The Diet of the serotine bat
A Comparison between rural and urban environments

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ABSTRACT. The diet of four maternity colonies of serotine bats in Southern Belgium was investigated by analysing faecal pellets collected from beneath the roost throughout the activity season. Their diet is composed of *Coleoptera Melolonthidae (Melolontha sp.*, *Amphimallon sp.*, *Rhizotrogus sp.*, *Serica brunnea)*, *Coleoptera Scarabaeidae (Aphodius sp.*, *Geotrupes sp.)*, *Coleoptera Carabidae, Diptera Tipulidae, Diptera Chironomidae, Lepidoptera, Hemiptera Pentatomidae, Hymenoptera Ichneumonoidea Ophionidae*, *Trichoptera* and *Arachnida*.

The diet of an urban colony of serotine bats was broadly the same as the diets of three rural colonies. Though some qualitative and quantitative variations were observed between study sites, the main source of variation in the diet was the seasonal availability of potential prey.

The prominence of agriculture-dependant prey (chafers in mid summer and *Aphodius* beetles in late summer and autumn) was observed at all study sites. Consequently, dietary breadth and diversity is smaller during these periods.

KEY WORDS : Food, *Eptesicus serotinus*, *Vespertilionidae*, foraging tactic.

RESUMÉ. Le régime alimentaire de quatre colonies de reproduction de sérotines communes dans le sud de la Belgique a été étudié par l'analyse d'excréments récoltés dans les gîtes durant toute la période d'activité.

Le régime alimentaire se compose de *Coleoptera Melolonthidae (Melolontha sp.*, *Amphimallon sp.*, *Rhizotrogus sp.*, *Serica brunnea)*, *Coleoptera Scarabaeidae (Aphodius sp.*, *Geotrupes sp.)*, *Coleoptera Carabidae, Diptera Tipulidae, Diptera Chironomidae, Lepidoptera, Hemiptera Pentatomidae, Hymenoptera Ichneumonoidea Ophionidae*, *Trichoptera* et d'*Arachnida*.

La composition du régime alimentaire d'une colonie urbaine est largement semblable à celle de colonies situées en zone rurale. Des différences qualitatives et quantitatives existent entre les quatre sites d'études, mais la variation du régime alimentaire est principalement tributaire de la disponibilité saisonnière des proies potentielles.

Dans tous les sites d'étude, la sérotine commune témoigne d'une forte dépendance alimentaire envers des proies liées à l'activité agricole: les hannetons au début de l'été et les *Aphodius* en fin d'été et en automne. Il en découle que la largeur de niche alimentaire et la diversité alimentaire sont réduites à ces périodes.

MOTS CLÉS : Nourriture, *Eptesicus serotinus*, *Vespertilionidae*, tactique de recherche de nourriture.

INTRODUCTION

Bat populations are declining world-wide as a result of a growing number of factors, including habitat loss and fragmentation, disturbances to roosts, exposure to toxins, and introduced predators (RACEY, 1998). This makes it difficult to draw general conclusions about bat conservation, which may require species-specific conservation plans (FENTON, 1997). Understanding the natural history of species and developing hypotheses about foraging strategies requires basic information on food habits (LITVAITIS, 2000).

The serotine bat (*Eptesicus serotinus*) is found throughout much of Western Europe and often roosts in houses. Relatively abundant species, such as the serotine bat, are important for conservation because of their role in ecosystems and the research opportunities they offer.

The rural environment is an usual habitat for the serotine bat since it can take advantage of current farming practices (CATTO et al., 1995; RACEY, 1998). In cities (GAISLER & BAUEROVA, 1986; MICKLEBURGH, 1987; 1989; GAISLER et al., 1998), the serotine bat could however face difficulties in finding food because urban ecosystems do not provide the same insect concentrations (qualitatively and quantitatively) as rural habitats (TAYLOR et al., 1978).

Recently, more attention has been devoted to the urban ecology of bats (*Chiroptera*) because of their ecological importance and the habit of some species to roost in artificial structures (GEGGIE & FENTON, 1984; BENZAL & MORENO, 1989; MICKLEBURGH, 1987; 1989; KURTA & TERAMINO, 1992; GAISLER et al., 1998; GEHRT & CHELSVIG, 2003a; 2003b; WHITAKER et al., 2006).

Numerous studies have documented the food habits of the serotine bat in Great Britain (ROBINSON & STEBBINGS,

1993; Catto et al., 1994; 1996; Vaughan, 1997), Netherlands (Labee & Voute, 1983), Germany (Kurtze, 1982; Dense, 1992), Luxembourg (Harbusch, 2003), Switzerland (Beck, 1995; Gerber et al., 1996) and Czech Republic (Zukal et al., 1997; Gajdosik & Gaisler, 2004) but none of these studies were conducted in urban surroundings, where habitat fragmentation and loss were likely to be of major importance.

We assumed that serotine bats could modify their trophic niche in order to adapt their dietary requirements to the urban availability of prey. In this way, they would exploit different insect resources from those in rural environments. In this study, data on the diet of an urban colony of serotine bats are presented and compared with similar data collected in rural habitats.

The goals of this paper are to (1) describe the diet of the serotine bat and its seasonal changes; (2) point out intra-specific dietary differences in relation to contrasting environmental conditions around the summer roost.

These issues have broad implications for other species and can be used to focus future research and conservation efforts.

STUDY SITES

Four colonies were studied in southern Belgium: three were in a rural landscape and one was in a city.

The first rural colony consists of circa 40 breeding females roosting in a house in Tintigny, Province of Luxembourg (UTM coordinates 31 U FR 81 06), a village situated in the Semois River valley in a landscape including pastures, and both coniferous and deciduous forests. On the south, it is bordered by beech forests and on the north by the southern slopes of the Ardennes. This colony dispersed in 1997 due to a visit by a stone marten, *Martes foina*. The second rural colony, similar in size, roosted approximately 3km from the first, in the church of Saint Vincent, Province of Luxembourg (UTM coordinates 31 U FR 78 05) in the same habitat type. A colony roosting in a house in Doische, Province of Namur (UTM coordinates 31 U FR 24 55), consisted of about 20 breeding females. This village is surrounded mainly by broadleaved and coniferous forests, pastures, and arable land.

