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# Foraging and diet of the northern bat *Eptesicus nilssoni* in Sweden

Jens Rydell

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Northern bats foraged predominantly in small individual and transient feeding sites usually in open places near trees and over water. Lakes were preferred as foraging habitat as compared to woodlands and farmlands. The pattern of habitat selection did not change drastically during the period of reproduction. The diet was probably unselective, consisting mainly of small dipterans and moths and also caddis flies, lacewings and mayflies (lake area) and dung beetles (farmland). Northern bats consumed insects of 3–30 mm body length, thus taking prey items of a broader size range than other bat species studied.

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## 1. Introduction

The northern bat *Eptesicus nilssoni* (Keyserling and Blasius 1839), weighing 8–15 g, is the most common bat species throughout most of Fennoscandia. Its range extends north to the Arctic circle, east to Korea, and south to the central European mountains (Corbet 1978).

The northern bat experiences short feeding seasons and coexists with few bat species throughout most of its range. In May females assemble into maternity colonies that consist of 10–50 individuals. Their roosts are usually located in heated houses, where one or two young per female are born in late June or early July. By early August females and juveniles have left the maternity roost and foraging grounds associated with them (Rydell, unpubl.).

No published data exist regarding the feeding ecology of the northern bat. This paper presents information about the foraging behaviour and the diet during pregnancy and lactation.

## 2. Study areas

The study was carried out at two sites northeast of the town of Ulricehamn in South-central Sweden (57°45'N, 13°25'E). Each area, about 100 hectares in size, was inhabited by maternity colonies of northern bats, composed of 25–30 females.

One study area includes parts of two oligotrophic lakes (28% of the area), connected by a small stream. The lakes and the stream are surrounded by mature deciduous woodlands (38%), a young spruce plantation (21%) and arable fields (13%). The woodlands are dominated by *Betula* spp., *Alnus glutinosa*, *Fraxinus excelsior*, *Ulmus glabra*, *Corylus avellana*, *Acer platanoides* and *Quercus robur*. This study area will be referred to as the "lake area".

The other study area is located near a small village, and is dominated by open farmland (covering 85% of the area). Apart from several isolated trees there are also small birch (*Betula* spp.) groves (8%), parkland (4%) and mature spruce forests (3%). The parkland is dominated by *Acer* spp., *Ulmus glabra*, *Tilia cordata* and *Fraxinus excelsior*. Ten houses and a church as well as several farm-buildings and barns are also found

within this study area which will be referred to as the "farmland area".

### 3. Methods

The bats of the lake area were studied from May to July 1981 and from June to July 1982 while the bats of the farmland area were observed from June to July 1982 and from May to July 1984.

The search for foraging bats was made on foot or by car, using a QMC S-100 bat detector which permitted species identification (Ahlén 1981). The positions and times of observations were marked on maps together with the routes travelled. The inventories started half an hour after the emergence of the first bats and continued as long as foraging bats were observed. The same routes were followed every night of observation. Bats foraging within 50 m of the roosts were excluded. The number of foraging bats per km of transect was calculated for each habitat type by dividing the number of observations with the distance travelled across the habitat type. Assuming 50 m detector range each km of transect equals about 5 hectares.

Temperature, occurrence of mist and rain and approximate wind speed, wind direction and cloud cover were recorded at the roost site every hour during the nights of observation.

Faeces for diet analysis were collected by spreading sheets of paper under the roosting bats. The faecal pellets were soaked in water and examined under a dissecting microscope. To identify the insect remains in the faeces they were compared with whole insects caught in the two areas. The approximate proportions (by volume) of each insect group in the faeces were estimated for each sampling period. The method of faecal analysis is discussed by Kunz and Whitaker (1983).

To monitor the relative abundance of insects, a 20 W light trap was run during one hour after the emergence of the bats on fifty nights in 1984. The light trap was placed in a parkland site close to the roost. Feeding attempts of northern bats that foraged near the light trap were recorded during nineteen of these nights, and the average attack rates were calculated for each hour of trapping.

G-statistics were performed according to Sokal and Rohlf (1981).

