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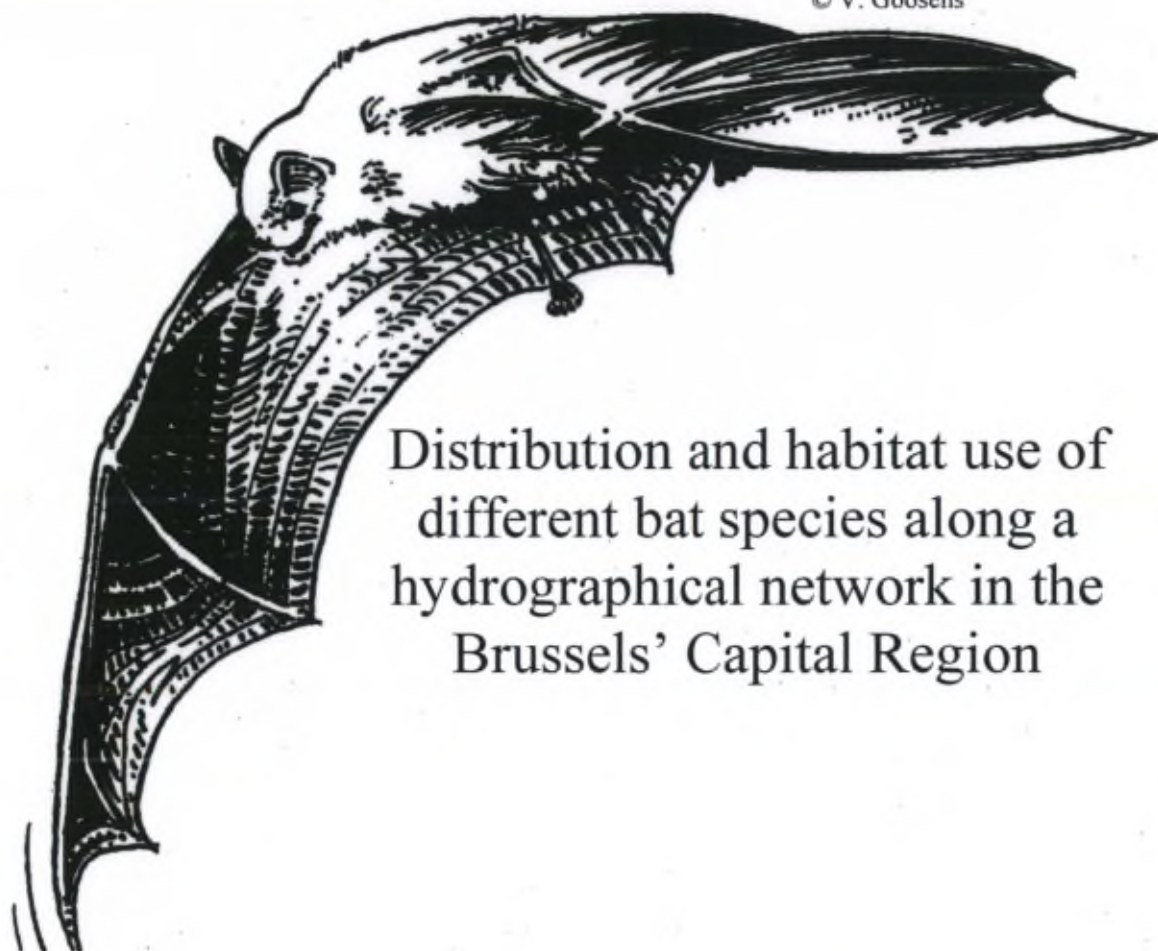
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Distribution and habitat use of  
different bat species along a  
hydrographical network in the  
Brussels' Capital Region

PhD thesis for the obtention of the grade of Docteur en Sciences  
Université Libre de Bruxelles

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## Abstract

The main goal of this PhD thesis was to provide a comprehensive data set on the distribution and habitat use of different bat species in the South-eastern part of the Brussels Region. Major outcomes of this work are the following:

- The confirmation of the particular high species richness in our study area and the discovery of a new species for the Region. We also give explanations for the differential distribution of the ten bat species identified along the string of ponds.
- The development of a reliable estimator of bat activity in a particular habitat: water bodies and the comprehension of temporal use of a pond by different bat species throughout the night but also the activity season,
- The importance of sampling both emerging and flying insects in assessing prey availability for bats in riparian habitats and the influence of temperature on the presence of some bat species around ponds,
- The improvement in the knowledge of roosting and hunting habitat preferences of Daubenton's bats.

## Résumé

Le principal objectif de cette thèse était de fournir des données permettant la compréhension de la distribution et l'utilisation de l'habitat par différentes espèces de chauves-souris exploitant le sud-est de la Région de Bruxelles-Capitale. Les découvertes les plus importantes de ce travail sont :

- La confirmation de la grande richesse spécifique en chauves-souris de notre zone d'étude avec en plus l'identification d'une nouvelle espèce pour la Région. Nous avons aussi apporté certains éclaircissements quant à la distribution des dix espèces identifiées le long de la série d'étang sur laquelle nous travaillions,
- Le choix d'une méthode pour estimer adéquatement l'activité de vol des chauves-souris au niveau des milieux particuliers que sont les zones humides tels les étangs, ainsi que son utilisation pour appréhender les variations temporelles d'activité par différentes espèces au cours de la nuit mais aussi de la saison d'activité,
- L'importance d'échantillonner les insectes émergents et volants dans l'évaluation de la disponibilité des proies pour les chauves-souris en milieu humide et l'influence de la température de l'air sur le comportement de certaines espèces de chauves-souris,
- L'amélioration de la connaissance du mécanisme de sélection des zones de gagnage et de gîte chez le Murin de Daubenton, espèce strictement inféodée aux étendues d'eau pour la chasse.

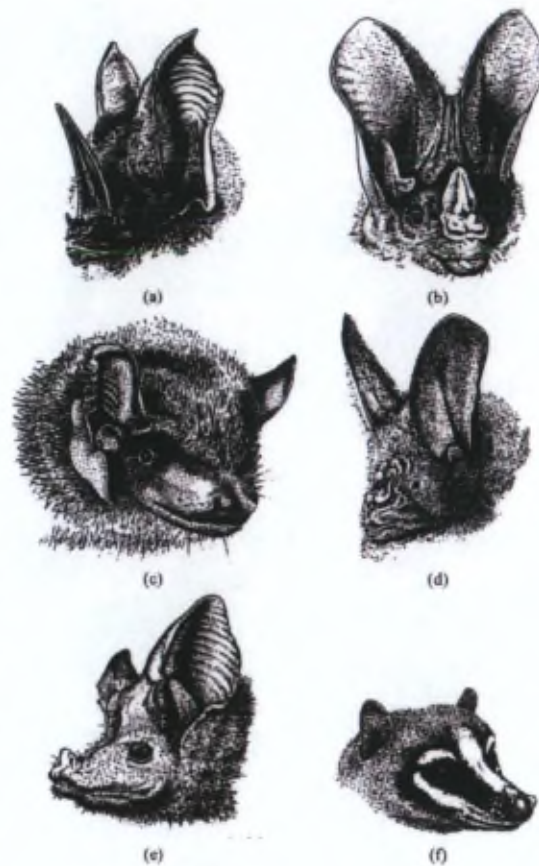
## **Introduction**

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# 1. Bats

## 1. 1.Generalities

Bats belong to the class of Mammals and are categorised as a distinct Order since 1980, the Chiroptera, characterised by having their arms transformed into wings, enabling flight. These flying mammals are found in every biome of the planet except the polar regions, high altitude mountains, isolated islands (i.e. French Polynesia), and the middle of deserts. There are at present 1001 identified species worldwide, making them the largest order of mammals after the Rodentia (Hutson et al., 2001). According to Hill & Smith (1984), the heads of bats show perhaps a wider range of variation than any other group of mammals (Figure 1.1). This is due to their different diets and food capture methods. The Order Chiroptera is divided into two suborders: Megachiroptera (167 species) and Microchiroptera (834 species). Megachiroptera is made up of a single family: the Pteropodidae, which is found in the tropical and sub-tropical regions of the Old World.

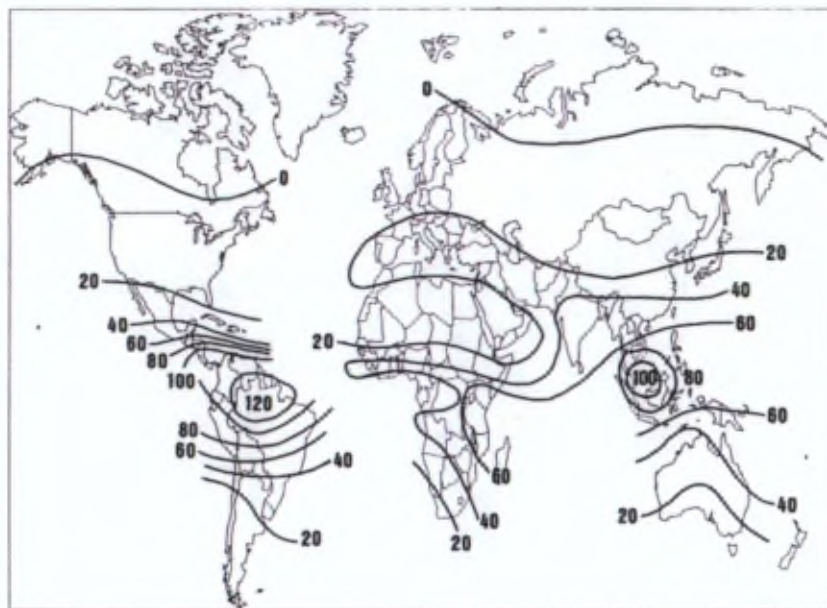


**Figure 1.1:** Illustrations of heads of several bat species: (a) *Lonchorhina auritus*, (b) *Macroderma gigas*, (c) *Nyctalus noctula*, (d) *Nycteris grandis*, (e) *Rhinopoma hardwickei*, and (f) *Pteropus personatus*. After Hill & Smith (1984).

This group includes the largest species of bats, called flying foxes because of their “dog-like” faces, with generally large eyes and simple ears. Flying foxes weigh up to 1.2 kg, and feed mostly on vegetal material. The second group is formed by species that barely reach 125g and that belong to 19 families. More than 75% of Microchiropterans feed on insects although food sources may include other invertebrates, fish, amphibians, small mammals, blood, fruits, nectar or flowers (Altringham, 1996; Hutson et al., 2001).

For the most part, Chiroptera live in tropical regions and only three major families (Rhinolophidae, Molossidae and Vespertilionidae) inhabit cool temperate zones. Based on bat species richness in quadrates of 500 km square, three main centres of species richness have been identified in the tropics: the Americas (up to 120 species are centred over Amazonia), the tropical rain forest of Southeast Asia and the savannah region of equatorial East Africa. In general, species richness decreases with increasing distance from the equator (Figure 1.2). The contrast between temperate and tropical regions is striking. Whereas 146 species have been

found in Venezuela, almost half this number was recorded for the entire Palaearctic region (Findley, 1993).



**Figure 1.2:** Species richness of bats throughout the world. Isograms are based on bat species richness in 500 km square quadrates (Willig & Selcer, 1989).

Low temperatures and food shortage during wintertime represent a major challenge for virtually all animals living in temperate latitudes. Insectivorous bats are small, with masses in the range of 2 to 90g. Smaller bats have a higher surface to volume ratio than larger ones, a great handicap to temperature regulation when the bat is resting. In response of this, bats in temperate regions enter into torpor and hibernate to save energy during cold periods (Ransome, 1990). The brevity of the period of abundant insect food supplies seems to be the major factor restricting temperate bats to a single breeding sequence. In the northern hemisphere, mating often takes place in autumn, but it may occur at any time from late summer to early spring, according to the species. A single sperm, stored throughout the winter inside the female's oviduct or uterus fertilizes the egg. Fertilisation occurs usually in April or May. The length of the gestation period of bats is determined by the foraging success of the female and the roost ambient temperature in her roost. Females congregate in maternity roosts at some time during pregnancy and may form large clusters which do not disperse until after lactation has ended; lactation lasts for at least a month. Females abandon their offspring in late summer or early autumn (Ransome, 1990).

## 1. 2. Echolocation

In 1938, Pierce & Griffin showed that the bat *Eptesicus fuscus* emits high frequency signals. Later, Griffin & Galambos (1941) demonstrated that bats listen to echoes from objects, allowing them to orient themselves in the dark while flying, and named this phenomenon echolocation. Echolocation is widespread in the animal kingdom. For instance, toothed whales generate sounds in the form of clicks, within their nasal sacs, situated behind the melon. The

lower jaw receives the echo, and the fatty tissue behind it transmits the sound to the middle ear and then to the brain (Thomas et al., 2004). Cave-dwelling birds also employ echolocation for navigating through caves (Leroy, 1979). With the exception of the genus *Rousettus*, megachiropteran bats do not echolocate, but rely on vision and smell for orientation (Holland et al., 2005). Echolocation is used by Microchiropteran bats to identify and track flying or standing prey, as well as to avoid obstacles. Microchiropteran bats generate their sonar calls with their particularly large larynx. Vocal membranes allow bats to produce both high-pitched and loud sounds (Mergell et al., 1999). Bats emit a series of brief, high-frequency pulses with the mouth or the nose according to the Family they belong to. The reception mechanism, including the ear and the auditory centres of the brain, enables the identification of the direction, distance, velocity and some aspects of the size, shape or nature of objects from the echo (Grinnell, 1995; Altringham, 1996). In the last decades, as a result of the development of bat detectors, behavioural studies have become possible. Many ecological questions remain unanswered, however, and bats still belong to one of the most mysterious and unknown mammal group.