A colony of approximately 40 females roosted in an attic in Namur (UTM coordinates 31 U FR 32 91), a town of 100000 inhabitants, located in the Meuse River valley at its confluence with the Sambre River. The surrounding area is heavily urbanized.

METHODS

Polythene sheets were placed on the attic floor, beneath the roosting bats, from the end of April to October. Faecal pellets were collected every two weeks, air-dried and stored in plastic bags. Five periods are distinguished according to the physiological stage of the females (Table 1).

Data gaps are due to the absence or scarcity of bats in the roost during the sampling period. Sample periods dur-

TABLE 1

Subdivision of bat activity period into fortnights and periods.

Date	Development of the young	Fort-night	Physiological state of females	Period
April II		1	post hibernation	I
May I		2	post hibernation	I
May II		3	late pregnancy	II
June I		4	late pregnancy	II
June II	Birth	5	lactation	III
July I		6	lactation	III
July II	First foraging flights	7	lactation	III
Aug. I		8	post lactation	IV
Aug. II		9	post lactation	IV
Sept. I		10	post lactation	IV
Sept. II		11	pre hibernation	V
Oct. I		12	pre hibernation	V

ing which bats were scarce (<3 individuals in the colony) are excluded from the study. Pellets were taken at random, using a random number generator, to reduce the probability of collecting pellets from the same individual. The sample size was assessed a posteriori by examining the variation of prey proportions relative to the number of analysed pellets (Kervyn, 1998; Kervyn, 2001). Serotine bats, in the roosts, used to crawl on the ridgebean rather than hang freely and this could have led to a weak contamination of faecal samples by older droppings.

Each faecal pellet was soaked in water on a microscope slide and teased apart under a binocular microscope using a pair of dissecting needles. Identification of insect pieces was facilitated by the descriptions of Whitaker (1988), McAney et al. (1991), Pir (1994), and Kervyn (1995; 2001). Insect fragments were also compared with whole insect specimens collected on the bat's foraging grounds or with the entomological collection of the Zoological Museum of Liège. No attempt was made to estimate accurately the frequency of fragments or percentage volume of prey taxa within a dropping, because most fragments cannot be attributed to a single taxon. Moreover, the remains of a single prey are distributed among many droppings (Robinson & Stebbings, 1993).

Relevance and limits of this method were evaluated by several authors (Kunz & Whitaker, 1983; Dickman & Huang, 1988; Robinson & Stebbings, 1993). Faecal analysis does not provide the exact composition of the ingested food. However, it allows an estimation of food composition, especially common prey items. Its use is valuable for seasonal or geographical comparisons of the diet. Results usually overestimate the proportion of large insects and of those leaving easily identifiable pieces even after ingestion and digestive transit. Soft bodied insects may be underrepresented.

Results are expressed in relative frequency of occurrence which represents the number of pellets containing the item among the sample of 40 pellets, divided by the total number of items.

Dietary diversity was calculated using the Shannon-Weaver index: $H'=-\Sigma p_i.\log_2 p_i$ where p_i is the proportion of the ith item and n is the total number of items (Brewer, 1994). Trophic niche breath was calculated as follow: $DB=((\Sigma p_i^2)^{-1}-1)/(n-1))$ (Hespenheide, 1974).

To detect possible temporal variations, a goodness-of-fit test (SOKAL & ROHLF, 1981) was performed for each individual colony, comparing the frequency distribution of prey items during successive fortnights. A Newman-Keuls test was used to identify the origin of the variations. Most analyses were performed on Minitab 10.1 for Windows (Minitab Inc., 1829 Pine Hall Rd State College PA 16801-3008 USA).

RESULTS

Diet Composition

Thirty-six faecal samples were collected: 9 at Doische in 1996, 11 at Tintigny in 1996, 4 at Saint-Vincent in 1996 and also in 1997, and 8 at Namur in 1998. Some fortnights were not studied because of movements of the colony inside the roost or to secondary roosts.

TABLE 2

Diet composition of the serotine bat over 12 fortnights (see Table 1) at four study sites (D96: Doische 1996, T96: Tintigny 1996, SV96: Saint-Vincent 1996, SV97: Saint-Vincent 1997, N98: Namur 1998).

Fortnight	Site and year	Melolontha sp.	Amphimallon sp. and Rhizotrogus sp.	Serica brunnea	Aphodius sp.	Geotrupes sp.	Carabidae	Tipulidae	Chironomidae	Lepidoptera	Ichneumonidae	Hemiptera	Trichoptera	Arachnidae	indéterminés	TOTAL
1	D96	5	34	0	0	0	0	2	0	0	2	0	0	0	8	51
	T96	29	0	1	8	0	0	3	0	3	1	2	0	0	2	49
	SV96	34	0	2	3	0	0	1	0	5	1	0	0	0	4	50
2	D96	7	35	0	0	0	0	5	1	2	0	0	0	0	4	54
	T96	36	0	0	4	0	1	1	0	2	0	0	0	0	1	45
	SV97	40	0	0	0	1	0	6	0	0	5	0	0	0	0	52
	N98	37	2	0	0	0	0	11	0	9	6	3	1	0	5	74
3	D96	33	17	0	0	0	1	5	0	0	1	0	0	1	0	58
	T96	40	0	0	0	0	0	11	0	0	9	0	0	0	0	60
	SV97	39	0	0	1	3	0	23	0	0	10	0	0	0	0	76
	N98	30	17	0	0	0	0	15	0	12	5	6	3	0	4	92
4	D96	15	3	0	0	0	0	1	0	0	3	0	17	0	2	41
	T96	36	0	0	0	0	1	32	0	6	25	0	0	0	3	103
	SV96	14	0	0	0	1	7	31	0	19	22	1	21	0	0	116
	N98	4	20	0	0	0	6	12	0	10	3	11	12	0	2	80
5	D96	1	3	0	0	0	0	4	0	0	1	0	35	0	5	49
	T96	29	0	2	1	0	0	30	0	19	11	0	0	0	1	93
	N98	2	27	0	0	0	1	8	0	8	2	2	5	0	4	59
6	D96	1	29	0	0	3	0	2	0	4	0	2	2	0	4	47
	T96	0	0	0	19	0	2	8	1	23	4	2	2	0	2	63
	N98	1	26	0	0	0	1	24	3	9	1	3	1	0	0	69
7	D96	14	16	0	1	1	0	3	5	4	0	0	6	0	3	53
	SV96	10	0	5	13	2	5	6	7	8	0	13	9	0	2	80
	SV97	0	0	3	39	0	0	20	0	14	1	8	16	0	2	103
	N98	0	26	0	2	0	7	10	0	15	0	18	1	0	2	81
8	D96	0	0	0	36	5	0	9	0	20	0	10	0	0	3	83
	T96	0	0	16	30	4	3	5	0	14	3	4	1	0	1	81
	SV97	0	0	7	32	8	3	17	0	9	2	18	0	0	7	103
	N98	0	11	0	9	0	1	2	0	15	0	35	1	0	1	75
9	T96	4	0	0	33	0	0	5	0	3	8	0	0	0	2	55
10	D96	0	0	12	38	6	0	5	0	3	6	0	0	0	4	74
	T96	0	0	0	40	1	0	2	0	0	7	1	0	0	2	53
	SV96	0	0	3	37	6	3	5	0	6	4	12	0	0	3	79
	N98	0	0	0	21	0	1	0	0	13	1	21	0	2	1	60
11	T96	0	0	0	40	6	0	1	0	0	6	0	0	0	2	55
12	T96	0	0	0	40	3	0	3	0	2	2	0	0	0	1	51