## 4. Results

### 4.1. Foraging behaviour

After emergence groups of female bats foraged among the trees near the roosts during 20–40 minutes. However, after having dispersed, they started to occupy specific foraging sites, which they aggressively defended against intruders (Rydell in press). Such a temporary feeding territory was normally used during several min-

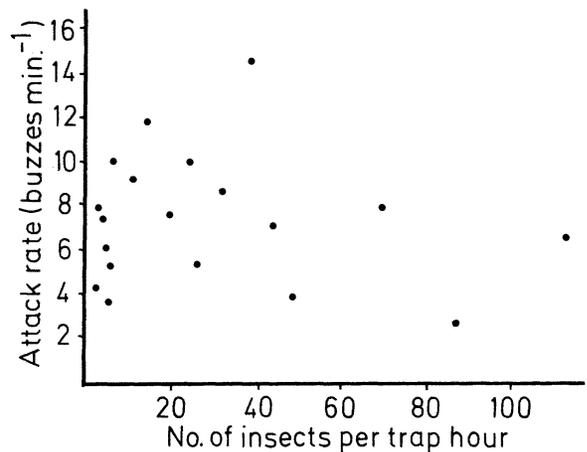


Fig. 1. Attack rates by foraging *E. nilssonii* in relation to the abundance of insects measured by means of a light trap.

utes before the bat moved to another feeding site. A few bats were sometimes observed to share a territory briefly, but intruders were most often evicted. Foraging groups consisted of 1.3 individuals on average (S.D. = 0.8,  $n = 156$  groups). Average group size did not differ significantly between habitats or between months ( $t$ -tests). Occasionally (4 nights), the bats foraged in large flocks ( $> 10$  bats) in overlapping flight paths, apparently exploiting large concentrations of insects. Under these circumstances group sizes could not be determined.

The food was always caught and eaten in the air. The attack rate of the bats did not increase continuously with the insect trap catch ( $r_s = 0.02$ ,  $p > 0.05$ , Spearman's rank correlation, Fig. 1). Instead, the highest average attack rate (14 feeding buzzes  $\text{min}^{-1}$ ) was recorded at an intermediate insect abundance. Thus, attack rate and insect abundance were significantly correlated as long as insects were scarce ( $< 20$  insects  $\text{h}^{-1}$ ) although not when abundant ( $r = 0.73$ ,  $p < 0.05$ , and  $r = -0.36$ ,  $p > 0.05$ , respectively).

Close observations of bats foraging in regular beats permitted measurements of handling times when large prey items were caught. After a successful attack against a large moth (about 10–30 mm body length), the bat immediately left its foraging beat for an average of 41 seconds (S.D. = 29,  $n = 19$ ), before foraging was resumed. Since the bat was seen to leave the foraging beat with the moth in its mouth, this time presumably represents the time needed to chew and swallow the insect. While doing this, the bat flew in a circuit in the vicinity of its hunting beat and emitted no feeding buzzes. When catching small prey items, however, the bats did not leave their foraging beats, but rather appeared to forage continuously. Less than a second sometimes elapsed between two attacks (feeding buzzes).

Tab. 1. Densities of foraging *E. nilssoni* in the main habitat types available near the roosts in the two study areas. One km of transect equals 5 ha assuming 50 m detector range. G-tests (Goodness of fit, d.f. = 2 and 1, respectively) for observed densities and those expected if distribution was random.

Study area	Habitat type	Number of bats observed		G	p
		Total	Per km of transect		
Lake area	Lakes	109	4.54	120.64	<0.001
	Woodlands	98	1.17		
	Farmlands	2	0.17		
Farmland	Woodlands	77	3.99	29.31	<0.001
	Farmlands	65	1.64		

#### 4.2. Habitat selection

All foraging bats were observed in open places and never within or below the tree canopies. They normally stayed a few meters from the vegetation. Foraging beats were established near trees usually at the height of the thickest foliage at 5–15 meters, along buildings or over open areas like meadows and lakes. In the latter cases the bats normally flew 2–5 meters above the ground or surface. Occasionally, the bats were observed to forage high above the tree canopies up to at least 100 meters above the ground.

When the observations were classified as associated with either of the three main habitat types available, it was found that the lakes were preferred as hunting grounds to the woodlands and the woodlands to the farmlands (Tab. 1). The hunting beats that were established in farmland were always associated with either isolated trees or buildings (82%) or with small meadows (18%). The large open fields and pastures as well as the young spruce plantation appeared not to be used for foraging, although they were often crossed by bats moving between feeding sites.

Weather conditions significantly influenced the habitat selection in the lake area (Tab. 2). However, neither

Tab. 2. Influence of some weather factors on habitat selection (lakes vs. woodlands/farmlands) by foraging *E. nilssoni* in the lake area. G-tests (d.f. = 1).