### **1. 3. Status and conservation of bats**

Approximately 22% of bat species are considered as threatened and another 23% as near threatened (Hutson et al., 2001). As far as we know, many European bat species have undergone large population declines during the 20<sup>th</sup> century (Stebbing, 1988). One of the driving causes of these declines is believed to be the loss of roosting and foraging habitat, which have deleterious consequences on bat populations (Walsh & Harris, 1996a, 1996b). Declines in insect abundance and diversity over the last decades associated with the intensification of agriculture linked with much less grazed pasture and the loss of hedgerows have been suggested as contributory factors to the decline of bat populations (Stebbing, 1988). In Europe, according to the country, bats are listed as protected species in the 'Fauna, Flora, Habitat European directive', the Bern Convention, and the Bonn convention with the Bat agreements also called Eurobats. Signatory countries of this latter agreement have the obligation to:

- forbid the destruction, detention and capture of bats,
- survey and protect important sites for bats (*i.e.*, hunting grounds),
- mandate organisations for information and sensitisation campaigns,
- support international research programs dealing with the conservation of threatened species and
- try to replace pesticides and highly toxic chemical products for wood treatment by less dangerous substitutes.

The Annex 4 of the 29<sup>th</sup> August 1991 order of the executive of the Brussels' Capital Region aspires to protect all vertebrates including bats, as well as their roost.

#### 1. 4. Ecological and economical roles of bats

Throughout tropical regions, fruit and nectar-eating bats are vital to the survival of rainforests. It has been estimated that they play an important role in the pollination of at least 500 neotropical species of plants (Vogel, 1969). In the savannas of East Africa, for instance, the white flowers of the giant baobab open only at night and are adapted to be pollinated by bats. In the Neotropics, Phyllostomid bats act as seed-dispersal agents for up to 24% of forest tree species present on certain sites (Humphrey & Bonaccorso, 1979; Galindo-Gonzales et al., 2000).

In many parts of the world, bats are by far the most important natural controllers of night-flying insects, consuming great quantities of mosquitoes, moths, beetles, crickets, as well as a variety of aquatic insects. A single little brown bat *Myotis lucifugus*, one of North America's most abundant species, is capable of capturing seven mosquitoes per minute and eating approximately 110% of its body weight per night (Anthony & Kunz, 1977). It has been estimated that the 20 million *Tadarida brasiliensis* that occupy the major maternity cave in central Texas (Figure 1.3) could eat up to several hundred tons of insects a night (McCracken, 1996). The loss of insectivorous bat populations leaves farmers dependant on pesticides.



**Figure 1.3:** Colony of free-tailed bats, *Tadarida brasiliensis*, leaving their roost, the Braken cave at dusk (Texas, USA).

Finally, in some developing countries, guano mining is still an important source of revenue for communities (Hutson et al., 2001). Indeed, bat guano, made of insect chitin is a natural and excellent fertiliser.

#### 1. 5. The study of bat communities

Communities are groupings of organisms living together in the same place. They have many characteristics including species composition, species diversity, the relative abundance of species, spatial and temporal patterning of species abundance, and morphological characteristics of the dominant species (Tilman, 1982). The study of communities is

rewarding because it leads to an understanding of the way organisms of different kinds affect each other and how they have adapted to each other's presence (Findley, 1993).

Communities are delineated arbitrarily, depending upon the preferences and goals of the investigator. In our work, the term 'bat community' and 'bat assemblage' refers to all the species occurring together in one geographical locality. No processes or theoretical context is implied.

Studying bat communities in temperate countries is of considerable interest for two reasons. First, the body size of bats is characteristic of r-selected mammals, short-lived, rapid reproducing organisms exhibiting pronounced population fluctuations, adapted to transient, unpredictable habitat. On the contrary, bats live longer than any other mammal of comparable body size (Austard & Fisher, 1991; Wilkinson & South, 2002); they have a low reproductive rate, adult females having mostly one young per year; and they show relative stable populations. In this respect, bats behave like K-strategists. Every facet of their biology suggests that they are occupying stable and predictable habitats such as humid, tropical regions offering quasi-constant and abundant presence of resources (insects, fruits or roosts), they maintain stable populations close to the carrying capacity of the environment (Findley, 1993). In Europe, however, thirty-five species of bats have been described, all being insectivorous. Understanding the mechanisms used by K-strategist species to adapt to unpredictable fluctuations in their environment, for example changes in food availability or climatic conditions, is one of the main goals of conservation biology. It is well-documented that bats living in temperate countries hibernate during wintertime to cope with reduced food resources and decreasing temperatures (Audet & Fenton, 1988; Hamilton & Barclay, 1994). During spring and summer, however, bats are strongly dependent on flying insect availability. Bell (1980) provided experimental evidence that all species present within the community he studied respond opportunistically to unpredictable patches of prey. The mechanisms allowing bats to effectively localise patches of insects every night during the activity periods remain, nevertheless, poorly understood. Second, bat species are considered as bio-indicators of unaltered, high-quality environments because of their high sensitivity to habitat disturbance (Medellin et al., 2000). Bats are multi-habitat users requiring distinct ecological conditions for feeding areas, day roosts, mating sites, and corridors. These resources are vital and can be used as cues when assessing changes in habitat (Fenton, 2003).

## **1. 6. Bats in urban ecosystems**

Cities are highly constraining habitats for most wildlife species because of habitat fragmentation, reduction of food sources and roosting sites, which are consequences of urbanisation. These effects are known to influence the distribution of bats (Walsh & Harris, 1996b; Gerell & Gerell-Lundberg, 1993; Jenkins et al., 1998). Urban bat communities compared with non-urban ones are characterised by a lower number of individuals, decreased species diversity, and strongly expressed dominance of a single species (Kurta & Teramino, 1992). In temperate countries, studies on bat community are rare (Bell, 1980), and those

concerning urban or sub-urban communities are often limited to surveys (De Cornulier & Clergeau, 2001).

### Fragmentation

The existence of linear landscape elements can play a major role in the presence/absence of bats in a given habitat. By linking patches to one another, biological corridors such as hedgerows or tree lines can increase bats' chances of survival in fragmented environments. In addition to functioning as flight paths and a protection from predators, linear landscape elements also give access to additional hunting grounds and can provide more food thanks to the windbreak effect (Lewis, 1969a, 1969b; Limpens & Kapteyn, 1991; Verboom & Spoelstra, 1999). Extensive urbanisation results in the progressive disappearance of this connectedness. For instance, some species seem to be particularly sensitive to the presence of corridors when commuting from one site to another. Daubenton's bats, *Myotis daubentonii*, will never choose a flight path if it implies crossing an open habitat even if this way is shorter. Rather, they will follow a corridor involving a large roundabout (Limpens & Kapteyn, 1991).



**Figure 1.4:** Bats in flight in an urban environment (Limpens et al., 1997)

### Insect availability

Urban areas of large cities have depleted insect faunas (Taylor et al., 1978) and some bat species have adopted different foraging behaviours in a rural vs. urban environments (Geggie & Fenton, 1985). Street lamps are frequently used as foraging sites by some bat species (Rydell & Racey, 1995) (Figure 1.4), certain lamps emitting high amounts of energy in the ultraviolet range which attract insects (Rydell, 1992). However, bat species are unequally affected by the presence of street lamps. Those most expected to benefit from artificial light sources are aerial hawking genera such as *Nyctalus*, *Eptesicus*, *Vespertilio* and *Pipistrellus*. None of the species of these genera are presently under threat (Hutson, 1993). On the other

hand, several European species of *Myotis*, *Plecotus* and *Rhinolophus*, which do not take advantage of street lamps, have seen their populations decline and are, at least in some countries, endangered (Kunz & Racey, 1998).

### Roost availability

Towns offer great amounts of diurnal roosts for synanthropic large (*Eptesicus serotinus*) or small (*Pipistrellus pipistrellus*) species that establish their colonies in buildings (Jenkins et al., 1991). Those species are usually well adapted to urban habitats and are thus widely distributed throughout Europe (Corbet & Harris, 1991). Conversely, most endangered species roost in trees, are lucifugus and are very sensitive to human disturbance (Hutson et al., 2003). It follows that these species should hardly be recorded in such urban habitats.

### 1. 7. Bats around ponds

Riparian habitats serve several ecological functions for bats. Ponds and streams are important drinking sites for animals, especially in urban areas, where these habitats are limited in numbers. As in xeric environments, where water sources are scarce, they typically concentrate high levels of bat activity (Adams & Simmons, 2002). Gaps created by ponds likely provide favourable structural edges that constitute preferred habitat for many species (Walsh & Harris, 1996a, 1996b; Law & Chidel, 2002). Water holes are concretely among the most insect productive grounds and constitute the preferred foraging sites for bats, which forage on emerging adult aquatic insects (Rydell et al., 1994; Walsh & Mayle, 1991). Stretches of water therefore are interesting habitats for undertaking studies of bat community studies because they concentrate many species and individuals (Figure 1.5).



**Figure 1.5:** Five bat species hunting over or at the vicinity of a pond: 1) *Nyctalus noctula*, 2) *Eptesicus serotinus*, 3) *Pipistrellus pipistrellus*, 4) *Myotis daubentonii*, and 5) *Plecotus auritus* (After Limpen et al., 1997).

## 2. Study area

### 2. 1. Brussels

Our experiments were carried out during five activity seasons between April and September, from 2001 to 2005, in the south-east of the Brussels Region, along the Woluwe River and the Forêt de Soignes. Brussels (50°48'N, 4°24'E) has an oceanic-temperate climate characterised by cool, humid winters and hot, humid summers. The mean temperature is 9.8°C and the mean rainfall 780.1mm (IBGE, 2002).

Although the town is highly urbanized, 53% of its surface is still unbuilt. Twenty five percent of the region's surface is covered by private gardens and parks, and 16% by forests and cemeteries, making the Region one of the greenest capitals in Europe. Semi-natural habitats of high biological value cover 15% of the regional territory and allow the establishment of a relatively diverse flora and fauna (Gryseels, 1998). However, parks and gardens are not equally distributed throughout the region, and decrease in size and number the closer one gets to the town centre (Figure 2.1).



**Figure 2.1:** Green spaces typology in the Brussels' Region. The legend indicates green cover of the different blocks in percentage (©IBGE, 2000).

The 1999 Regional Development Plan introduced the 'green network' concept, which aims at remedying this imbalance by creating new public parks in areas where they are scarce. This program also aspires at progressively creating a network of green corridors in the city which would enable bats to move more easily from one park or garden to another (Figure 2.2).



**Figure 2.2:** Green network in the Brussels' Region (©IBGE, 2000)

## 2.2. The Woluwe



**Figure 2.3:** Blue network of Woluwé basin, green spaces and the Forêt de Soignes (in dark green).

The 'blue network' concept is specifically concerned with rivers and ponds located within the region's various hydrographical networks (Molenbeek in the north; Broekbeek, Neerpèdebeek and Vogelzangbeek in the west; Geleytsbeek in the south and the Woluwe in the south-east). The network tackles social and economical issues, as well as ecological ones. Indeed, this project aims to: (1) guarantee water-surface quality; (2) re-establish the continuity of the surface network; (3) improve social, visual and entertainment value of the rivers, ponds and wetlands and (4) develop the biodiversity of these environments and preserve as many species as possible (IBGE, 2000).

Our study area extends over a surface of about 20 km<sup>2</sup> and spans four municipalities: Woluwé-Saint-Lambert, Woluwé-Saint-Pierre, Auderghem and Watermael-Boitsfort. The Woluwe is an urban river located in the south-east of the region. It is 21 km long, of which 9 km belong to the Brussels Region. The river has its source in the Forêt de Soignes situated in the south of Brussels and flows into the Senne near Vilvorde. It constitutes a pond network, made-up of about 20 ponds enclosed within 8 km<sup>2</sup>. These ponds have different hydrological and environmental characteristics (IBGE, 2003). This network includes: the Silex-Moulin complex, Ten Reuken, the Rouge-Cloître ponds, the Mellaerts ponds, and the ponds found in the Woluwe, Sources and Malou parks (Figure 2.3).

### 2. 3. The Forêt de Soignes

This forest is located on a relatively flat plateau at a height of 120m in the south of the region where permanent streams, springs, wetlands and ponds are poorly represented. The forest massif covers 4383 ha spread over all three Belgian regions: 38% of the surface is managed by the Brussels Region (1657 ha), 56% by the Flemish Region and 6% by the Walloon Region. These 1657 ha represent 60% of all parks and gardens found within Brussels. The forest itself is mostly composed of deciduous trees (92%): beeches (*Fagus sylvatica*) and oaks (*Quercus* spp.) cover 74% and 16% of the surface, respectively. The most common coniferous are pines (*Pinus sylvestris* and *Pinus nigra laricio* var. *corsicana*) and larches (*Larix decidua*). The Forêt de Soignes is famous for the cathedral aspect of its beech stands, characterised by mature trees and non-existent understory and herb layers. These trees are still present on 65% of the forest surface. The management undertaken under the Austrian regime at the end of the XVIII<sup>th</sup> century gave to the Forêt de Soignes its current aspect (Van der Ben, 1997). Beeches in cathedral stands are old (between 150 and 200 years old) and are particularly tall (up to 40 meters) with the base of the crown perched at more than 20 meters.

Surveys have shown that this environment presents a low biodiversity. However, this old forest shelters rare organisms, including bryophytes (*Ephemerum stellatum*), the stag beetle (*Lucanus cervus*), a variety of beetles endemic to the forest massif (*Carabus auronitens* var. *putseysi*), spiders (*Achaearanea simulans*, *Walckenaeria corniculans*), the fire salamander (*Salamandra salamandra*), the black woodpecker (*Dryocopus maritius*), the honey buzzard (*Pernis apivorus*), the goshawk (*Accipiter gentilis*) as well as many bat species (IBGE, 2002). Diversity in flora and myceta is stable over years, although population size tends to decrease progressively. On the contrary, the fauna shows generally a significant reduction in the richness as well as in population size (IBGE, 2002).