A total of 2467 insect fragments were recorded from 1440 droppings (Table 2). 2380 items were identified and 87 were not. The mean number of prey taxa per dropping was 1.61±0.84 (n=1440), with a maximum of 6.

Coleopterans accounted for the majority of identified prey: *Melolontha sp.* (19.4%), *Amphimallon sp.* and *Rhizotrogus sp.* (11.2%), *Serica brunnea* (2.1%), *Aphodius sp.* (18.8%), *Geotrupes sp.* (2.1%), and *Carabidae* (e.g. *Harpalus sp.*, 1.8%). The second most frequently consumed group of insects belonged to the order *Diptera*: *Tipulidae* (13.8%), and *Chironomidae* (0.7%). Other prey were from the orders *Lepidoptera* (10.8%), *Hemiptera* (*Pentatomidae* 7.2%), *Hymenoptera* (*Ichneumonoidea*

Ophionidae 6.4%) and *Trichoptera* (5.6%), and non-insect Arachnids (0.1%) (Fig. 1).

Seasonal and spatial variations

Considered fortnight by fortnight, the results are significantly heterogeneous between the different colonies. The G values are always highly significant ($p < 0.001$) indicating that the frequency distribution of the prey items vary from one colony to another, independently of the time of the year. Table 3 shows the prey categories involved in these significant changes and Table 4 the localities (colonies) deviating from random.f

TABLE 3

Partial values of G for composition of prey types.

ortnight	1	2	3	4	5	6	7	8	10
d.f.	13	13	13	13	13	13	13	13	13
Melolontha sp.	<0,001	<0,001	<0,025	<0,001	<0,001	ns	<0,001	ns	ns
Amphimallon sp. / Rhizotrogus sp.	<0,001	<0,001	<0,001	<0,001	<0,001	<0,001	<0,001	<0,001	ns
Serica sp.	ns	ns	ns	ns	ns	ns	ns	<0,001	<0,005
Aphodius sp.	ns	ns	ns	ns	ns	<0,001	<0,001	<0,005	<0,05
Geotrupes sp.	ns	ns	ns	ns	ns	ns	ns	ns	ns
Carabidae	ns	ns	ns	ns	ns	ns	<0,025	ns	ns
Tipulidae	ns	ns	<0,05	<0,001	<0,01	<0,005	ns	<0,025	ns
Chironomidae	ns	ns	ns	ns	ns	ns	<0,005	ns	ns
Lepidoptera	ns	ns	<0,01	<0,025	<0,01	<0,01	ns	ns	<0,005
Ichneumonidae	ns	ns	<0,05	<0,001	ns	ns	ns	ns	ns
Hemiptera	ns	ns	ns	<0,001	ns	ns	<0,001	<0,001	<0,001
Trichoptera	ns	ns	ns	<0,001	<0,001	ns	<0,025	ns	ns
Arachnidae	ns	ns	ns	ns	ns	ns	ns	ns	ns
unidentified	ns	ns	ns	ns	ns	ns	ns	ns	ns

TABLE 4

Partial values of G for food composition at four study sites ('–' means no data).

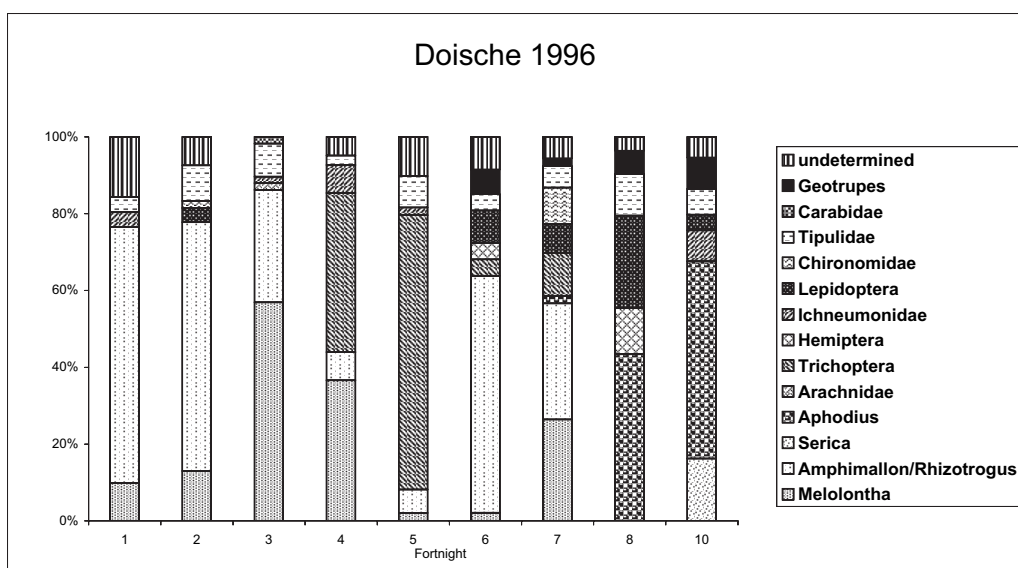| fortnight	1	2	3	4	5	6	7	8	10
d.f.	2	3	3	3	2	2	3	3	3
D96	<0,001	<0,001	ns	<0,001	<0,001	<0,005	<0,001	ns	<0,025
T96	<0,001	<0,025	ns	<0,001	<0,001	<0,001	–	<0,005	<0,05
SV96	<0,001	–	–	<0,01	–	–	<0,01	–	ns
SV97	–	<0,025	<0,025	–	–	–	<0,001	ns	–
N98	–	ns	<0,025	<0,001	<0,001	<0,005	<0,001	<0,001	<0,001

