

Of the two feeding sites observed intensively, each was used regularly by only two to four marked bats each year and occasionally by other marked individuals (Table 1). Unmarked bats also were observed almost daily. Females that regularly used the sites defended them against intruders; linear dominance orders were evident among them (Rydell, 1986b). Hence, dominance, used according to Kaufmann (1983), implies priority of access to the site. Territories were kept by the same individuals from year to year as long as they remained in the colony (Table 2). Individuals maintained dominance ranks in most instances; two reversals were observed. In 1984, a two-year-old bat, breeding for the first time, acquired permanent dominance over two others through frequent interactions; a similar situation occurred in 1985 when another bat became dominant at the same site (Table 2, site A). Except for these reversals, the territories were defended only against individuals of lower rank or unmarked ones.

Data from feeding site A in 1984 and 1985 (Tables 1 and 2) suggest that dominance was correlated only loosely with the time spent at the site ($r_s = 0.40$ and 0.10 in 1984 and 1985, respectively, $d.f. = 3$, $P > 0.05$ in both years). However, a correlation with foraging efficiency is suggested because the territorial individuals spent 1–5% (2–8 min) of the observed foraging time involved in territorial disputes, as compared to 9% (1.4 min) for all nonterritorial individuals combined. The fraction increased with decreasing rank ($r_s = -1.00$, $d.f. = 3$, $P < 0.05$ in both years).

The available data suggest that northern bat maternity colonies conform to the general mammalian pattern (Greenwood, 1980), having structurally stable groups characterized by natal dispersal of males and fidelity to natal areas among females. The study area apparently provided an abundance of roosting sites for house-dwelling bats; therefore, roost shortage does not seem to be the main reason for the observed site fidelity (Humphrey, 1975). However, some houses may provide particular conditions that enhance reproductive success, thereby making them superior to superficially similar houses (Brigham and Fenton, 1986).

Alternatively, the location of the roost may contribute more to its use than conditions that prevail inside. Assuming that efficient foraging is a prerequisite for successful reproduction, proximity to profitable feeding

TABLE 2.—Number of wins in territorial disputes and computed ranks of individual female *Eptesicus nilssonii* observed at two feeding sites near the roost in southern Sweden, June–July, 1983–1985. Dash indicates that individual was present in the colony and reproducing; blank indicates that individual was not present or not reproducing.

Individual	Site A						Site B					
	1983		1984		1985		1983		1984		1985	
	Wins	Rank	Wins	Rank	Wins	Rank	Wins	Rank	Wins	Rank	Wins	Rank
RW	11	1	13	3			—		—			
BR			25	2	5	2			—			—
GB	2	3	4	4	1	4			—		3	1
RY					22	3					1	2
OW			10	1	6	1			—			—
B	2	2					11	1				
YG							1	2	1	1		
Others									—			—

sites may be a determinant of roost selection (Kunz, 1982). In particular, this would apply to the lactation period, when females return to suckle the young in the roost during the night and, therefore, must make several commuting flights. The park where the bats roosted was situated near the center of the home range of the maternity colony. If shifts among roosts did not imply changes in use of feeding sites, a shift to the nearest house outside the park (350 m) would mean a doubling in average distance from roost to feeding site (from 220 to 460 m).

Site fidelity often is promoted by defensible resources (Greenwood, 1983). In bats, defensibility of mating stations (Gerell and Lundberg, 1985; Morrison and Morrison, 1981) and all purpose territories (McWilliam, 1987) seem to facilitate strong site fidelity in males, but observations of resource defense by female bats are rare. Profitable feeding sites apparently were in short supply in the study area, and the possibility of defending them probably was facilitated by their small sizes (usually about 100 m²) and predictable food supplies (Brown, 1964).

Observations of foraging bats suggest at least three potential advantages of site fidelity related to the distribution of the food: knowledge of the location of profitable food patches presumably enhances foraging efficiency; priority of access to feeding sites seems to require an initial investment in time and energy through fighting, but once acquired, territories probably are maintained at relatively low costs; it may be advantageous to be among individuals whose dominance status is known because fighting may then be kept at a minimum and foraging efficiency may be increased.

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ECOLOGY OF SPOTTED BAT (*EUDERMA MACULATUM*) ROOSTING AND FORAGING BEHAVIOR

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Until the advent of small (<1-g) radio transmitters, knowledge of the foraging and roosting behavior of insectivorous bats came from population studies. Transmitters representing $\leq 5\%$ of the body mass of a bat (Aldridge and Brigham, 1988) should make it possible to verify some of the inferences about the behavior of bats drawn from population studies (unmarked individuals).

The spotted bat, *Euderma maculatum*, is an excellent subject for this kind of investigation because a 0.9-g transmitter is <5% of its body mass and there is a reasonable base of sometimes conflicting literature about its behavior and ecology. For example, Watkins (1977) noted that captures of this bat in mist nets suggest that it is most active after midnight. Leonard and Fenton (1983), however, monitored foraging behavior and concluded that activity spanned the entire night and was little affected by weather or by lunar conditions. The absence of a lunar effect on activity does not agree with data from some other species of bats (Erkert, 1982). There is general agreement that *E. maculatum* roosts in cliffs (Leonard and Fenton, 1983; Watkins 1977), but disagreement about its foraging habits. Watkins (1977) reported that *E. maculatum* lands and chases insects on the ground, whereas Leonard and Fenton (1983) monitored 263 feeding buzzes (high-pulse-repetition rates associated with attacks on airborne prey—Griffin et al., 1960) none of which involved flights <1 m above the ground.

Data on behavior and ecology of a species are essential for making conservation decisions. *Euderma maculatum* is a spectacular mammal that appears to be widespread but rarely abundant (Fenton et al., 1987), but assessing its status means knowing the size of its populations. Leonard and Fenton (1983) used emergence counts at roosts to estimate the population of *E. maculatum* in south-central British Columbia, but the accuracy of these counts depends upon the pattern of roost use by the bats. Some species of bats are roost-faithful, but others often switch roosts (Fenton, 1983). The timing of departures from roosts and of appearances at foraging sites suggests that individuals are predictable in their roosting and foraging behavior and, if so, that emergence counts can be used to estimate population size.

The purposes of this study were to compare data collected on populations of *E. maculatum* with those obtained from radio-tracking known individuals in south-central British Columbia, and to use data from known individuals to determine if counts of bats emerging from roosts can provide a reliable index to numbers of *E. maculatum*.

The study was conducted between early May and late August 1986, and early May and late September 1987. Intensive radio-tracking was done in 1987. We worked in the general vicinity of Okanagan Falls, British Columbia (Fig. 1) and collected data on populations of *E. maculatum* (unknown individuals) by observation and by listening to their audible (to us) echolocation calls, and by radio-tracking.

We used Skin Bond® adhesive to attach 0.9-g Holohil BD1 transmitters (Holohil, R.R. 2, Woodlawn,