## References

- Adams, R. A. & J. A. Simmons, 2002. Directionality of drinking passes by bats at water holes: is there co-operation? *Acta Chiropterol.*, 4: 194-199.
- Anthony, E. L. P. & T. H. Kunz, 1977. Feeding strategies of the little brown bat, *Myotis lucifugus*, in southern New Hampshire. *Ecology*, 58: 775-786.
- Altringham, J. D., 1996. *Bats: Biology and Behaviour*, Oxford University Press, 262p.
- Audet, D. & M. B., Fenton, 1988. Heterothermy and the use of torpor by the bat *Eptesicus fuscus* (Chiroptera: Vespertilionidae): a field study. *Physiol. Zool.*, 61: 197-204.
- Austard S. N & K. E., Fisher, 1991. Mammalian aging, metabolism, and ecology: evidence from the bats and marsupial. *J. Gerontol.*, 46: 47-53.
- Bell, G. P., 1980. Habitat use and response to patches of prey by desert insectivorous bats. *Can. J. Zool.*, 58: 1876-1883.
- De Cornulier, T. & P., Clergeau, 2001. Bat diversity in French urban areas. *Mammalia*, 65: 540-543.
- Corbet, G. B. & S., Harris, 1991. *The Handbook of British Mammals* Blackwell Science, 583p.
- Fenton, M. B., 2003. Science and the conservation of bats: where to next? *Wildlife Society Bulletin*, 31: 6-15.
- Findley, J. S., 1993. *Bats a community perspective*. Cambridge University Press, 167p
- Galindo-Gonzales, J., Guevara, S. & V. J., Josa, 2000. Bat- and bird-generated seed rains at isolated trees in pastures in a tropical rainforest. *Cons. Biol.*, 14: 1693-1703.
- Geggie, J. F. & M. B., Fenton, 1985. A comparison of foraging by *Eptesicus fuscus* (Chiroptera: Vespertilionidae) in urban and rural environments. *Can. J. Zool.*, 63: 263-267.
- Gerell, R. & K., Gerell-Lundberg, 1993. Decline of a bat *Pipistrellus pipistrellus* population in an industrialized area in south Sweden. *Biol. Cons.*, 65: 153-157.
- Griffin, D. R. & R., Galambos, 1941. The sensory basis of obstacle avoidance by flying bats. *J. Exp. Zool.*, 86: 486-506.
- Grinnell, A. D., 1995. Hearing in bats: An overview. In Popper, A. N. & R. R., Fay (eds.), *Hearing by bats*, pp 1-36.
- Gryseels, M., 1998. "Natuur en Groene Ruimten in het Brussels Hoofdstedelijk Gewest". In: IRSNB-KBIN & IBGE-BIM, 1998. *Qualité de l'Environnement et Biodiversité en Région de Bruxelles-Capitale. Inventaire et suivi de la Flore et de la Faune. Document de travail de l'IRScNB 93*, 185p.
- Hamilton, I. M. & R. M. R., Barclay, 1994. Patterns of daily torpor and day-roost selection by male and female big brown bats (*Eptesicus fuscus*). *Can. J. Zool.*, 72: 744-749.
- Hill, J. E. & J. D., Smith, 1984. *Bats – A natural history*. University of Texas Press, Austin, Texas, 243p.
- Holland, R. A., Winter, P. & D. A., Waters, 2005. Sensory systems and spatial memory in the fruit bat *Rousettus aegyptiacus*. *Ethology*, 111: 715-725.
- Hutson, A.M., 1993. *Action plan for the conservation of Bats in the United Kingdom*. The Bat Conservation Trust. UK.
- Hutson, A. M., Mickleburgh, S. P. & P. A. Racey, 2001. *Microchiropteran Bats. Global Status Survey and Conservation Action Plan*. IUCN, 49p.
- Humphrey, S.R. & F.J. Bonaccorso. 1979. Population and community ecology. In R.J. Baker, J.K. Jones & D.C. Carter. (eds.). *Biology of Bats of the New World Family Phyllostomatidae, Part III*. Spec. Publ. Mus. Texas Tech. Univ., Lubbock, pp. 409-441.
- IBGE-BIM, 2000. *Maillages vert et bleu*. 32p
- IBGE, 2002. *Projet de plan de gestion de la Forêt de Soignes, partie de Bruxelles-Capitale*, 192p.

- IBGE, 2003. Life-Nature project LIFENAT/B/5167. Inrichting van Speciale Beschermingszones in het Brussels Hoofdstedelijk Gewest. Technisch rapport, 252p.
- Jenkins, E. V., Laine, T., Morgan, S. E., Cole, K. R. & J. R., Speakman, 1998. Roost selection in the pipistrelle bat, *Pipistrellus pipistrellus* (Chiroptera : Vespertilionidae), in northeast Scotland. *Anim. Behav.* 56: 909-917.
- Kurta, A. & J. A., Teramino, 1992. Bat community structure in an urban park. *Ecography*, 15: 257-261.
- Kunz, T.H. & Racey, P.A. (eds.), 1998. *Bat biology and conservation*. Smithsonian Institution Press, Washington DC, 365p.
- Law, B.S. & Chidel, M. (2002) Tracks and riparian zones facilitate the use of Australian regrowth forest by insectivorous bats. *J. App. Ecol.*, 39: 605-617.
- Leroy, Y., 1979. L'univers sonore animal. *Ecologie fondamentale et appliquée*, Gauthier-Villars, 350p
- Lewis, T., 1969a. The diversity of the insect fauna in a hedgerow and neighbouring fields. *J. Applied Ecology*, 6: 453-458.
- Lewis, T., 1969b. The distribution of flying insects near a low hedgerow. *J. App. Ecol.*, 6: 443-452.
- Limpens, H. J. G. A. & K., Kapteyn, 1991. Bats, their behaviour and linear landscape elements. *Myotis*, 29: 39-48.
- Limpens, H., Mosters, K. & W., Bongers, 1997. Atlas van de Nederlandse vleermuizen. Onderzoek naar verspreiding en ecologie. KNNV Uitgeverij.
- McCracken, G.F. 1996. Bats Aloft: A study of high altitude feeding. *Bats*, 14: 7-10.
- Medellin, R. A., Equihua, M. & M. A., Amin, 2000. Bat Diversity and Abundance as Indicators of Disturbance in Neotropical Rainforests. *Cons. Biol.*, 14: 1666-1675.
- Mergell, P., Fitch W. T. & H., Herzel, 1999. Modeling the role of nonhuman vocal membranes in phonation. *J. Acou. Soc. Am.*, 84: 1676-1679.
- Pierce G. W. & D. R., Griffin, 1938. Experimental determination of supersonic notes emitted by bats. *J. Mamm.*, 19: 454-455.
- Ransome, R. D., 1990. The Natural History of Hibernating Bats. 235p
- Rydell, J., 1992. Exploitation of insects around streetlamps by bats in Sweden. *Funct. Ecol.*, 6: 744-750.
- Rydell, J., Bushby, A., Cosgrove, C. C. & P. A., Racey, 1994. Habitat use by bats along rivers in north east Scotland. *Folia Zoologica*, 43(4): 417-424.
- Rydell, J. & P. A., Racey, 1995. Street lamps and the feeding ecology of insectivorous bats. *Symp. zool. Soc. Lond.*, 67: 291-307.
- Stebbing, R.E. 1988. Conservation of European Bats. Christopher Helm, London, 246p.
- Taylor, L. R., French, R. A. & I. P., Woiwod, 1978. The Rothamsted insect survey and the urbanization of land in Great Britain. In: Frankie, G. W. & C. S., Koehler (eds.), *Perspectives in urban entomology*. 31-65 pp.
- Tilman, D., 1982. Resource competition and community structure. Princeton University Press, 296p.
- Thomas, J. A., Moss C. F. & M., Vater, 2004. Echolocation in bats and dolphins. University of Chicago Press, 631p.
- Van der Ben, D., 1997. La Forêt de Soignes. Passé, présent, avenir. Editions Racine, Bruxelles, 250p.
- Verboom, B. & K., Spoelstra, 1999. Effects of food abundance and wind on the use of tree lines by an insectivorous bat, *Pipistrellus pipistrellus*. *Can. J. Zool.*, 77: 1393-1401.
- Vogel, S., 1969. Chiropterophilie in der neotropischen Flora. II. *Flora* 158: 185-350.
- Walsh, A. L. & B. A., Mayle, 1991. Bat activity in different habitats in a mixed lowland woodland. *Myotis*, 29: 97-104.

- Walsh, A. L. & S., Harris, 1996b. Foraging habitat preferences of vespertilionid bats in Britain. *J. App. Ecol*, 33: 508-518.
- Walsh, A. L. & S., Harris, 1996b. Factors determining the abundance of vespertilionid bats in Britain: geographical, land class and local habitat relationships. *J. App. Ecol*, 33: 519-529.
- Wilkinson, G. S. & J. M., South, 2002. Life history, ecology and longevity in bats. *Aging cell*, 1: 124-131.
- Willig, M. R. & K. W., Selcer, 1989. Bat species density gradients in the New World: A statistical assessment. *J. Biogeog.*, 16:189-195.

### **3. Problematic and research questions**

In the northern hemisphere, activity season ranges from March to October. Therefore, insectivorous bats have only a few months ahead to give birth, raise their young, and make reserve forecasting winter. During this period, bats can face day to day heterogenic climatic conditions and non-negligible fluctuations in the localization, nature and quantity of available prey. Convenient roosting sites, corridors to commute and hunting areas are hard to acquire; this is still exacerbated in urban habitats because of the patchwork-like nature of parks and gardens. This PhD thesis deals with species distribution, temporal and spatial use of resources and site fidelity along a string of ponds located in a sub-urban area.

My research addressed four ecological questions, each one constituting a different chapter in this thesis.

1/ What is the composition of the different bat communities along the pond network? I defined bat assemblages along the Woluwe hydrographical network, and discuss the presence or absence of the different species in relation to the distance to the forest and pond productivity. Surveys allowed records of the soprano pipistrelle for the first time in the Brussels region.

2/ Bat densities are usually particularly high around ponds. How can we assess relative bat activity in such habitat? We tested and compared two methods based on acoustic sampling used to monitor bat activity. Then, we focused our attention on a single pond, investigating overnight changes and seasonal variation in flight, foraging activities and social interactions.

3/ What is the relationship between insect availability in terms of quality and quantity, and bat activity around ponds? We first tested different sampling methods to assess emerging and flying insect abundance. Then, we studied the influence of prey availability on bat activity around a single pond on two consecutive years.

4/ How do bats decide where to hunt? We concentrated my efforts on Daubenton's bats, a species strictly dependent on the presence of water bodies. I studied activity patterns in Daubenton's bats by means of telemetry in order to investigate whether hunting and/or roosting fidelity occurs in this species.

## Chapter 1

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## **Bat community composition in a sub-urban area along a hydrographical network**

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### **Abstract**

We studied overall species richness, species occurrence and relative Daubenton's bat density, and species distribution around ponds spread along a hydrographical network located in the south-east of the Brussels' Region. We also measured arrival times of the two most common bat species (common pipistrelle and Daubenton's bat) to investigate connectivity between sites and site attractiveness. Our results reveal high species richness in the study area, with up to ten bat species recorded. There is strong contrasting occurrence at the different ponds, which might stem from habitat configuration and/or species biology. Neither species richness nor Daubenton's bats density were linked to insect productivity of ponds, which was probably linked to insect sampling protocol. Consistent with the different timing of species emergence from their roost, Daubenton's bats arrived later to foraging sites than common pipistrelles. Furthermore, arrival time of Daubenton's bats measured at foraging sites increased with increasing distance to the forest.

## Introduction

Urban areas include natural, semi-natural, and artificial habitats. Some parts of cities as paved surfaces and lawns are biological deserts, whereas stream valleys, rail lines, or parklands can harbour many wild species. Urbanisation typically results in both a reduction in the total area of a native habitat and habitat fragmentation within a built environment (Forman & Godron, 1986; Czech & Krausman, 1997). In areas of human settlement, bats face additional stresses due to reduction of biological corridors or increased light pollution, noise and traffic (Nyholm, 1965; Krull et al., 1991; Rydell, 1992; Rodt et al., 1998; Lodé, 2000). Only few species using aerial-hawking away from obstacles have adapted to perturbations induced by increased urbanisation and are the most common foragers in European cities (e.g., *Nyctalus*, *Vespertilio*, *Eptesicus* and *Pipistrellus*) (Rydell & Racey, 1995). Most of these species have changed their roosting habitat and/or modification in their foraging strategies to roost in buildings or under bridges (Thompson, 1992; Entwistle et al., 1997; Bihari, 2004; Evelyn et al., 2004), and take advantage of light sources as 'hot spots' to hunt insects (Kunz, 1982; Furlonger et al., 1987; Blake et al., 1994; Rydell & Racey, 1995; Rydell et al., 1996; Gaisler et al., 1998; Lee & McCracken, 2002). Other species are rarely encountered in urbanised areas (e.g., *Myotis*, *Plecotus* and *Rhinolophus*) because they are light-phobic, need corridors of vegetation for their movements and/or are particularly selective in their foraging grounds. Most of the European bat species that are currently regarded as endangered belong to the latter group (Rydell & Racey, 1995).

Ponds and lakes are major components of the composite feeding range of bats (Walsh & Mayle, 1991; Law et al., 1998). This is particularly marked in urban and sub-urban areas where insect availability is limited in comparison to more rural places (Geggie & Fenton, 1985). Aerial plankton over water body surface produced by emergence or attracted by the lake surface is one of the main food sources in such environments. In this study, we analyzed bat community structure and distribution around ponds spread along a hydrographical network in a sub-urban area. We took advantage of a relatively rich species assembly of bats confined to the use of a limited number of water bodies contrasted in both productivity and location with respect to shelter providing habitats. First, we determined overall species richness and species occurrence at each pond. We also estimated the relative density of Daubenton's bat *Myotis daubentonii* around each pond, a species highly sensitive to habitat perturbations such as loss of linear landscape elements (LLE) (Limpens et al., 1989; Kretschmer, 2001). Second, we measured arrival time at each pond of the first individuals belonging to the two most common species in the study area, the common pipistrelle and the Daubenton's bat. Third, we assessed how remoteness of ponds to the forest and pond productivity affect bat community structure.

## Material & Methods

### *Study area and sampling*

Our study was conducted from March to September 2001 and 2002 in the Woluwe basin (Brussels, Belgium). The Woluwe basin covers a third of the Brussels' Region in its south-eastern part and is well supplied with parks, green areas, tree alignments, standing and flowing water (IBGE, 2000). The Woluwe River rises in the Forêt de Soignes in the extreme south of our study area. The stream is uncovered in some parts of its watercourse and supplies more than 20 water bodies (figure 1). It is also skirted or crossed by large boulevards (figure 1) with high traffic, noise, and lighting levels. Bats were sampled around seven ponds or groups of ponds: Silex, Rouge-Cloître, Ten Reuken, Woluwé, Mellaerts, Sources and Malou (figure 1).