Fig. 1. – Seasonal variations of the food composition (relative frequency of occurrence) of the serotine bat in Tintigny, Saint-Vincent, Doische and Namur. Fortnights are explained in Table 1.

Namur 1998

Saint Vincent 1996   Saint Vincent 1997

Tintigny 1996
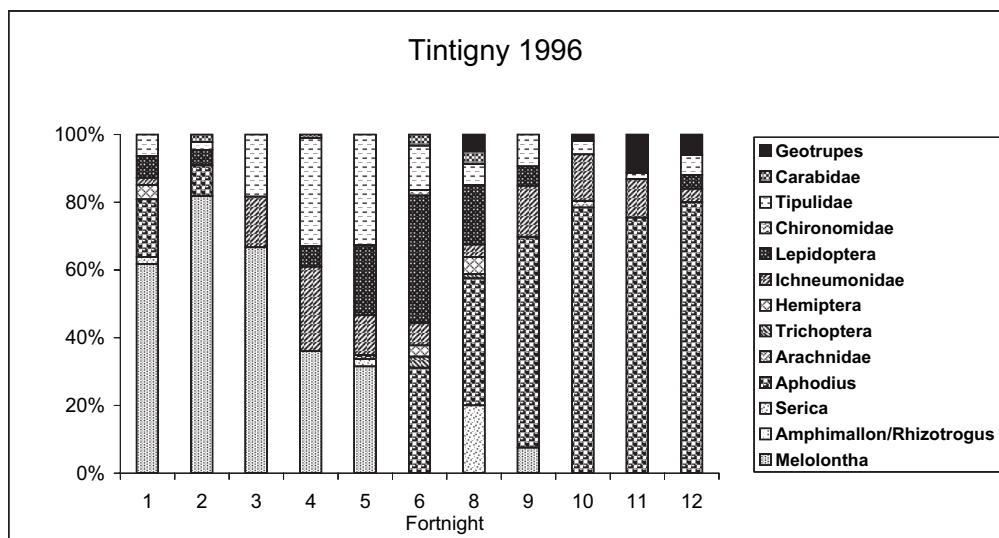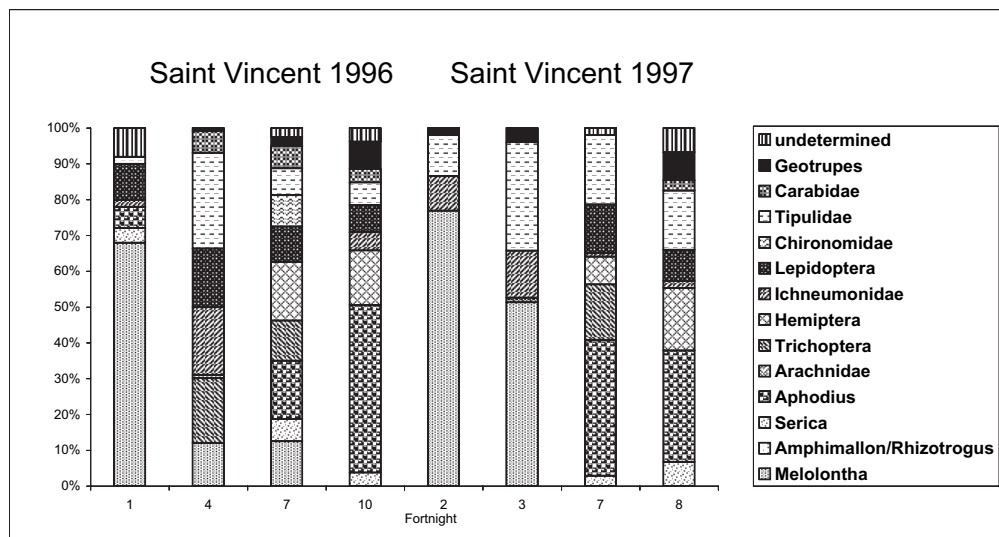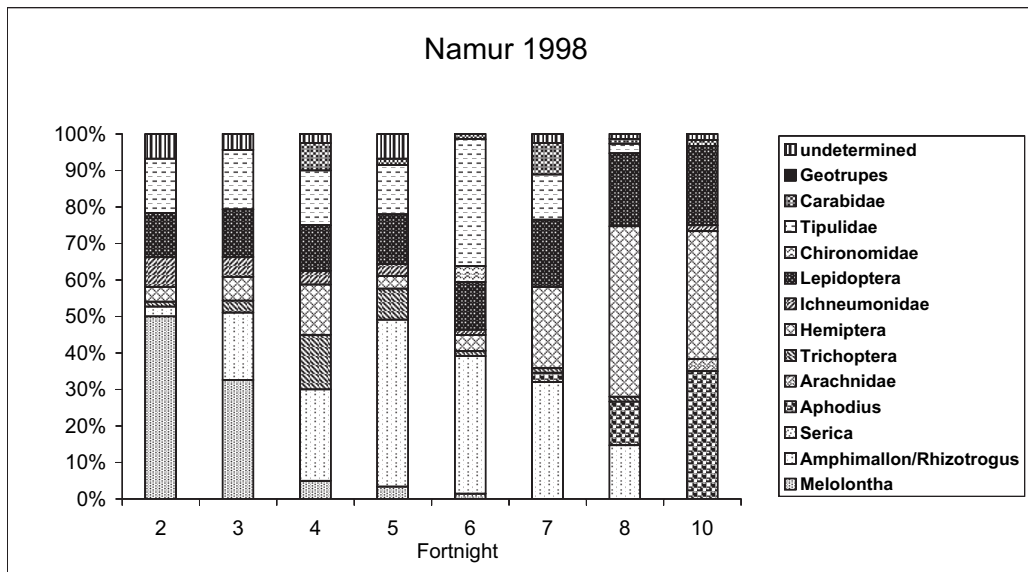
At each colony, the G value is highly significant (p<0.001), indicating the diet changes dramatically. Prey changes by sites are illustrated in Table 5 whereas periods (fortnights) deviating from random are in Table 6.