		Percentage of the observations over water		G	p
		N			
Temperature	<10°C	50	64.0	3.74	n.s.
	≥10°C	159	48.4		
Windspeed	<2 ms <sup>-1</sup>	113	70.8	35.23	<0.001
	≥2 ms <sup>-1</sup>	96	30.2		
Cloudyness	<100%	138	41.3	19.75	<0.001
	100%	71	73.2		
Rain	No	190	48.4	13.35	<0.001
	Yes	19	89.5		

Tab. 3. Habitat selection (lakes vs. woodlands/farmlands) by foraging *E. nilssoni* in the lake area during successive fortnight periods and in relation to windspeed and cloudyness.

Period	Windspeed	Cloudyness	No. of observations	
			over water	over land
May 15–31 (2 nights)	<2 ms <sup>-1</sup>	<100%	2	0
		100%	0	0
	≥2 ms <sup>-1</sup>	<100%	0	28
		100%	5	0
June 1–15 (3 nights)	<2 ms <sup>-1</sup>	<100%	29	15
		100%	0	0
	≥2 ms <sup>-1</sup>	<100%	0	0
		100%	0	0
June 16–30 (4 nights)	<2 ms <sup>-1</sup>	<100%	0	0
		100%	27	6
	≥2 ms <sup>-1</sup>	<100%	2	9
		100%	3	13
July 1–15 (6 nights)	<2 ms <sup>-1</sup>	<100%	14	7
		100%	0	0
	≥2 ms <sup>-1</sup>	<100%	2	17
		100%	17	0
July 16–31 (2 nights)	<2 ms <sup>-1</sup>	<100%	8	5
		100%	0	0
	≥2 ms <sup>-1</sup>	<100%	0	0
		100%	0	0
Total			109	100

wind speed nor cloudyness did so independently ( $G = 9.06$ ,  $p < 0.005$ , d.f. = 1, test for three way interactions). There was also a significant shift in habitat selection in the lake area in May ( $G = 20.03$ ,  $p < 0.001$ , d.f. = 4, test for independence, Tab. 3), but since 94% of the May observations were made during windy weather, it was probably caused by the prevailing wind conditions. No significant differences in habitat selection were observed with respect to season or weather factors in the farmland area.

#### 4.3. Diet

The body length of the prey items ranged from 3 mm (Nematocera) to about 30 mm (Lepidoptera). The bats hunting in the lake area fed primarily on small dipterans (mainly Chironomidae), moths and caddis flies, while the bats of the farmland area predominantly fed on small dipterans, moths and dung beetles (Scarabaeidae) (Tab. 4). The smaller insects (Nematocera) occurred in the faeces throughout the summer, but were particularly common during early June in both years. Larger insects were scarce during these periods. The relative volumes of each insect group occurring in the faeces roughly followed those of the trap catches; the correlations being significant in two out of four cases (Tab. 5).

#### 5. Discussion

The lakes were clearly preferred to other habitats as

Tab. 4. Percentages of different insect groups (volume) found in faecal pellets from *E. nilssoni* in the two study areas. N denotes the number of faecal pellets analyzed.

Study area, year	Insect group	May		June		July	
		15–31	1–15	16–30	1–15	16–31	
Lake area, 1982	N:	34	38	41	46	27	
	Diptera						
	Nematocera	68.5	60.5	35.1	31.5	33.0	
	Others	2.9	8.2	7.1	5.9	7.4	
	Lepidoptera	13.8	16.0	12.0	41.7	20.7	
	Trichoptera	8.8	9.5	34.6	14.6	27.0	
	Ephemeroptera	0.0	0.0	4.9	6.3	8.5	
	Neuroptera	5.9	5.3	0.0	0.0	0.0	
Coleoptera	0.0	0.5	6.3	0.0	3.3		
Farmland, 1982	N:	0	11	29	64	34	
	Diptera						
	Nematocera	–	77.3	38.3	31.1	35.3	
	Others	–	0.0	0.0	0.0	2.9	
	Lepidoptera	–	18.2	37.2	44.8	34.7	
	Trichoptera	–	0.0	4.8	3.1	5.9	
	Ephemeroptera	–	0.0	0.0	0.0	0.0	
	Neuroptera	–	4.5	1.7	0.0	0.0	
Coleoptera	–	0.0	17.9	20.9	21.2		
Farmland, 1984	N:	61	72	112	77	0	
	Diptera						
	Nematocera	44.3	74.0	48.4	45.2	–	
	Others	0.0	1.4	0.0	0.0	–	
	Lepidoptera	30.0	16.7	26.3	26.1	–	
	Trichoptera	3.1	5.3	2.6	6.1	–	
	Ephemeroptera	4.3	0.0	0.0	0.0	–	
	Neuroptera	0.0	0.0	0.0	0.0	–	
Coleoptera	18.4	2.6	22.8	22.6	–		

feeding grounds. Since obstacles are absent, insects may be relatively easy to catch over lakes as compared to more cluttered habitats. Furthermore, the temperature over large water bodies is comparatively even over the 24 hour period, and may thus remain high when the air temperature over land drops and insects there become less active. The lakes may therefore still provide enough insects when foraging over land has become unprofitable.