**Figure 1:** Map of the Woluwe basin showing green spaces, ponds, large roads and the ten bat species identified.

We calculated the distance between ponds and the Forêt de Soignes and pond surface (table 1). Data on insect productivity were available for six out of the seven ponds studied (table 1). They were obtained from macro-invertebrate samples collected from 1999 to 2002 (Goddeeris, 2003), and 2004 for Sources (unpublished data), based on twelve silt samples taken in each pond by means of a Petite Ponar grab sampler of 240 cm<sup>2</sup>. Diptera, especially Chironomidae and Ceratopogonidae, represented the vast majority (98%) of the insects sampled (Goddeeris, 2003).

**Table 1:** Compilation of data available on the ponds studied and maximum densities of Daubenton's bats observed over the ponds.

Ponds	Size (ha)	Distance to the forest (km)	Insects /m <sup>2</sup>	Daubenton's bats /ha
Malou	0.7	2.4	-	0.71
Sources	0.8	1.6	390	0.79
Woluwé	5.2	1.2	1340	0.82
Gd Mellaerts	3.7	0.8	2630	3.62
Ten Reuken	3.1	0	4850	3.68
Rouge-Cloître	8.8	0	792	3.02
Silex	1	0	4638	6.0

Species identification was based on ultrasound monitoring. Monitoring was performed during two hours following sunset. Each pond was visited from seven up to eleven times in total; starting point of monitoring changed each night. Bat calls were recorded using a time expansion bat detector (D-980, Pettersson Elektronik, Sweden), and stored on DAT recorder or Mini Discs (Sony). Species were identified in the field when possible, or through analysis of bat call recordings with Batsound software (Pettersson Elektronik, Sweden) using spectrogram analysis. Echolocation calls of many *Myotis* species are difficult to discriminate based on echolocation records only (Warren et al., 2000), and the behaviour of bats has to be simultaneously observed to make reliable identification. Therefore, a few additional mist-netting sessions were carried out around ponds where some bat species remained enigmatic for correct species identification.

#### *Bat community structure*

Bat community structure on each pond was determined as overall species richness, species occurrence and relative Daubenton's bat density. Species richness was estimated by counting the total number of species identified around each pond. We assessed species occurrence by calculating the percentage of sampling days a given species was recorded over a pond. Bat activity on a pond is difficult to assess. Bats are nocturnal animals and it is to date not possible to achieve an absolute count of all the individuals flying in an area by means of bat detectors or other devices. Moreover, bat activity over ponds can be exceptionally intense (see Chapter 2), and it is often unfeasible to differentiate between five or ten bats flying at a distance of a few meters from the observer by means of a bat detector (pers. obs). Therefore, we measured relative density of Daubenton's bat *Myotis daubentonii* as an estimator of their activity. This species is well suited for such a study for at least two reasons. First, *M. daubentonii* is a trawling species hunting insects close to the water surface, and the number of

foraging individuals may be estimated by scanning the surface of water bodies with a torch. Second, Daubenton's bats are lucifugous and highly dependent on the presence of biological corridors for commuting flight between roosting and foraging sites (Limpens et al., 1989). Thus, the species is also a good indicator of relatively unaltered habitat. To assess Daubenton's bat density, the water surface was scanned during a few seconds every 30 minutes, and the highest number of individuals recorded over the night was reported and divided by the area of the pond. In Rouge-Cloître, we counted individuals over a single water body because other ponds were either covered by macrophytes or too large for being scanned with a torch.

Each night, we also measured arrival time of the very first individuals belonging to the two most common bat species (common pipistrelle and Daubenton's bat) providing inquiries about sites' connectivity and attractiveness. Data from 'Rouge-Cloître' were excluded from the analysis because the prospecting path included a detour from the pond's bank.

### *Statistical analysis*

To test whether bats exploited differently the seven ponds of the study area, we compared species richness and Daubenton's bats density between ponds using Kruskal-Wallis and Dunn's post-hoc tests. Difference in mean arrival times at each pond between the common pipistrelles and the Daubenton's bats was tested using Student *t*-test. Arrival times at each pond were compared for each species with Kruskal-Wallis and Dunn's post hoc tests. To measure the link between arrival time of Daubenton's bats and increasing distance to the forest, we used a Spearman rank Correlation test. To assess the effect of the distance separating each pond to the forest and pond productivity over bat community composition, both factors were correlated with species richness or with Daubenton's bats densities by means of multiple regressions. Statistica 6.0 and SPSS 11.0.4 were used for data analyses, and Map Info 5.5 to draw habitat and species distribution map.

## **Results**

We identified ten bat species in the study area: common pipistrelle *P. pipistrellus*, Nathusius' pipistrelle *P. nathusii*, soprano pipistrelle *P. pygmaeus*, Daubenton's bat, whiskered bat *M. mystacinus*, notch-eared bat *M. emarginatus*, serotine bat *Eptesicus serotinus*, noctule bat *Nyctalus noctula*, Leisler's bat *N. leisleri*, and a long-eared bat *Plecotus* sp. We did not discriminate among echolocation calls of two long-eared bat species *P. auritus* and *P. austriacus*. Species richness greatly varied between ponds (table 2).

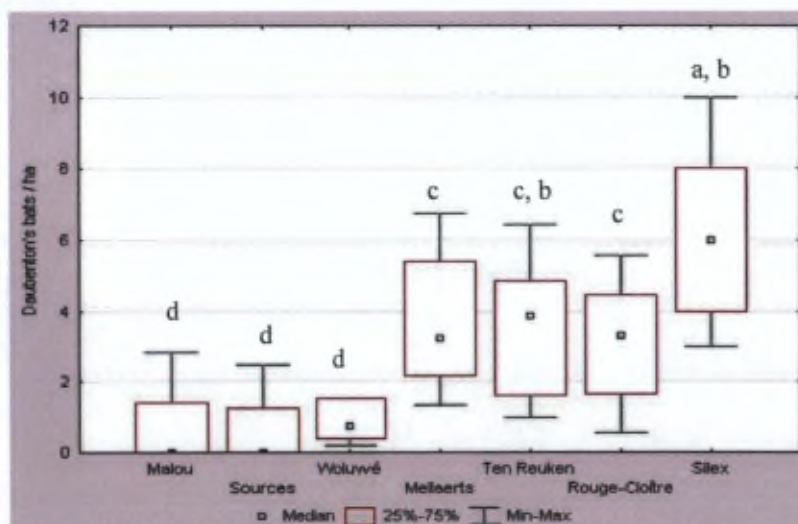
**Table 2:** Species occurrence (%) and species richness at ponds.

	Malou	Sources	Woluwé	Gd Mellaerts	Ten Reuken	Rouge-Cloître	Silex
<i>P. pipistrellus</i>	100	100	100	100	100	100	100
<i>P. nathusii</i>	78	29	75	100	91	70	90
<i>P. pygmaeus</i>	0	0	0	0	0	10	30
<i>M. daubentonii</i>	44	43	100	100	100	100	100
<i>M. mystacinus</i>	0	0	0	0	9	0	10
<i>M. emarginatus</i>	0	0	0	0	0	10	0
<i>E. serotinus</i>	0	0	50	0	63	0	40
<i>N. noctula</i>	0	0	75	45	18	40	20
<i>N. leisleri</i>	0	0	0	27	45	30	80
<i>Plecotus sp</i>	0	0	0	0	9	0	20
<b>Species richness</b>	3	3	5	5	8	7	9

Silex, Ten Reuken and Rouge-Cloître showed the highest diversity with nine, eight and seven species, respectively. Woluwé and Mellaerts harboured five species, and Malou and Sources were visited by three species only. Species occurrence differed significantly between ponds (Kruskall-Wallis  $H=44.79$ ,  $p=0.001$ ; table 2). From the ten species identified, common pipistrelle, Nathusius pipistrelles and Daubenton's bats were recorded over the seven ponds and occurred more frequently than the other species (Dunn's test,  $p<0.05$ ). Occurrence between common pipistrelles, Nathusius' pipistrelles and Daubenton's bats varied significantly ( $H=8.52$ ,  $p<0.02$ ). Nathusius' pipistrelles were less regularly observed around ponds than common pipistrelles ( $p<0.05$ ), whereas no difference occurred with Daubenton's bats ( $p>0.05$ ). Occurrence of common pipistrelles and Daubenton's bats over the seven ponds sampled showed no differences ( $p>0.05$ ), although the latter species appeared less regularly in Malou and Sources.

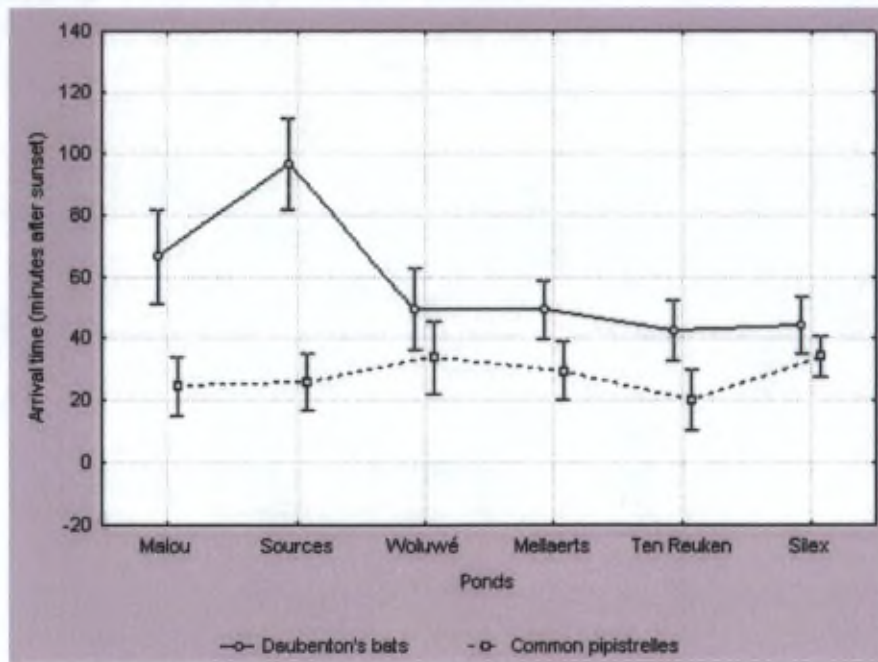
#### *Arrival time, pond productivity and distance to the forest*

After sunset, Daubenton's bats arrived later at foraging grounds than common pipistrelles (mean arrival time  $\pm$  SD =  $52.21 \pm 3.78$  min. and  $28.75 \pm 1.46$  min., respectively;  $t=6.62$ ,  $p<0.001$ ; figure 3).



**Figure 2:** Numbers of Daubenton's bats per hectare observed while flying over the seven ponds studied. Treatments with lower case letters differed significantly (Kruskall-Wallis and Dunn's tests,  $p<0.05$ ).

Arrival time of Daubenton's bats also differed among ponds ( $H= 11.68$ ,  $p< 0.04$ ); they were recorded 20 and 45 minutes later at Malou and Source than at the other ponds (figure 3). By contrast, no significant difference was found among ponds in the arrival time of common pipistrelles ( $H= 10.81$ ,  $p> 0.05$ ). Arrival time of Daubenton's bats followed positively increasing distance to the forest (Spearman Rank Correlation,  $r= 0.91$ ,  $p< 0.017$ ).



**Figure 3:** Arrival times on the different ponds of Daubenton's bats and common pipistrelles ( $\bar{x} \pm$  SD).

Species richness significantly decreased with increasing distance between ponds and the forest, but not with insect productivity (multiple regression,  $r^2= 0.94$ ,  $p< 0.02$ ; richness vs. distance:  $p< 0.03$ ; richness vs. insect productivity:  $p= 0.23$ ). Regarding Daubenton's bats, their density was significantly different over the seven ponds ( $H= 39.12$ ,  $p< 0.001$ ; figure 2). Silex was the most frequented site compared with Ten Reuken, Mellaerts and Rouge-Cloître, showing intermediate levels of activity, and with Woluwé, Malou and Sources presenting the lowest levels ( $p< 0.05$ ) (figure 2). Daubenton's bats' density was neither associated with the distance of ponds to the forest nor with their productivity (multiple regression,  $r^2= 0.78$ ,  $p= 0.10$ ).

## Discussion

Our results revealed a high species richness of bats in the studied area. We identified common pipistrelles and serotine bats, which are often found in urban or sub-urban backgrounds because they take advantage from resources available in towns, such as buildings and streetlamps for roosting and hunting (Blake et al., 1994; Catto et al., 1996; Lesiński et al., 2000). Whereas Daubenton's bat, Nathusius' pipistrelle and soprano pipistrelle are usually unrelated to urban areas, they are often found exploiting aquatic environments (Helmer, 1983; Jones & Rayner, 1988; Oakeley & Jones, 1998; Lesiński et al., 2000). That is probably this latter factor that influenced their records in our zone. We also sampled species strictly associated to wood and forests, such as whiskered bat, notch-eared bat, long-eared bat and

Leisler's bat, and the noctule bat known to roost in trees but to hunt in large open areas as parks (Schober & Grimmberger, 1991). The high species richness found in this study (the Woluwe basin covers about 50 km<sup>2</sup>) is consistent with that previously reported in summer by Devillers et al. (2004) for the whole Brussels-region (about 161 km<sup>2</sup>). Species richness in our studied area likely resulted from the close contiguity of ponds, streams, hedgerows, gardens, buildings, parks, woods, and a large forest, which offer many roosting and hunting opportunities.

Our data indicated contrasting occurrence between bat species at different ponds. Common pipistrelle was recorded recurrently at all ponds. This opportunistic species is also the most widespread and common bat species in Europe (Corbet & Harris, 1991). Nathusius' pipistrelle was relatively common and spread along the Woluwe basin. This occurrence is somewhat surprising since the species is unusual in urban settings (Lesiński et al., 2000). Daubenton's bat was identified each night over every pond, except at Malou and Sources. The remaining seven species sampled occurred less frequently. This might stem from habitat configuration and/or the species biology. Indeed, while moving away from the forest, we observed a decline in the number of species identified around ponds. A few species were restricted to large wooded area and thus presumably to the Forêt de Soignes because they use forest drives or glean arthropods on the foliage (whiskered bats, notched-eared bats and long-eared bats; Anderson & Racey, 1991; Krull et al., 1991). Long-eared bats are known to use very discreet calls (Anderson & Racey, 1991) and their presence might have been overlooked; this species also covers short flight distances (<1 km) (Entwistle et al., 1996), which limits population expansion. Bigger bats such as noctules and serotines often fly more than 8 km to reach hunting grounds and also fly in altitude (Robinson & Stebbings, 1997; Waters et al., 1999; Kronwitter, 1988). Thus, presence of streetlamps and absence of biological corridors do not limit their dispersal. These species hunt in open environments and avoid cluttered locations, which might account for their absence in Malou and Sources.