TABLE 5

Total values of G for the prey types versus the four study sites.

site	D96	T96	SV96	SV97	N98
d.f.	104	143	39	39	104
G-test	<0,001	<0,001	<0,001	<0,001	<0,001

TABLE 6

Partial values of G for food composition by fortnight ('-' means no data).

site	D96	T96	SV96	SV97	N98
d.f.	8	11	3	3	8
1	<0,001	<0,01	<0,001	-	-
2	<0,001	<0,001	-	<0,001	<0,001
3	<0,001	<0,001	-	<0,001	<0,001
4	<0,001	<0,001	<0,001	-	<0,025
5	<0,001	<0,001	-	-	<0,005
6	<0,001	<0,001	-	-	<0,001
7	ns	-	<0,025	<0,001	<0,005
8	<0,001	<0,001	-	<0,001	<0,001
9	-	<0,01	-	-	-
10	<0,001	<0,001	<0,001	-	<0,001
11	-	<0,001	-	-	-
12	-	<0,001	-	-	-

Chafers made up most of the diet during late April – May at all study sites (Fig. 1). *Rhizotrogus – Amphimallon* predominate in Doische, whilst *Melolontha sp.* was the main prey elsewhere. During late June – July, *Rhizotrogus – Amphimallon* predominated again in Doische and was present in Namur. Tipulids were found mainly in May and June but also in September. Ophionids were taken in May and June but in small quantities. *Trichoptera* were consumed in June – July, especially in late June in Doische where they accounted for more than two thirds of the diet. Lepidopterans were mainly consumed in late June – July, except in Doische. Chironomids were eaten in July in moderate quantities. *Hemiptera* were encountered, mainly in Namur, in late July – August. This order is mainly represented by *Pentatomidae,* especially *Pentatoma* sp. *Serica brunnea* was identified in the diet in August – September in Saint-Vincent, Tintigny and Doische. *Aphodius* beetles appeared in July and were a major part of the diet until the end of the season at all sites. A weak contamination by older droppings could explain the presence of *A. rufipes* in the samples of April-May. *Geotrupes* and Arachnids were rarely found and do not show a seasonal trend.

Dietary breadth and diversity

Shannon-Weaver diversity indices were not significantly different between study sites for each of the first four periods (F-test at a=0.05: F_1=1.29; df_1=6; p_1=0.480; F_2=3.79; df_2=7, p_2=0.151; F_3=1.08, df_3=9, p_3=0.455; F_4=1.13, df_4=8, p_4=0.455). The fifth period was not included because of the small sample size (n=2).

An F-test indicated the diversity was significantly different (F-test at a=0.05: F=4.22, df=35, p=0.008) among the five periods. A Newman-Keuls test (a=0.05) showed that the first and the last periods were significantly different from the others (Fig. 2).

Similar results were obtained for dietary breadth indices (F-test at a=0.05: F_1=1.51; df_1=6; p_1=0.436; F_2=4.99; df_2=7, p_2=0.109; F_3=5.12, df_3=9, p_3=0.051; F_4=0.59, df_4=8, p_4=0.688) (F-test at a=0.05: F=2.90, df=35, p=0.038).
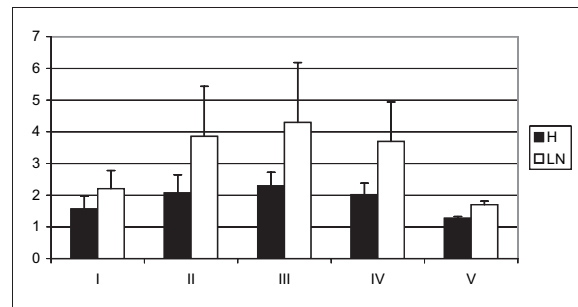

Fig. 2. – Shannon-Weaver diversity index and dietary breadth index in relation to the serotine bat activity periods. Periods are defined in Table 1.

DISCUSSION

Composition

The diet composition was similar to that reported by other authors (KURTZE, 1982; LABEE & VOUTE, 1983; ROBINSON & STEBBINGS, 1993; CATTO et al., 1994; BECK, 1995; GERBER et al., 1996; VAUGHAN, 1997; HARBUSCH, 2003). The most striking result is the lack of qualitative differences between the diet of urban and rural colonies of serotine bats.

A goodness of fit test showed quantitative differences between the four study sites. However, the difference between the urban study site and the three rural sites is not more important than within the three rural sites, except the two last fortnights (8 and 10) where *Hemiptera* are more frequent in the diet in Namur and *Aphodius* beetles are less important (Fig. 1).

In Doische, summer chafers were eaten instead of cockchafers elsewhere. Similarly trichopterans were more consumed in Doische than by the other colonies, reducing the proportion of lepidopterans and tipulids.

Influence of the phenology of prey

Seasonal variations observed in the diet of the Serotine bat can easily be explained when considering the phenology of its main prey. Cockchafers (*Melolontha sp.*) are a major prey in May and June, i.e. at the peak of their flight activity (KERVYN, 1996; GERBER et al., 1996; HARBUSCH, 2003).

The food item *Rhizotrogus sp. – Amphimallon sp.* shows a bimodal pattern in Doische corresponding to the respective emergence of *Rhizotrogus sp.* (late April – May) and *Amphimallon solstitialis* (June – July). Tipulids, mainly represented by the large *Tipula* genus, emerge from the soil in late May – June (*Tipula oleracea*)

and again in July and August (*T. paludosa*) (COULSON, 1959; 1962). The same pattern of occurrence of this prey item (*T. oleracea*) was also observed in the diet of *Myotis myotis* in southern Belgium (KERVYN, 1996).