Slow windspeed is probably a prerequisite for profitable foraging over lakes, since most water insects are slow fliers that avoid open air on windy nights. Thus, for instance Chironomidae (Nematocera) and *Sialis* sp. (Neuroptera) were observed to swarm over the lakes during calm weather in early June, and their remains were found in the faeces of the bats.

The foraging behaviour of the northern bat is similar to that of some other bat species of larger size, for example *Euderma maculatum* (Leonard and Fenton 1983) and *Lasiurus cinereus* (Belwood and Fullard 1984), in that they generally keep to open areas and defend individual feeding territories. Group foraging, in contrast, appear to be more common among females of some smaller species, for example *Myotis daubentoni* (Wallin 1961, Nyholm 1965) and *Pipistrellus pipistrellus* (Racey and Swift 1985).

Northern bats usually foraged singly (76%), but occasionally most of the bats were observed foraging with overlapping flight paths. The latter behaviour occurred when the bats exploited swarms of water insects, concentrations of insects around flowering trees and when congregating along rows of street lamps. Foraging theory predicts that such large and ephemeral food patches should be less likely to be economically defensible (Brown 1964) than small and predictable ones (Davies and Houston 1984). Large food patches may attract potential competitors but may also locally provide food in superabundance, in both cases decreasing the defensibility by increasing the cost/benefit ratio of territoriality. The spacing patterns of foraging northern bats thus changes from individual beat foraging and territoriality to flock foraging when large concentrations of insects appear.

Most bats are opportunistic feeders (Fenton 1982). The diet of the northern bat varied somewhat between the areas and from time to time, but apparently included all groups of insects that were available except the smallest ones (< 3 mm). Why did the bats bother to capture small Nematocera even when large moths were abundant? When capturing small prey items, the handling times can probably be considered close to zero because searching is resumed while the last captured insect is still handled (Swift et al. 1985). Theoretically, this implies that small prey items should not be rejected once detected no matter how common the larger insects are (MacArthur and Pianka 1966). Under these circumstances unselective feeding is the optimal strategy. However, a bat's ability to detect the prey item may still depend on its size (Barclay 1985). A lower size limit of detection is thus the most likely reason why the smallest insects were not included in the diet.

Assuming that feeding is unselective and that handling times are negligible, the attack rate should increase linearly with increasing insect availability. This was apparently the case as long as insects were scarce. Large insects (moths) were very rare on such nights and their relative abundance generally increased with the trap catches. Thus, when larger insects were captured, handling times were no longer negligible and the attack rate should therefore decrease as larger insects became more frequently encountered.

Tab. 5. Relationships (Spearman's rank correlation,  $r_s$ ) between the percentage volumes of different insect groups found in faecal pellets of *E. nilssoni* in the farmland area (1984) and the estimated volumes of those of a light trap sample obtained during the same periods. N denotes the number of insect groups ranked.

Period	N	$r_s$	p
May 15–31	6	0.90	<0.05
June 1–15	6	0.94	<0.05
June 16–30	5	0.80	n.s.
July 1–15	5	0.90	n.s.

The maximum attack rate as well as the minimum sizes of the prey items observed among the northern bats are comparable to those of *Myotis* spp. (Griffin et al. 1960, Belwood and Fenton 1976) and *Pipistrellus pipistrellus* (Racey and Swift 1985, Swift et al. 1985). These bats are smaller than the northern bat and they normally do not eat insects larger than 10–12 mm body length (Anthony and Kunz 1977, Swift et al. 1985). Northern bats, however, frequently consume moths as large as 30 mm body length as well, sizes that appear to be preferred by larger bats like *Eptesicus fuscus* (Whitaker 1972) and *Lasiurus cinereus* (Black 1974, Belwood and Fullard 1984). The northern bat thus seems to feed on a comparatively broader range of prey sizes than other bat species that are known to forage in flight.

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