Neither species richness nor Daubenton's bat density were linked to insect productivity. The lack of association between species richness and insect productivity might stem from some species avoiding insect rich areas because vegetation types or biological corridors do not enable successful hunting and/or secured displacement. On the other hand, that Daubenton's bat density was not associated with productivity contrasts with previous studies showing a strong relationship between both factors in this species (Warren et al., 2000; Kretschmer, 2001). Nevertheless, our data must be considered with caution since our estimate of insect productivity was based on the sole number of invertebrates collected from benthos samples. Yet, it could not reflect the effective productivity of imagoes by the pond, since predation rate by fishes (Hanson & Riggs, 1995) or water quality may greatly affect emergence of insect larvae (Holloway, 1983).

Daubenton's bat densities over water bodies were not associated with the distance of ponds to the forest. Two explanations may account for this result. First, the number of Daubenton's bats foraging on a pond does not depend exclusively from individuals roosting in the forest. Indeed, this species may find shelters in parks provided with many mature trees. Two such parks, Woluwé and Duchesse Anne, are located in our study area and Daubenton's

bats roosting in these parks could have biased our analyses. Second, the number of Daubenton's bat foraging over a pond could depend on insect availability, rather than distance of the pond to the forest. Although our data do not reveal an association between bat densities and insect productivity, such a relationship has been documented in other studies (see above).

Daubenton's bats arrived later at foraging sites than common pipistrelles. This is consistent with the different timing of species emergence from roost, common pipistrelles leaving roost before Daubenton's bats (Gaisler et al., 1998; Warren et al., 2000). Excepting the late arrival of Daubenton's bats at Malou and Sources (figure 3), both species seemed to need little time for commuting from their roost to the pond. Several hypotheses may account for the low number, low occurrence and late arrival time of Daubenton's bats at Malou and Sources. First, the small size of ponds might have increased competition for access to resources and, hence, lead to avoidance of both ponds by most individuals. Daubenton's bats prey close to water surface (Jones & Rayner, 1988), a behaviour that may still increase competition among individuals. This hypothesis seemed to us unlikely because other ponds such as the Silex were not significantly larger than Malou and Sources, but supported on average six times more individuals. Second, individuals recorded at Malou and Sources might be roosting farther and need longer time to reach the pond. Whereas common pipistrelles roost in buildings available along the entire study area, females and males Daubenton's bats usually roost in deciduous trees provided with many cavities (Schober & Grimberger, 1991; Kretschmer, 2001). Further, females Daubenton's bats usually exploit roosting areas enclosing many hollow trees over a small surface (see Chapter 5). Thus, surrounding areas in the vicinity of Malou and Sources might have been poorly provided in suitable trees. Moreover, linear landscape elements (LLE) are essential for Daubenton's bats movements, since their displacements occur exclusively under or near vegetation cover (Limpens et al. 1989). Both Malou and Sources are isolated from the other ponds by the large and very illuminated Tervuren Boulevard. Daubenton's bats might therefore use tortuous paths to avoid an exposed crossing, which increases their commuting time (Kapteyn, 1995; Mostert, 1997; Arthur & Lemaire, 1999). Our result showing that arrival time of Daubenton's bats at foraging grounds is positively associated with their distance to the forest is consistent with this hypothesis. Third, only males might exploit Malou and Sources. Females Daubenton's bats are known to evict males from rewarding hunting places (Encarnação et al. 2005). Males therefore fall back on the ponds of poorer quality. Malou and Sources were located downstream to the river (figure 1) and were probably of poorer water and mud quality than the other ponds. In 2004, Cyanobacteria were sampled in Sources (unpublished data), the less productive pond among studies ponds. Capture and radio-tracking of Daubenton's bats hunting at Malou and Sources would allow testing the two latter hypotheses, by providing information on localisation of their roosts, their commuting paths and their sex.

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## References

- Anderson, M. E. & P. A., Racey, 1991. Feeding behaviour of captive brown long-eared bats, *Plecotus auritus*. *Anim. Behav.*, 42: 489-493.
- Arthur, L. & M., Lemaire, 1999. Les chauves-souris maîtresses de la nuit. La Bibliothèque du Naturaliste. Lausanne, Delachaux et Niestlé, 265p.
- Bihari Z. 2004. The roost preference of *Nyctalus noctula* (Chiroptera, Vespertilionidae) in summer and the ecological background of their urbanization. *Mammalia*, 68: 329-336.
- Blake, D., Hutson, A. M., Racey, P. A., Rydell, J. & J. R., Speakman, 1994. Use of lampits roads by foraging bats in southern England. *J. Zool., Lond.*, 234: 453-462.
- Catto, C.C.M., Hutson, A.M., Racey, P.A. & P.J., Stephenson, 1996. Foraging behaviour and habitat use of the serotine bat (*Eptesicus serotinus*) in southern England. *J. Zool., Lond.*, 238: 623-633.
- Corbet, G. B. & S., Harris, 1991. The Handbook of British. Mammals Blackwell Science, 583p.
- Czech, B., and P. R. Krausman. 1997. Implications of an ecosystem management literature review. *Wildl. Soc. Bull.*, 25:667-675.
- Devillers P., Kapfer G., Devillers-Terschuren J., Lafontaine R.-M. & Y., Laurent, 2004. Les Chauves-souris de la Région bruxelloise: Distribution et Habitats. *Nat. Belg.*, 85: 1-50.
- Encarnação, J. A., Holweg, D., Jasnoch, U., Kierdorf, U. & V., Wolters, 2005. Sex-related differences in roost-site selection of Daubenton's bats (*Myotis daubentonii*) during the nursery period. *Mamm. Rev.*, 35: 285-294.
- Entwistle, A. C., Racey, P. A. & J. R., Speakman, 1996. Habitat exploitation by a gleaning bat, *Plecotus auritus*. *Phil. Trans. R. Soc. Lond. B.*, 351: 921-931.
- Entwistle, A. C., Racey, P. A. & J. R., Speakman, 1997. Roost selection by the brown long-eared bat *Plecotus auritus*. *J. App. Ecol.*, 34: 399-408.
- Evelyn, M. J., Stiles, D. A. & R. A., Young, 2004. Conservation of bats in suburban landscapes: roost selection by *Myotis yumanensis* in a residential area in California. *Biol. Cons.*, 115: 463-473.
- Forman, R. T. T. & M., Godron, 1986. Landscape Ecology. John Wiley, New York., 619p.
- Furlonger, C. L., Dewar, H. J. & M. B., Fenton, 1987. Habitat use by foraging insectivorous bats. *Can. J. Zool.*, 65: 284-288.
- Gaisler, J., Zukal, J., Rehak, Z. & M., Homolka, 1998. Habitat preference and flight activity of bats in a city. *J. Zool., Lond.*, 244: 439-445.
- Geggie, J. F. & M. B., Fenton, 1985. A comparison of foraging by *Eptesicus fuscus* (Chiroptera: Vespertilionidae) in urban and rural environments. *Can. J. Zool.*, 63: 263-267.
- Goddeeris, B., 2003. Benthische Macro-Invertebrated van de Brussels vijvers. In IBGE, 2003. Inrichting van Speciale Beschermingszones in het Brussels Hoofdstedelijk Gewest. Technisch rapport, 34-56 pp.
- Hanson, M. A. & M. R., Riggs, 1995. Potential effects of fish predation on wetland invertebrates: a comparison of wetlands with and without fathead minnows. *Wetlands*, 15:167-175.
- Helmer, W., 1983. Boombewonende watervleermuizen *Myotis daubentonii* (Kuhl, 1817) in het van nijmegen. *Lutra*, 26: 1-11.
- Holloway, J.D., 1983. Insect surveys – an approach to environmental monitoring. A tti XII Congresso naz. Ital. Ent. (Roma, 1980), 239-261.
- IBGE-BIM, 2000. Maillages vert et bleu. 32p

- Jones, G. & M. V., Rayner, 1988. Flight performance, foraging tactics and echolocation in free-living Daubenton's bats *Myotis daubentonii* (Chiroptera: Vespertilionidae). *J. Zool., Lond.*, 215: 113-132.
- Kapteyn, K., 1995. Vleermuizen in het landschap. Haarlem, Schuyt, 224p.
- Kronwitter, F., 1988. Population structure, habitat use and activity patterns of the noctule bat *Nyctalus noctula* Schreber, 1774 (Chiroptera: Vespertilionidae) revealed by radio-tracking. *Myotis*, 26: 23-88.
- Kretschmer, M., 2001. Untersuchungen zur Biologie und Nahrungsökologie des Wasserfledermaus, *Myotis daubentonii* (Kuhl, 1817), in Nordbaden. *Nyctalus*, 8: 28-48.
- Krull, D., Schumm, A., Metzner, W. & G., Neuweiler, 1991. Foraging areas and foraging behavior in the notched-eared bat, *Myotis emarginatus* (Vespertilionidae). *Behav. Ecol. Sociobiol.* 28: 247-253.
- Kunz, T. H., 1982: Ecology of bats. Plenum Press, New York and London, 425p.
- Law, B., Anderson, J. & M., Chidel, 1998. A bat survey in state Forests on the south-west slopes of New South Wales with suggestions of improvements for future surveys. *Austr. Zool.*, 30: 467-479.
- Lee, Y.-F. & F., McCracken, 2002. Foraging activity and food resource use of Brazilian free-tailed bats, *Tadarida brasiliensis* (Molossidae). *Ecoscience*, 9: 306-313.
- Lesiński, G., Fuszara, E. & M., Kowalski, 2000. Foraging area and relative density of bats (Chiroptera) in differently human transformed landscapes. *Z. Säugetierk.*, 65: 129-137.
- Limpens, H. J. G. A., Helmer, W., van Winden, A. & K., Mostert, 1989. Vleermuizen (Chiroptera) en lintvormige landschapselementen. *Lutra*, 32: 1-20.
- Lodé, T., 2000. Effect of a Motorway on Mortality and isolation of Wildlife Populations. *Ambio*, 29: 163-166.
- Mostert, K. 1997. Watervleermuis *Myotis daubentonii* (Kuhl, 1817). In H. Limpens, K. Mostert & W. Bongers, (Ed.). 1997. Atlas van de Nederlandse vleermuizen. Utrecht, Koninklijke Nederlandse Natuurhistorische Vereniging. pp 113-123
- Nyholm, ES. 1965. Zur Ökologie von *Myotis mystacinus* (Leisl.) und *M. Daubentoni* (Leisl.) (Chiroptera). *Ann. Zool. Fenn.*, 2: 77-123.
- Oakeley, S. F. & G., Jones, 1998. Habitat around maternity roosts of the 55 kHz phonic type of pipistrelle bats (*Pipistrellus pipistrellus*). *J. Zool., Lond.*, 245: 222-228.
- Robinson, M. F. & R. E., Stebbings, 1997. Home range and habitat use by the serotines bat, *Eptesicus serotinus*, in England. *J. Zool., Lond.*, 243: 117-136.
- Rodts, J., Holsbeek, L. & S., Muyldermans, 1999. Dieren Onder onze Wielen, over het effect van het wegverkeer op de inlandse fauna. VUB Press, 200p.
- Rydell, J., Entwistle, A. & P. A., Racey, 1996. Timing of foraging flights of three species of bats in relation to insect activity and predation risk. *Oikos*, 76: 243-252.
- Rydell, J. & P. A., Racey, 1995. Street lamps and the feeding ecology of insectivorous bats. *Symp. zool. Soc. Lond.*, 67: 291-307.
- Rydell, J., 1992. Exploitation of insects around streetlamps by bats in Sweden. *Functional Ecology*, 6: 744-750.
- Schober W. & E., Grimmberger, 1991. Guide des Chauves-souris d'Europe. Biologie-Identification-Protection. Delachaux & Niestlé, 225p.
- Thompson, M. J. A., 1992. Roost philopatry in female pipistrelle bats *Pipistrellus pipistrellus*. *J. Zool., Lond.*, 228: 673-679.
- Walsh, A. L. & B. A., Mayle, 1991. Bat activity in different habitats in a mixed lowland woodland. *Myotis*, 29: 97-104.
- Warren, R. D., Waters, D. A., Altringham, J. D. & D. J., Bullock, 2000. The distribution of Daubenton's bats (*Myotis daubentonii*) and pipistrelle bats (*Pipistrellus pipistrellus*) (Vespertilionidae) in relation to small-scale variation in riverine habitat. *Biol. Cons.*, 92: 85-91.
- Waters, D., Jones, G. & M., Furlong, 1999. Foraging ecology of Leisler's bat (*Nyctalus leisleri*) at two sites in southern Britain. *J. Zool., Lond.* 249: 173-180.