Consumption of caddisflies (*Trichoptera)* in June – July reflects emergence of these insects observed in the field. Predation of chironomids also reflects local availability of swarms.

Serica brunnea are known to fly in late summer (DU CHATENET, 1986). This small chafer is also consumed at that time by the greater horseshoe bat and the serotine in neighbouring Luxembourg (PIR, 1994; HARBUSCH, 2003).

Since most identified hemipterans were *Pentatoma rufipes*, the occurrence of the hemipterans in the diet in late summer is explained by its phenology (VILLIERS, 1945).

Aphodius beetles are represented by *A. rufipes*, a large species that emerges in late summer (DESIÈRE, 1974). This prey is observed during that period in all dietary studies of the serotine in Western Europe (LABEE & VOUTE, 1983; CATTO et al., 1994; BECK, 1995; GERBER et al., 1996).

The phenology of lepidopterans in the diet is hard to interprete because there are many species that are impossible to distinguish from one other in bat droppings.

KURTZE (1982) and ROBINSON & STEBBINGS (1993) reported a peak in predation of *Geotrupes* in spring and in July.

Previous studies revealed the predation of other insects. *Hymenoptera* were observed (BECK, 1995), especially *formicids* by GERBER et al. (1996) and ZUKAL et al. (1997). The predation of *hydrophilids* (LABEE & VOUTE, 1983), of the burying beetle *Necrophorus humator* (ROBINSON & STEBBINGS, 1993; CATTO et al., 1994) and of the chafer *Polyphylla fullo* has also been reported (GERBER et al., 1996). CATTO et al. (1994) also report the incidental identification of *Neuroptera*, *Plecoptera* and *Aphidae.*

Dietary diversity

Dietary diversity is greatly reduced in early spring and late autumn because of a heavy dependence upon cockchafers – summer chafers and *Aphodius* beetles respectively. A higher diversity from late May to early September can be due to a higher diversity of available insects, to increased foraging periods during the night by lactating females (DENSE, 1992; CATTO et al., 1995, pers obs.), or to the presence in the colony of individuals of various physiological states (non reproductive, pregnant, lactating, young) (CATTO et al., 1994) or that forage in different habitats. This seasonal pattern of food diversity contrast with those obtained by HARBUSCH (2003) and is very different from the one observed in *Rhinolophus ferrumequinum*, a similarly-sized bat eating the same prey types, but focusing on lepidopterans during late pregnancy (JONES, 1990; RANSOME, 1996). Food availability should be regarded as a major source of variability in dietary diversity (HARBUSCH, 2003). Horseshoe bats have a specialised echolocation system enabling them to prey on lepidopterans. Their echolocation clicks (frequency range near 80KHz) fall indeed outside the hearing possibilities of the

moths, ranging from 15 to 60KHz, whereas the frequency of the serotine bat signals ranges around 25KHz.

Differences among study sites

Intraspecific geographic variation in bat diets likely reflects geographic variation in the availability of insects (BELLWOOD & FENTON, 1976; WHITAKER, 1995; GERBER et al., 1996; AGOSTA & MORTON, 2003; BRACK & LAVAL, 2006).

However, in this study, chafers and *Aphodius* beetles were invariably, at all study sites, the key prey eaten respectively in spring and in autumn.

Two hypotheses can explain the absence of difference between rural and urban bat diets. On the one hand, insect prey could be present in the city (parks, urban gardens), in close vicinity (residential areas), or could disperse from the countryside towards the cities. On the other hand, serotine bats could compensate for local urban food shortage by foraging further away, in unbuilt areas.

Both hypotheses are valid, depending on the prey concerned. For instance, summer chafers (*Amphimallon solstitialis*) were seen flying along tree-lined streets and were hunted by foraging serotine bats. Parks, cemeteries, fallow lands, and football playing fields in urban areas are not ploughed or sprayed with insecticide. They are the urban equivalent of unimproved pasture and a good source of chafers. So are also many gardens. However, *Aphodius* beetles are closely associated with cow-dung and are therefore quite rare in cities. Therefore, their presence in the food of urban serotine bats suppports the hypothesis that bats travel to rural areas to forage.

Foraging strategy and habitats

Serotines take advantage of insect populations emerging in a short period of time in the night as well as over the season. A large prey item (e.g. chafer, tipulid, *Hemiptera*,..) could be energetically beneficial These insects fly noisily and can therefore be detected at a distance of up to 10 meters (pers. obs.). Passive acoustic detection is undoubtedly a cue used to locate them, especially just prior to take off (ROBINSON & STEBBINGS, 1993, pers. obs.). This does not exclude use of echolocation to avoid obstacles, locate precisely a flying noisy insect or identification of other potential prey (e.g., lepidopterans).

The ecology of cockchafers, summer chafers, tipulids and ichneumonids indicates that the serotine bat is likely to forage from May to July along broad-leaved forest edges, in orchards, and over hay meadows and pastures (CATTO et al., 1996; SCHMIDT, 2000). Lepidopterans frequent the same habitats, and are found in the vicinity of street lamps (CATTO et al., 1996; SCHMIDT, 2000). *Aphodius* beetles are strongly associated with cow-dung and are eaten in autumn by serotines foraging over grazed pastures. The importance of *Aphodius* in the diet may explain why BARTONICKA & ZUKAL (2003) failed to find foraging serotines in towns from the end of August on. In the urban study site of Namur, the nearest grazed pasture is 2.5km from the roost. This distance is therefore a minimal activity radius for this colony. Swarms of insects (chironomids, trichopterans) along stream and small riv-

ers also attract foraging serotine bats (LABEE & VOUTE, 1983, pers. obs.).

Conservation

Cockchafers and summer chafers emerge in large quantities and are consumed not only by the serotine bat (CATTO et al., 1994), but also by other large and rare bats such as *Rhinolophus ferrumequinum* (JONES, 1990; PIR, 1994), and *Myotis myotis* (KERVYN, 1995). Our results indicate that these insects are key-species for serotine bats since they are the first – and nearly the only – prey taken between and after the last hibernation bouts. Current farming practices, especially ploughing and sowing of pastures, destroy large quantities of larvae of these preys.