## SHORT NOTES

First recordings of the soprano pipistrelle *Pipistrellus pygmaeus* (Leach, 1825) in BelgiumGéraldine Kapfer<sup>1,2</sup>, Marc Van de Sijpe<sup>3</sup>, Ben Van der Wijden<sup>4,5</sup>, Wout Willems<sup>3</sup>, Bob Vandendriessche<sup>3</sup> and Bart Mulkens<sup>3</sup><sup>1</sup> Institut Royal des Sciences Naturelles de Belgique, Biologie de la conservation, Belgium<sup>2</sup> Eco-Ethologie Evolutive, Université Libre de Bruxelles, Brussels, Belgium<sup>3</sup> Natuurpunt v.z.w., Vleermuizenwerkgroep, Mechelen, Belgium<sup>4</sup> Evolutionary Biology Research Group, University of Antwerp, Belgium<sup>5</sup> A.B.Consultancy g.c.v., Dendermonde, Belgium

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Microchiropteran bats species can be discriminated according to morphometrical, behavioural and genetical features (1) (2). In addition, as bat species often emit distinct echolocation calls, the analysis of signal characteristics is a good identification tool and can even lead researchers to the discrimination of sibling species. In 1993, JONES & VAN PARIJS (3) showed a bimodal distribution in the echolocation calls of the common pipistrelle *Pipistrellus pipistrellus* (Schreber, 1774) with individuals emitting calls with maximum energy peak around 45kHz and others around 55kHz. Subsequent works have shown that the two phonic types also showed differences in diet, habitat use (4) and social calls (5) (6). Genetic analysis finally separated the two phonic types into different cryptic species *P. pipistrellus* and *P. pygmaeus* (Leach, 1825), the common name given to the latter species being soprano pipistrelle (7). The distribution of *P. pygmaeus* is poorly known because of the recent distinction between the two phonic types. To date, it seems that soprano pipistrelles occur in Portugal, Sweden (8), Norway (9) and Denmark (7) (9) (10), whereas its sibling species, *P. pipistrellus*, does not. In other countries : Greece (11), Great Britain (3), Switzerland (12) (13), Northern Ireland (14), Germany (15) (16), France (17), Italy (18), and Spain (19) (16), the two species (*P. pipistrellus* and *P. pygmaeus*) are sympatric. Despite its presence in bordering countries, *P. pygmaeus* has never been identified in the Benelux so far. Two species of pipistrelles are known to occur in Belgium (20) : *P. pipistrellus* is widely distributed in Europe whereas *P. nathusii* (Keyserling & Blasius, 1839) is much less frequent and usually found around forest edges and riparian habitats (21). Here, we present the first acoustic records of the soprano pipistrelle in Belgium.

Echolocation calls were recorded by means of time expansion bat detectors (D-240(x) and D-980, Pettersson Elektronik AB, Sweden) and stored on a Mini-disc recorder (Sony) or a DAT (Sony). They were then analysed with Bat Sound software (Pettersson Elektronik AB, Sweden). The shape of the signal and maximum energy frequency were used to identify the species. Pipistrelles all use FM-qCF echolocation calls (22), a Fre-

quency Modulated signal that ends up in a quasi Constant Frequency. However, as illustrated (Fig. 1), the different species can be discriminated according to the ending frequency of the qCF : *P. nathusii* around 35kHz, *P. pipistrellus* around 45kHz and *P. pygmaeus* around 55kHz (8) (23).

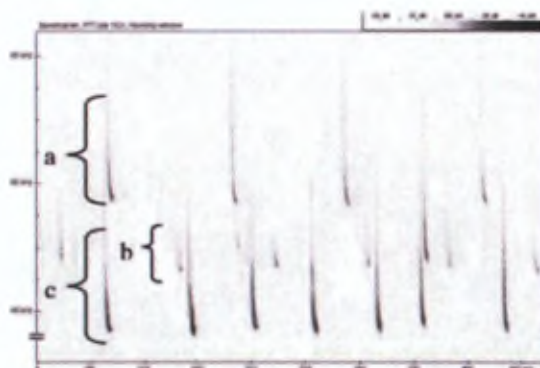


Fig. 1. – Sonogram of three *Pipistrellus* species recorded simultaneously at the Silex pond : a/ *P. pygmaeus*, b/ *P. pipistrellus*, c/ *P. nathusii*.

The first records of the soprano pipistrelle in Belgium came from different locations in the Flemish Region : Ieper (May 1998), Moen (June 1999) and Beernem (July 2000) in the Province of West-Flanders, in Zoersel (February 2002 and May 2003) and Merksem (May 2004) in the Province of Antwerp and, in Bree (September 2003) in the Province of Limburg. In April and June 2002 the species was first recorded in the Brussels Region respectively in the Silex domain (natural reserve in Boitsfort) and the Rouge Cloître domain (Auderghem). In the Walloon Region no confirmed observations were made until now (F. Forget, pers. comm.). Results are presented Table 1. In the Silex Domain (Brussels), soprano pipistrelles were recorded by chance in 2002 on two occasions. In 2003 a sustained monitoring experiment was performed during 50 nights, from April to September. The

species was noted on 38 nights throughout the activity season. In summer 2004 and 2005 additional recordings confirmed that the species was still present on the site.

In the Flemish Region, despite our increasing sampling effort in places where typical signals of *P. pygmaeus* had been recorded, in most cases, we never record the species

again. So far, all our recordings referred to single bats, most of which were recorded during spring (Table 1). This might suggest a temporally presence of the species in the Flanders, as a result of migration or accidental transportation.

TABLE 1

First records of the soprano pipistrelle in Belgium

Date	Location	Recorded (R) Observed (O)	Terminal QCF frequency (kHz)	Peak frequency (kHz)	N recorded signals	Habitat description
May 17, 1998	Ieper	R	54.3	55.2	15	Bank of a moat
June 06, 1999	Zwevegem (Moen)	R/O	57.9	58.7	10	Near a bridge, over a canal
July 02, 2000	Beernem	R/O	55.8	56.4	9	Ruins of a castle in a private woodland
February, 2002	Zoersel forest	R	56.7	59.6	7	Forest path
May, 2003	Zoersel forest	R	55.0	59.4	17	Forest path
September 3-4, 2003	Zuid-Willemsvaart Beek (Bree)	R	59.2	60.6	5	Near a bridge, over a canal
May 6 & 9, 2004	Fort Merkssem	R	55.7	56.7	18	Bank of a moat
April 4, 2002	Boitsfort (Brussels)	R/O	56.0	57.8	16	Bank of a pond
June 20, 2002	Auderghem (Brussels)	R/O	56.9	57.6	7	Bank of a forest pond

Terminal QCF frequency = terminal frequency of the signal derived from spectrogram analysis (BatSound) (average calculated from N recorded signals)  
Peak frequency = frequency of the highest peak derived from power spectrum (BatSound) of the selected signal (average calculated from N recorded signals)

A recent study has shown that *P. pipistrellus* and *P. pygmaeus* are sometimes mis-identified because of intra-specific variation, with some individuals using frequencies above or below the mean value (13). These authors found that false identification occurred in 50%, based on echolocation calls only. Is it possible that *P. pygmaeus* does not occur in Belgium and that we misidentify the species? It seems not likely. First of all, it is generally admitted that the frequency at maximum intensity of the search phase calls is the parameter showing the lowest inter-specific overlap and that best discriminates those two sibling species (1) (3) (4) (11) (18) (23). Second, WICHT et al. (2003) (13) only compared genetic and acoustical data of four soprano pipistrelles, which is a rather small sample to make any valuable interpretation. Third, they recorded their signals from hand-released animals, which could influence the emission of sounds (24). Finally, the distribution range of *P. pygmaeus* is particularly large in comparison with that of other European bat species ranging from Scandinavia to the Mediterranean area (1). The species is present in France, Germany and England and it would be surprising if the species was absent in the Benelux.

Our recordings suggest that *P. pygmaeus* is not widely distributed in Belgium but present. However, many areas have not been intensively surveyed. Moreover, this species has been overlooked in the past, because bat researchers did not expect thus did not look for bats at frequencies over 50kHz.

## REFERENCES

- MAYER, F. & O. VON HELVERSEN (2001). Cryptic diversity in European bats. *Proceedings of the Royal Society of London. Series B*, 268 : 1825-1832.
- ARLETTAZ, R., M. RUEDI, C. IBANEZ, J. PALMEIRIM & J. HAUSER (1997). A new perspective on the zoogeography of the sibling mouse-eared bat species *Myotis myotis* and *Myotis blythii* : morphological, genetical and ecological evidence. *Journal of zoology*, London, 242 : 45-46.
- JONES, G. & S.M. VAN PARIJS (1993). Bimodal echolocation in pipistrelle bats : are cryptic species present? *Proceedings of the Royal Society of London. Series B*, 251 : 119-125.
- BARLOW, K.E. (1997). The diet of the phonic types of the bat *Pipistrellus pipistrellus* in Britain. *Journal of zoology*, London, 243 : 597-609.
- BARLOW, K.E. & G. JONES (1997). Differences in songflight calls and social calls between two phonic types of the vespertilionid bat *Pipistrellus pipistrellus*. *Journal of zoology*, London, 241 : 315-324.
- BARLOW, K.E. & G. JONES (1997). Function of pipistrelle social calls : field data and a playback experiment. *Animal behaviour*, 53 : 991-999.
- BARRATT, E.M., R. DEAVILLE, T.M. BURLAND, M.W. BRUFORD, G. JONES, P.A. RACEY & R.K. WAYNE (1997). DNA answers the call of pipistrelle bat species. *Nature*, London, 387 : 138-139.
- GERELL-LUNDBERG, K. & R. GERELL (1994). The mating behaviour of the Pipistrelle and the Nathusius' Pipistrelle (Chiroptera) - A comparison. *Folia Zoologica*, 43(4) : 315-324.
- BAAGOE, H.J. (2001). Danish bats (Mammalia : Chiroptera) : Atlas and analysis of distribution, occurrence and abundance. *Steenstrupia*, 26 : 1-117.
- JONES, G. (1997). Acoustic signalling and speciation : the roles of natural and sexual selection in the evolution of cryptic species. *Advances in the Study of Behaviour*, 26 : 317-354.
- WEID, R. & O. VON HELVERSEN (1987). Ortungsrufe europäischer Fledermäuse beim Jagdflug im Freiland. *Myotis*, 25 : 5-27.
- ZINGG, P. (1990). Akustische Artidentifikation von Fledermäusen (Mammalia : Chiroptera) in der Schweiz. *Revue Suisse de Zoologie*, 97 : 263-294.

13. WICHT, B., M. MORETTI, D. PREATONI, D. TOSI & A. MARTINOLI (2003). The presence of soprano pipistrelle *Pipistrellus pygmaeus* (Leach, 1825) in Switzerland: first molecular and bioacoustic evidence. *Revue Suisse de Zoologie*, 110: 411-426.
14. RUSS, J.M. (1996). First record of bimodality in the echolocation calls of the common pipistrelle *Pipistrellus pipistrellus* in Ireland. *The Irish naturalists' journal*, 25: 225-226.
15. HÄUSSLER, U., A. NAGEL, M. BRAUN & A. ARNOLD (2000). External characters discriminating sibling species of European pipistrelles, *Pipistrellus pipistrellus* (Schreber, 1774) and *P. pygmaeus* (Leach, 1825). *Myotis*, 37: 27-40.
16. F. MAYER & O. VON HELVERSEN (2001). Sympatric distribution of two cryptic bat species across Europe. *Biological Journal of the Linnean Society*, 74: 365-374.
17. LUSTRAT, P. (1999). Première mention de Pipistrelle "commune", *Pipistrellus* sp., émettant en fréquence terminale à plus de 50 kHz en France. *Arvicola*, 11: 34-35.
18. RUSSO, D. & G. JONES (2000). The two cryptic species of *Pipistrellus pipistrellus* (Chiroptera: Vespertilionidae) occur in Italy: evidence from echolocation and social calls. *Mammalia*, 64 (2): 187-197.
19. RUEDI, M., Y. TUPINIER & O. DE PAZ (1998). First breeding record for the noctule bat (*Nyctalus noctula*) in the Iberian Peninsula. *Mammalia*, 62: 301-304.
20. DEVILLERS, P., G. KAPPER, J. DEVILLERS-TERSCHUREN, R.M. LAFONTAINE & Y. LAURENT (2004). Les Chauves-souris de la Région bruxelloise: Distribution et Habitats. *Les Naturalistes Belges*, 85: 1-50.
21. MITCHELL-JONES, A.J., G. AMORI, W. BOGDANOWICZ, B. KRSTUFK, P.J.H. REININDERS, F. SPITZENBERGER, M. STUBBE, J.B.M. THISEN, V. VOHRALIK & J. ZIMA (1999). *The Atlas of European Mammals*. 496p.
22. BARATAUD, M. (1996). *Balades dans l'in audible*. Edition Sitelle, 49 p.
23. BARLOW, K.E. & G. JONES (1999). Roosts, echolocation calls and wing morphology of two phonic types of *Pipistrellus pipistrellus*. *Zeitschrift für Säugetierkunde – International Journal of Mammalian Biology*, 64: 257-268.
24. PARSONS, S. (1998). The effect of recording situation on the echolocation calls of the New Zealand lesser short-tailed bat (*Myotis tuberculatus* Gray). *New Zealand Journal of Zoology*, 25: 147-156.

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## Chapter 2

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## **Comparison of two methods for determining relative activity of free flying bats**

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### **Abstract**

Bats have a high conservation value and measuring their activity is of prime importance for estimating the efficiency of management actions aimed at their maintenance. Yet, determining bat densities in the field is complicated because of the inherent difficulties in surveying nocturnal flying animals. Measuring activity of flying bats therefore remains semi-quantitative. By using frequency division, we compared Bat Passes counts (BP) and Activity Duration (AD), two methods used for bat activity estimation. Our results show that when overall activity is low, BP and AD are convenient tools, since both vary simultaneously. By contrast, when overall activity increases, AD becomes a much more reliable estimator of bat activity.

**Key words:** Bat, Activity, Bat detector, Methodology

## Introduction

Because of their high sensitivity to habitat disturbances, bats are recognised as relevant biological indicators of habitat quality and integrity (Brinkmann & Limpens, 1999, Entwistle *et al.*, 1997; Medellín *et al.*, 2000). Bats are also considered as “umbrella” species; *i.e.*, preservation of their habitat results in protection of numerous other animals and plants that rely on the same environment. This stems largely from the large home ranges used by many bat species for foraging and commuting (Racey & Swift, 1985; Waters *et al.*, 1999). Despite their small size, most bats are K-strategists and are less easily inclined to recover from a significant population decline (Horáček, 1985; Gaisler, 1989). Riparian habitats usually support high bat densities, with activity levels near rivers and ponds reaching 2 to 100 times those in forests, pastures, grasslands, or arable lands (Walsh & Harris 1996, Vaughan *et al.*, 1997). By contrast, in cities where green spaces are mostly patchily distributed, water bodies represent main foraging and drinking sites, being primordial for the maintenance of bat populations in urban environments.

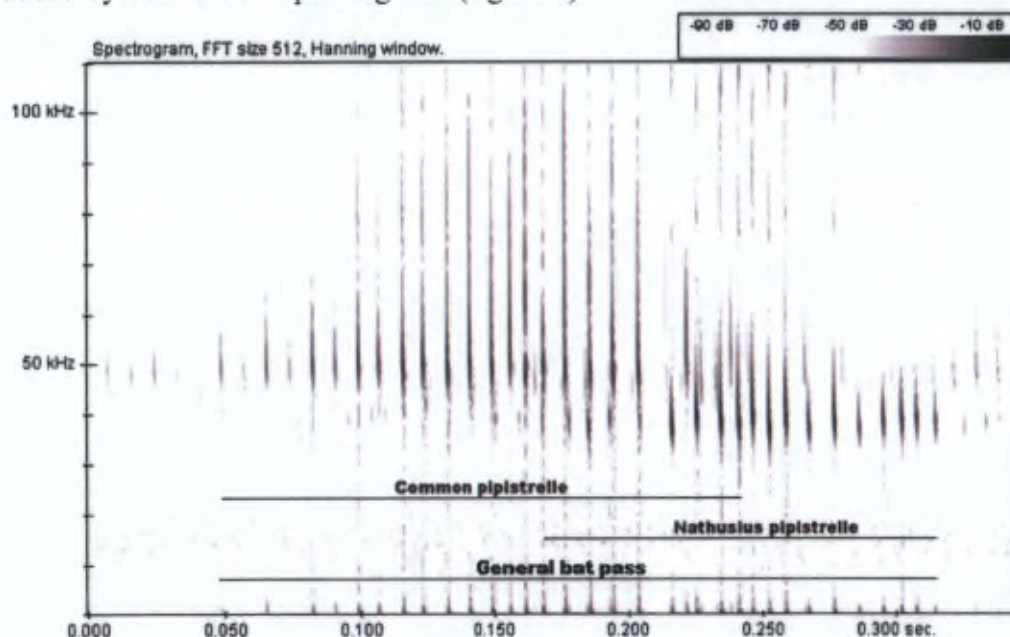
Estimating the efficiency of management actions for habitat quality improvement requires estimation of bat densities at different locations, before and after undertaking management operations. Yet, determining bat densities in the field is impossible because of the inherent difficulties in surveying nocturnal flying animals. Measuring bat activity therefore remains semi-quantitative and relies on various methods, including capture-recapture (O’Farrell and Bradley, 1970, Park *et al.*, 1998), photography (Daan, 1970), night vision scopes (Kretschmer, 2001) or acoustic sampling. The latter process offers several advantages. First, ultrasonic recordings are non-disruptive. Second, it is recognized as more effective than other methods for determining the presence of specific bat groups, even for species emitting weak or inconspicuous calls (O’Farrell, 1998; Anderson & Racey, 1991). Third, acoustic sampling can be automated *i.e.*, recordings can be carried out over long periods or simultaneously at distinct locations (Hayes, 1997).

To date, acoustic sampling of bat activity has been performed in two ways: (1) by counting the frequency of bat passes (BP) (Negraeff & Brigham 1995; Grindal & Brigham, 1999) or (2) by determining activity duration (AD) that is, the amount of time bats are heard (McAney & Fairley, 1988; Carmel & Safriel, 1998). Here, we compared reliability of both methods for estimating bat activity in habitats with variable bat densities by using frequency division.

## Materials and Methods

Bat activity was recorded around the Silex pond in a natural reserve at Boitsfort-Brussels (Belgium), between April and September 2003. The pond is adjacent to the “Forêt de Soignes”, an old-stand forest covered with 65% of 150-200 year-old “cathedral” beeches (*Fagus sylvatica*). Bat calls were recorded using a Pettersson D-980 (Pettersson Elektronik AB, Sweden) and recorded on a DAT-Sony recorder. Signals were then analysed with “Bat Sound” software (Pettersson Elektronik AB, Sweden). Frequency division (division factor:

10) was chosen as transformation mode because it allows both broadband and real-time recordings. We identified species by analysing echolocation calls' characteristics on spectrograms. The shape of the signal was used to determine the genus, whereas the frequency of maximum intensity was used to differentiate between species. When a species remained unidentified, the corresponding recording sequence was removed from the analysis. Two-minute recordings were performed during the two hours following sunset at six contact points located on the bank of the pond and separated 50m from each other. Overall, our sample represented 867 two-minute recordings over 50 sampling nights during the six-month period. Activity was recorded for each bat species sampled in our study area. Flight activity was estimated by counting the number of bat passes (BP) and activity duration (AD) per unit of time. We considered one BP as equivalent to a sequence of at least two echolocation pulses produced by one or more passing bats (figure 1).



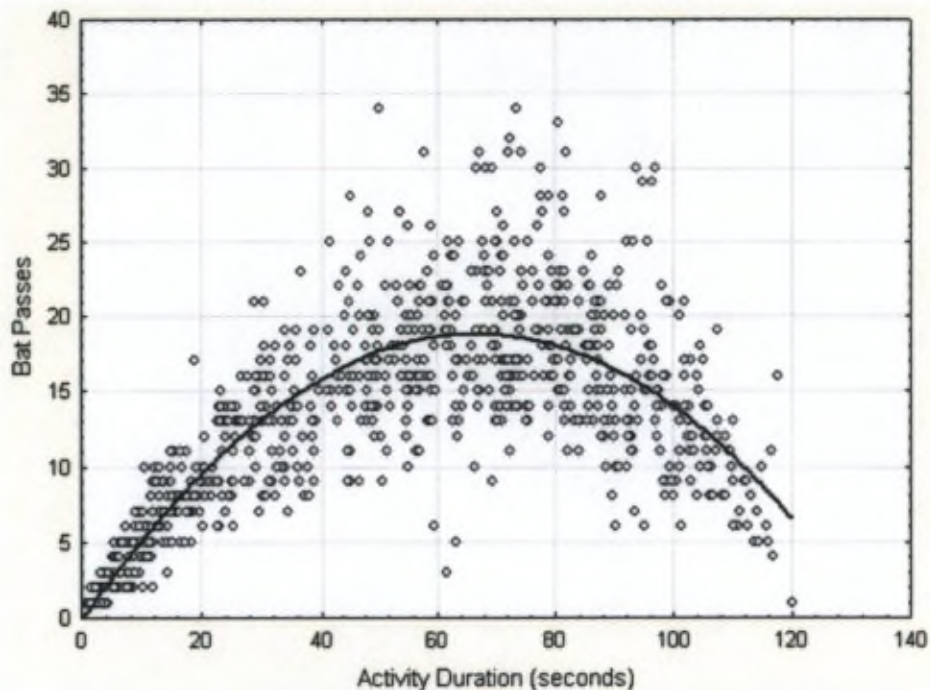
**Figure 1:** Frequency division sonogram. Black vertical lines show activity duration (AD) of one passage for the common pipistrelle, the Nathusius' pipistrelle, and the total activity duration for the general bat pass.

Two bat passes were separated by a silence or by a very low signal intensity of at least one second. AD was defined as the time (in seconds) during which bats were detected. It corresponds to the addition of the duration of every bat pass per unit of time (here, per two minutes). We compared the number of BP and the corresponding AD for each 2-min recording by using non linear regression.

## Results

Frequency division associated with time expansion allowed identification of seven bat species in the study area: *Pipistrellus pipistrellus* (Schreber 1774), *P. nathusii* (Keyserling and Blasius 1839), *P. pygmaeus* (Leach 1825), *Myotis daubentonii* (Kuhl 1817), *Nyctalus noctula* (Schreber 1774), *N. leisleri* (Kuhl 1817), and *Eptesicus serotinus* (Schreber 1774). Over the

whole sampling period, mean activity ( $\pm$ SD) around the pond reached  $12.9 \pm 7.1$  BP (range: 0 - 34) and  $51.9 \pm 33.9$  sec of AD per two minutes (range: 0 - 120 sec).



**Figure 2:** Relationship between general bat passes (BP) and activity duration (AD). Given is the general activity for the 7 bat species sampled in the study population (see Fig.1) ( $n = 867$ ; non linear regression:  $Y = -0.004 X^2 + 0.596 X - 0.130$ ).

There was a significant relationship between BP and AD during the two minutes sampling periods ( $r^2 = 0.67$ ,  $F = 974.5$ ,  $p < 0.001$ ; figure 2). This relationship followed a polynomial curve: as AD increased, BP initially increased, reached a maximum at 65 sec, and subsequently decreased. Thus, relatively low BP values (approximately less than 12 BP per two minutes) correspond to two extremely different AD values (on average, below 40 sec. and over 80 sec.). The same pattern occurred when considering the common pipistrelle ( $r^2 = 0.76$ ,  $F = 698.5$ ,  $p < 0.001$ ).

## Discussion

Our results show that BP counts are not reliable as estimator of bat activity in highly frequented habitats; a single, low BP value corresponds to two very different AD values. When overall activity is low, both estimators increase simultaneously and may be used reliably. However, with increasing activity, passage of several bats simultaneously or even successively results in the disappearance of breaks between passages, and AD becomes a more consistent estimator of bat activity than BP. The same pattern of the association between both estimators was obtained around other ponds and in open or semi-open environments, such as parks or forest edges (unpubl. data), indicating that it is reproducible in other habitats.

Bat activity has been mostly assessed by counting bat passes (e.g., Fenton *et al.*, 1973; Bell, 1980; Rydell *et al.*, 1994; Grindal, 1998). However, the definition of BP varies among studies, making comparisons difficult. Recently, several authors tried alternative methods

based on the use of Anabat-system or other frequency division detectors. For instance, Miller (2001) proposed an Activity Index based on the presence/absence of a species during a given period of time. According to Broders (2003), the ideal unit for activity estimations is a species-specific number of echolocation calls recorded in a standardised recording space per unit of time. He showed that the file size (bytes) of Anabat-recorded echolocation of the little brown bat *Myotis lucifugus* was closely associated with the number of calls. Our data show that measuring AD is also convenient for estimating bat activity when using Broder's (2003) definition. The first use of an AD index was proposed by Carmel and Safriel (1998), who introduced the "cumulative time-length" in bat activity monitoring. However, these authors carried out the species identification directly in the field, which explains their difficulties in estimating activity parameters for each species separately.

Although analysis in the laboratory is time consuming, semi-quantitative estimation of bat activity using AD based on frequency division recordings presents significant benefits. First, it can be automated and allows gathering data at multiple sites. Second, it enables the measure of activity durations for each species flying in the reception area of the microphone (or at least genera if these species are not easily identifiable thanks to frequency division). Third, even if some species are not discernible from others, frequency division is a convenient measure to assess the overall attraction of a particular site by bats and its evolution over time. High AD, as high bat passes frequency, does not necessarily mean more individuals flying in front of the receptor but indicates that the place is more rewarding. Our method is thus convenient for estimating the efficiency of management actions devoted to improve habitat quality for bats. Experiments in flight cages investigating the association between our estimates of bat activity and the absolute number of flying bats await further study.

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## References

- Anderson, M.E. & P.A. Racey (1991): Feeding behaviour of captive brown long-eared bats, *Plecotus auritus*. - *Austral. Zool.* **30**(4): 467-479.
- Bell, G.P. (1980): Habitat use and response to patches of prey by desert insectivorous bats. - *Can. J. Zool.* **58**: 1876-1883.
- Brinkmann, R. & H.J.G.A. Limpens (1999): The role of bats in landscape planning. In *Proceedings of the third European Bat Detector Workshop*. Eds Harbusch, C. & J., Pir. Ministère de la Culture. Travaux scientifiques du musée national d'histoire naturelle de Luxembourg, **31**: 119-136
- Broders, H.G. (2003): Another quantitative measure of bat activity and sampling intensity considerations for the design of ultrasonic monitoring studies. - *Acta Chiropterol.* **5**(2): 235-241.
- Carmel, Y. & U. Safriel (1998): Habitat use by bats in a Mediterranean ecosystem in Israel-conservation implications. - *Biol. Cons.* **84**(3): 245-250.
- Daan, S. (1970): Photographic recording of natural activity in hibernating bats. - *Bijdr. tot de Dierk.* **40**: 13-16.
- Entwistle, A.C., P.A. Racey, & J.R. Speakman (1997): Roost selection by the brown long-eared bat *Plecotus auritus*. - *J. App. Ecol.* **34**: 399-408.
- Fenton, M.B., S.L. Jacobson & R.N. Stone (1973): An automatic ultrasonic sensing system for monitoring the activity of some bats. - *Can. J. Zool.* **51**: 291-299.
- Gaisler J. (1989): The r - K selection model and life-history strategy in bats. in *European Bat Research 1987*. Hanák, Horáček & Gaisler (Eds.) Charles Univ. Press, Prague. pp. 117-124.
- Grindal, S.D. (1998): Habitat Use by Bats, *Myotis* spp., in Western Newfoundland. - *Can. Field-Nat* **113**(2): 258-263.
- Grindal, S.D. & R.M. Brigham (1999): Impacts of forest harvesting on habitat use by foraging insectivorous bats at different spatial scales. - *Ecoscience* **6**(1): 25-34.
- Hayes, J.P. (1997): Temporal variation in activity of bats and the design of echolocation-monitoring studies. - *J. Mamm.* **78**(2): 514-524.
- Horáček, I. (1985): Population ecology of *Myotis myotis* in central Bohemia (Mammalia: Chiroptera). - *Acta Univ. Carolin - Biol.*, 1981: 161-267 VIII.
- Kretschmer, M. (2001): Untersuchungen zur Biologie und Nahrungsökologie des Wasserfledermaus, *Myotis daubentonii* (Kuhl, 1817), in Nordbaden. - *Nyctalus* **8**(1): 28-48.
- McAney, C.M. & J.S. Fairley (1988): Habitat preference and overnight and seasonal variation in the foraging activity of lesser horseshoe bats. - *Acta Theriol.* **33**(28): 393-402.
- Medellin, R.A., M. Equihua & M.A. Amin (2000): Bat diversity and abundance as indicators of disturbance in Neotropical rainforests. - *Cons. Biol.* **14**(6): 1666-1675.
- Miller, B.W. (2001): A method for determining relative activity of free flying bats using a new activity index for acoustic monitoring. - *Acta Chiropterol.* **3**: 93-105.
- Negraeff, O. E. & R. M. Brigham (1995): The influence of moonlight on the activity of little brown bats (*Myotis lucifugus*). - *Zeitsch. Säugetierk.* **60**: 330-336.
- O'Farrell, M.J. (1998): A passive monitoring system for Anabat II using a laptop computer. - *Bat Res. News* **39**: 147-150.
- O'Farrell, M.J. & W.G. Bradley (1970): Activity patterns of bats over a desert spring. - *J. Mamm.* **51**(1): 18-26.
- Park, K.J., E. Masters & J.D. Altringham (1998): Social structure of three sympatric bat species (Vespertilionidae). - *J. Zool., Lond.* **244**: 379-389.
- Racey, P. A. & S. Swift (1985): Feeding ecology of *Pipistrellus pipistrellus* (Chiroptera: Vespertilionidae) during pregnancy and lactation. I. Foraging behaviour. - *J. Anim. Ecol.* **54**: 205-215.
- Rydell, J., A. Bushby, C.C. Cosgrove & P.A. Racey (1994): Habitat use by bats along rivers in north east Scotland. - *Folia Zool.* **43**(4): 417-424.