Aphodius beetles can also be considered key prey species since they are almost the only prey eaten in autumn. This illustrates a close association between this bat and human activities, in addition to roost sites (CATTO et al., 1995; RACEY, 1998). This relationship is fragile since use of antihelminthic drugs affects development and survival of dung beetles (WALL & STRONG, 1987; MADSEN et al., 1990; RANSOME, 1996).

The main conclusion is that, when in cities, the serotine bat does not adapt its diet to other prey but instead uses a restricted array of prey, probably energetically important large flying insects and/or insects available in large quantities.

We suggest that the absence of key-prey in the proximate surroundings of the colony induces, for the serotine bat, longer commuting flights and could consecutively decrease fitness – highlighted for the greater horseshoe bat (RANSOME, 1996) – or force the colony to use roosts located closer to profitable foraging grounds. Further studies taking fitness into account (e.g. reproductive success of adults and juvenile survival) should be completed to evaluate the impact of key-prey habitat loss or fragmentation near urban colonies.

CONCLUSION

The food composition of an urban colony of *E. serotinus* is broadly the same as in rural environment. Some qualitative and quantitative variations of food composition are observed among study sites. The main source of variation in the diet – both in rural and urban environments – is the phenology of available prey. Altough dietary diversity is higher in mid summer, the serotine bats prey on a restricted set of insects in early summer (chafers) and in late summer and autmn (*Aphodius* beetles).

In Namur, some prey are present within the city (*Amphimallon*), whereas other prey can only be found outside a radius of minimum 2.5km (*Aphodius rufipes*), supporting the hypothesis that bats are likely to forage outside the city.

This study confirms adaptation of the serotine bat to an anthropogenic environment, but because it feeds mainly on key prey species from agricultural lands, including species dependant upon cattle husbandry (Cockchafers – summer chafers, and *Aphodius* beetles) it is also potentially sensitive to current farming practices.

REFERENCES

AGOSTA SJ & MORTON D (2003). Diet of the big brown bat, *Eptesicus fuscus*, from Pennsylvania and Western Maryland. Northeastern Naturalist, 10(1): 89-104.

BARTONICKA T & ZUKAL J (2003). Flight activity and habitat use of four bat species in a small town revealed by bat detectors. Folia Zoologica, 52(2): 155-166.

BECK A (1995). Fecal analyses of European bat species. Myotis, 32-33: 109-119.

BELLWOOD JJ & FENTON MB (1976). Variation in the diet of *Myotis lucifugus* (*Chiroptera: Vespertilionidae*). Canadian Journal of Zoology, 54: 1674-1678.

BENZAL J & MORENO E (1989). On the distribution of bats in Madrid (Central Spain). In: HANAK V, HORACEK I & GAISLER (eds), European Bat Research 1987, Charles Univ. Press Praha: 363-371.

BRACK V & LAVAL RK (2006). Diet of the gray myotis (*Myotis grisescens*): variability and consistency, opportunism, and selectivity. Journal of Mammalogy, 87(1): 7-18.

BREWER R (1994). The science of ecology. International edition Saunders college Publishing, Philadelphia, Pennsylvania, USA: 773 pp.

CATTO CMC, HUTSON AM & RACEY PA (1994). The diet of *Eptesicus serotinus* in Southern England. Folia Zoologica, 43(4): 307-314.

CATTO CMC, RACEY PA & STEPHENSON PJ (1995). Activity patterns of the serotine bat (*Eptesicus serotinus*) at a roost in southern England. Journal of Zoology (Lond.), 235(4): 635-644.

CATTO CMC, HUTSON AM, RACEY PA & STEPHENSON PJ (1996). Foraging behaviour and habitat use of the serotine bat (*Eptesicus serotinus*) in southern England. Journal of Zoology (Lond), 238: 623-633.

COULSON JC (1959). Observations on the *Tipulidae* (*Diptera*) of the Moor House Nature Reserve, Westmorland. Transactions of the Entomological Society of London, 3(7): 157-174.

COULSON JC (1962). The biology of *Tipula subnodicornis* Zetterstedt, with comparative observations on *Tipula paludosa* Meigen. Journal of Animal Ecology, 31: 1-21.

DENSE C (1992). Telemetrische Untersuchungen zur Habitatnutzung und zum Aktivitätsmuster der Breitflügelfledermaus *Eptesicus serotinus* Schreber 1774 im Osnabrücker Hügelland. Diplom arbeit, Osnabrück: 118 pp.

DESIÈRE M (1974). Ecologie des coléoptères coprophiles en prairie pâturée et forêt. Thèse doctorale, Univ. Liège: 235 pp.

DICKMAN CR & HUANG C (1988). The reliability of fecal analysis as a method for determining the diet of insectivorous mammals. Journal of Mammalogy, 69(1): 108-113.

DU CHATENET G (1986). Guide des coléoptères d'Europe. Delachaux & Niestlé, Neuchâtel Paris: 479 p.

FENTON MB (1997). Science and the conservation of bats. Journal of Mammalogy, 78: 1-14.

GAJDOSIK M & GAISLER J (2004). Diet of two *Eptesicus* bat species in Moravia (Czech Republic). Folia Zoologica, 53(1): 7-16.

GAISLER J & BAUEROVA Z (1986). The life of bats in a city. Myotis, 23-24: 209-215.

GAISLER J, ZUKAL J, REHAK Z & HOMOLKA M (1998). Habitat preference and flight activity of bats in a city. Journal of Zoology (Lond.), 244: 439-445.

GEGGIE JF & FENTON MB (1984). A comparison of foraging by *Eptesicus fuscus* (Chiroptera: *Vespertilionidae*) in urban and rural environments. Canadian Journal of Zoology, 63: 263-267.

GEHRT SD & CHELSVIG JE (2003a). Bat activity in an urban landscape: patterns at the landscape and microhabitat scale. Ecological Applications, 13(4): 939-950.

GEHRT SD & CHELSVIG JE (2003b). Species-specific patterns of bat activity in an urban landscape. Ecological Applications, 14(2): 625-635.

GERBER E, HAFFNER M & ZISWILER V (1996). Vergleichende Nahrungsanalyse bei der Breitflügelfledermaus *Eptesicus serotinus* (Schreber, 1774) (Mammalia, Chiroptera) in verschiedenen Regionen der Schweiz. Myotis, 34: 35-43.

HARBUSCH C (2003). Aspects of the ecology of serotine bats (*Eptesicus serotinus,* Schreber 1774) in contrasting landscapes in southwest Germany and Luxembourg. PhD Thesis, Univ. Aberdeen: 206 pp.

HESPENHEIDE MA (1974). Prey characteristics and predator niche width. In: CODY ML & DIAMOND JM (eds), Ecology and evolution of communities. Harvard University Press.

JONES G (1990). Prey selection by the greater horseshoe bat (*Rhinolophus ferrumequinum*): optimal foraging by echolocation? Journal of Animal Ecology, 59(2): 587-602.

KERVYN T (1995). Contribution à l'étude de la tactique alimentaire du grand murin *Myotis myotis* (Borkhausen, 1797) (Mammalia: Chiroptera). Mémoire lic. Zool., Univ. Liège: 53 pp.

KERVYN T (1996). Le régime alimentaire du grand murin *Myotis myotis* (Chiroptera: Vespertilionidae) dans le sud de la Belgique. Cahiers d'Ethologie, 16(1): 23-46.

KERVYN T (1998). Méthodes de détermination du régime alimentaire des chiroptères insectivores. Arvicola, 10 (h.s.): 53-56.

KERVYN T (2001). Ecologie et éthologie de la sérotine commune (*Eptesicus serotinus*) (*Chiroptera, Vespertilionidae*): perspectives en vue de la conservation des chauves-souris. Thèse doctorale, Univ. Liège: 164 pp.

KUNZ TH & WHITAKER JOJr (1983). An evaluation of fecal analysis for determining food habits of insectivorous bats. Canadian Journal of Zoology, 61(6): 1317-1321.

KURTA A & TERAMINO JA (1992). Bat community structure in an urban park. Ecography, 15 (3): 257-261.

KURTZE W (1982). Beobachtungen zur Flugaktivität und Ernärhung der Breitflügelfledermaus, *Eptesicus serotinus* (Schreber). Drosera, 1: 39-46.

LABEE AH & VOUTE AM (1983). Voedselkeuze van een kolonie laatvliegers *Eptesicus serotinus*. Lutra, 26: 12-19.

LITVAITIS JA (2000). Investigating food habits of terrestrial vertebrates. In: BOITANI L & FULLER TK (eds), Research Techniques in Animal Ecology: Controversies and Consequences. Columbia University Press. New York, NY: 165-190.

MADSEN M, OVERGAARD NIELSEN B, HOLTER P, PEDERSEN OC, BRÖCHNER JESPERSEN J, VAGN JENSEN K-M, NANSEN P &

GRONVOLD J (1990). Treating cattle with ivermectin: effects on the fauna and decomposition of dung pats. Journal of Applied Ecology, 27: 1-15.

MCANEY CM, SHIEL C, SULLIVAN C & FAIRLEY J (1991). The analysis of bat droppings. Occasional publications of the Mammal Society, 14: 1-48.

MICKLEBURGH S (1987). Distribution and status of bats in the London area. The London Naturalist, 66: 41-91.

MICKLEBURGH S (1989). Distribution and status of bats in the London area. In: HANAK V, HORACEK I & GAISLER (eds), European Bat Research 1987, Charles Univ. Press Praha: 327-329.

PIR J (1994). Etho-ökologische Untersuchungen einer Wochenstubenkolonie der Grossen Hufeisennase (*Rhinolophus ferrumequinum,* Schreber 1774) in Luxemburg. Diplom arbeit. Justus-Liebig-Univ. Giessen.

RACEY PA (1998). Ecology of European bats in relation to their conservation. In: KUNZ TH & RACEY PA (eds), Bat biology and conservation. Smithsonian Institution Press. Washington and London: 249-260.

RANSOME RD (1996). The management of feeding areas for the greater horseshoe bats. English Nature Research Reports, 174: 1-74.

ROBINSON MF & STEBBINGS RE (1993). Food of the serotine bat, *Eptesicus serotinus* is faecal analysis a valid qualitative and quantitative technique? Journal of Zoology (Lond.), 231: 239-248.

SCHMIDT C (2000). Jagdgebiete und Habitatnutzung der Breitflügelfledermaus (*Eptesicus serotinus*) in der Teichlausitz (Sachsen). Säugetierkundliche Informationen, 4: 497-504.

SOKAL R & ROHLF J (1981). Biometry. Second edition Freeman & Co, New York: 859 p.

TAYLOR LR, FRENCH RA & WOIWOD IP (1978). The Rothamsted insect survey and the urbanization of land in Great Britain. In: Academic Press, London & New York, Perspectives in urban Entomology: 33-65.

VAUGHAN N (1997). The diets of British bats (*Chiroptera*). Mammal Review, 27(2): 77-94.

VILLIERS A (1945). Hémiptères de France, Hétéroptères Gymnocérates. Boubée, Paris: 83 pp.

WALL R & STRONG L (1987). Environmental consequences of treating cattle with the antiparasitic drug ivermectin. Nature (Lond.), 327: 418-421.

WHITAKER JOJr (1988). Food habits analysis of insectivorous bats. In: KUNZ TH (ed), Ecological and behavioural methods for study of bats. Smithsonian Inst. Press, Washington D.C. & London: 533 p.

WHITAKER JOJr (1995). Food of the big brown bat *Eptesicus fuscus* from maternity colonies in Indiana and Illinois. American Midland Naturalist, 134: 346-360.

WHITAKER JO, SPARKS DW & BRACK V (2006). Use of artificial roost structures by bats at the Indianapolis International Airport. Environmental Management, 38: 28-36.

ZUKAL J, GAJDOSIK M & REHAK Z (1997). The diet and foraging strategy of *Eptesicus serotinus* in southern Moravian agrocoenoses. Bat Research News, 38: 30-31.