- Vaughan, N., G. Jones and S. Harris (1997): Habitat use by bats (Chiroptera) assessed by means of a broad-band acoustic method. - *J. App. Ecol.* **34**: 716-730.
- Walsh, A. L. & S. Harris (1996): Factors determining the abundance of vespertilionid bats in Britain: geographical, land class and local habitat relationships. - *J. App. Ecol.* **33**: 519-529.
- Waters, D., Jones, G. & M. Furlong (1999): Foraging ecology of Leisler's bat (Nyctalus leisleri) at two sites in southern Britain. - *J. Zool., Lond.* **249**: 173-180.

## Temporal variation in flight activity, foraging activity and social interactions by bats around a sub-urban pond

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### Abstract

We investigated both overnight and seasonal activity patterns of a bat assemblage around a sub-urban pond between April and September 2003. Among the seven species identified, three (*Pipistrellus pipistrellus*, *P. nathusii* and *Myotis daubentonii*) showed the highest level of occurrence and/or flight activity. Flight activity of *P. pipistrellus* greatly varied over time, with the highest levels occurring just after sunset. In *P. nathusii* and *M. daubentonii*, activity remained constant for at least the first hours after sunset. Moreover, flight and foraging activities changed with the reproductive period. Whereas flight activity increased from pregnancy to post-lactation in *Pipistrellus*, it decreased during post-lactation in *M. daubentonii*. We demonstrated an increase in vocalisation rate of social calls in *P. pipistrellus* during the first hours of the night but also markedly during the post-lactation period. These different results are discussed in relation to the species' ecology and behaviour.

**Key words:** Chiroptera, flight activity, foraging activity, social calls

### Samenvatting

Ons onderzoek spitte zich toe op nacht- en seizoensactiviteit van een vleermuispopulatie rond een voorstadvijver tussen april en september 2003. Van zeven gedetermineerde soorten, waren er drie (*Pipistrellus pipistrellus*, *P. nathusii* en *Myotis daubentonii*) dominant wat betreft voorkomen en/of vliegactiviteit. De vliegactiviteit van *P. pipistrellus* fluctueerde sterk in tijd, met een piek net na zonsondergang. De activiteit van *P. nathusii* en *M. daubentonii*, bleef vrij constant gedurende minstens twee uur na zonsondergang. De vlieg- en jachtactiviteit varieerden met het voortplantingsseizoen. Waar de vliegactiviteit toenam van zwangerschap tot de post-lactatieperiode bij het genus *Pipistrellus*, nam deze af gedurende de post-lactatie bij *M. daubentonii*. Een toename van sociale roepen werd aangetoond bij *P. pipistrellus* gedurende de eerste uren van de nacht maar ook tijdens de post-lactatieperiode. Deze resultaten worden besproken in relatie met de ecologie en het gedrag van de soorten.

**Key words:** Chiroptera, vlieg activiteit, jacht activiteit, sociale roepen

## Introduction

Unlike tropical bats, which can be separated into guilds based on diet (Aguirre 2002), all European bat species are insectivorous, although some representatives of the genus *Myotis* have found to be partially feeding on fish (Levin et al. 2006). In temperate regions, insect eating bats face ecological constraints such as food restrictions due to winter and associated cold temperatures. Because most temperate bats hibernate, time devoted to breeding and fat accumulation is limited (Ransome 1990). Monitoring bat activity during the active season can thus provide insight into bat requirements during this critical period. For insectivorous species, activity patterns, *i.e.* changes in flight or foraging activities, might vary on a daily or seasonal basis in response to many factors: insect availability (Anthony et al. 1981, De Jong & Ahlén 1991) or weather conditions (Avery 1985, Ruedi 1993, Verboom & Spoelstra 1999). For example, 'aerial hawking' species depend on the evening peak in the abundance of flying insects, while 'gleaning' species can potentially emerge later from their roost as they primarily feed on diurnal perched insects or moths that remain available throughout the night (Entwistle et al. 1996). Sex, age and reproductive status also influence activity patterns, as they affect energy demand (Swift 1980, Catto et al. 1995, Wilkinson & Barclay 1997).

Few studies have investigated activity patterns of bat assemblages over the night and the season (Gaisler et al. 1998, Bartonička & Zúkal 2003), and they generally focused on species distribution in different habitats. Analyses of temporal variations of bat communities in a single site are even scarcer (O'Farrell & Bradley 1970, Bartonička 2002). Riparian habitats are important centres for bat activity (Grindal et al. 1999). Flying insects emerging from the surface of water bodies likely represent a plentiful and predictable supply of prey; calm water provide suitable drinking sites (e.g., Geggie & Fenton 1985, Brigham et al. 1992, Rautenbach et al. 1996). In addition, these highly frequented habitats may be chosen as mating grounds by males, to increase their chance to find females (Gerell & Lundberg 1985). Riparian environments are therefore particularly interesting for investigating the coexistence of bat species throughout summer in temperate regions.

In this study, we investigated both overnight and seasonal activity patterns of a bat assemblage around a sub-urban pond based on data collected in a standardised way. We determined the occurrence, flying and foraging activity patterns for different bat species identified. Because these parameters may be affected by the reproductive status (Audet 1990, Barclay 1991), our data were analysed with regard to three reproductive periods: pregnancy, lactation and post-lactation. We also studied whether emission of social calls by common pipistrelles does vary after sunset and throughout the activity season.

## Material & Methods

### *Study area and sampling*

Our study was conducted from April to September 2003 around the Silex pond, located in the south-east of Brussels, Belgium. This 1 ha pond stands 100 m from the nearest house and 150 m from the nearest illuminated road. It is surrounded by the Forêt de Soignes on one side and

by more open habitats on the other side: wet meadows, a pasture with a few hedgerows, and a few apple trees.

We recorded bat activity over 50 nights ( $\bar{X} \pm \text{SD}$ :  $8.7 \pm 2.7$  nights per month). Recordings were performed during the first hours following sunset, which corresponds to the time when bats display the highest activity (Anthony & Kunz, 1977). Each night, bat activity was sampled 45, 90, and 135 minutes after sunset referred to as Round 1 (R1), Round 2 (R2) and Round 3 (R3), respectively. For each of these nightly sampling rounds, two-minute recordings were performed at random at six contact points located on the bank of the pond and separated by at least 50 m from each other. Overall, our survey represented 870 two-minute recordings. Recording was performed during warm ( $t^{\circ} > 10^{\circ}\text{C}$  at starting point), calm and dry nights to minimize the influence of temperature, airstreams and rain on bat activity.

To determine how reproductive status affects activity patterns, data were separated into three periods: April to Mid-June, Mid-June to end of July, and August-September (18, 14, and 18 recording nights respectively). These periods correspond to distinct phases of the reproductive cycle of most common European bat species: pregnancy, lactation and post-lactation respectively (Swift 1980, Bartonicka & Zukal 2003). Isolated captures by mist-netting of Daubenton's bats over the pond confirmed that the selected periods were consistent with reproductive status of females.

#### *Recording and identification*

Bat activity was monitored with a Pettersson D-980 (Pettersson Elektronik AB, Sweden) and signals were stored on a DAT recorder (Sony). Time expansion was chosen as the first recording mode, as it provides the most reliable species identification (Barataud 1996). Frequency division (FD, division factor 10) was selected as the second recording mode because of its broadband and real-time recording properties (Barataud 1996). FD recordings were used to measure bat activity patterns. Recordings were analysed with Bat Sound software (Pettersson Elektronik AB, Sweden) using spectrogram analyses. Parameters used for species identification were the shape of the signal, maximum energy peak frequency, and bandwidth (Barataud 1996).

#### *Occurrence, flight and foraging activities*

Occurrence is defined as the percentage of recording days a given species was found over the pond. For each species, flight activity (FA) was estimated by measuring activity duration, calculated as the accumulated duration of every bat pass per unit of time (*i.e.*, during the two-minute recording time). Foraging activity was assessed by counting the number of feeding buzzes per unit of time. Feeding buzzes were recognised by high pulse repetition rates associated with attacks on prey (Griffin 1958). Capture time was assessed by estimating the number of seconds between two foraging attempts, *i.e.*, by dividing the sum of flight activity levels by the sum of the feeding buzzes recorded during the same laps of time.

### Emission of social calls

Social calls are signals with low-frequency components that may occur between echolocation calls and which have communication purposes (Fenton 2003). Because the common pipistrelle *Pipistrellus pipistrellus* was the most abundant in the study area, social calls were analysed for this species only. Emission of social calls was assessed by counting the number of those vocalisations registered per two minute interval, through simultaneous recordings in time expansion and frequency division.

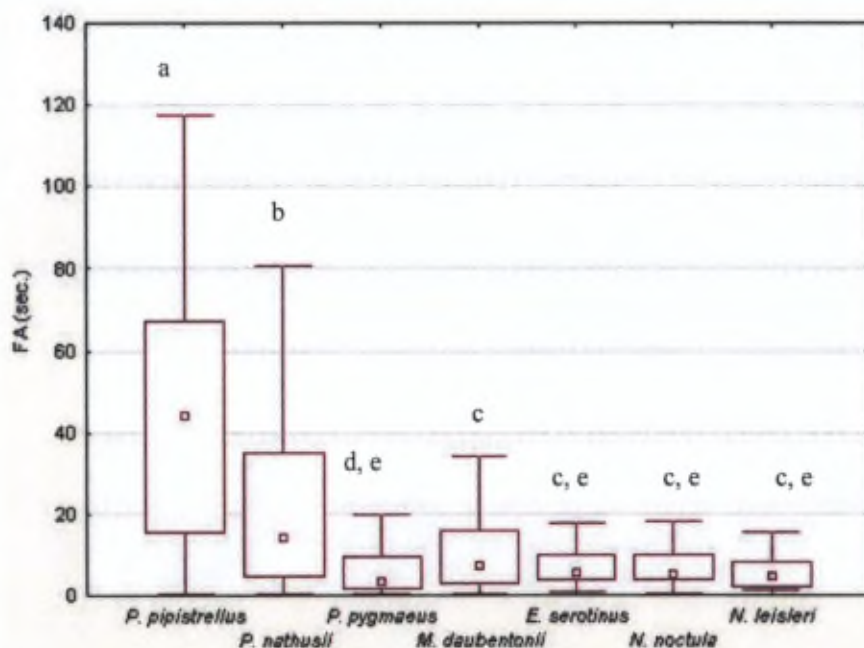
### Statistical analysis

Data were compared by using nonparametric Kruskal-Wallis, Mann-Whitney and Dunn's post hoc tests with Statistica 6.0. For activity level comparisons, records in which we did not register bats were excluded from the analyses to move the median value from zero and obtain clearer graphs.

## Results

### Occurrence, overall flight activity and foraging rate

Recordings allowed to identify seven species (figure 1): common pipistrelle *Pipistrellus pipistrellus* (Schreber, 1774), Nathusius' pipistrelle *P. nathusii* Keyserling & Blasius, 1839, soprano pipistrelle *P. pygmaeus* (Leach, 1825), Daubenton's bat *Myotis daubentonii* (Kuhl, 1817), noctule *Nyctalus noctula* (Schreber, 1774), Leisler's bat *N. leisleri* (Kuhl, 1817) and serotine *Eptesicus serotinus* (Schreber, 1774).



**Figure 1:** Overall flight activity (FA) (medians, percentiles 25%, 75%, maximum and minimum), measured as the duration of bat passes per two minute periods, for the seven species identified around the pond. Treatments with the same lowercase letters did not differ significantly (Dunn's tests,  $P < 0.05$ ).

Flight activity levels differed significantly between species (Kruskal-Wallis test,  $H=517.2$ ,  $P<0.001$ ; figure 1). Overall activity was higher for *P. pipistrellus* ( $P<0.001$ ); this species was also identified in 100% of the nightly samplings. *P. nathusii* was more active than *M. daubentonii* over the pond ( $P<0.001$ ), primarily because of the high flight activity of *P. nathusii* during post-lactation (see below). However, whereas *P. nathusii* was identified in 76% of our recording nights, this value reached 96% for *M. daubentonii* indicating that this species is a regular visitor in our study area. *P. pygmaeus*, *E. serotinus*, *N. leisleri*, and *N. noctula* did not differ significantly in their activity levels ( $P>0.05$ ) and were excluded from further analyses due to their low activity level and/or occurrence.

Capture time also varied according to the species considered ( $H=18.38$ ,  $P<0.001$ ). *M. daubentonii* captured insects more rapidly, feeding attempts occurring approximately every six seconds, than *P. pipistrellus* and *P. nathusii* that captured insects each 13 and 24 seconds respectively ( $P<0.05$ ; table 1).

#### *Flight and foraging activities after sunset during each reproductive period*

Flight activity of *P. pipistrellus* decreased after sunset for each reproductive period (**P** (pregnancy):  $H=19.8$ ,  $P<0.001$ ; **L** (lactation):  $H=32.5$ ,  $P<0.001$ ; **PL** (post-lactation):  $H=61.0$ ,  $P<0.001$ ), with activity on round R1 being significantly higher than on R3 ( $P<0.05$ ). By contrast, both *M. daubentonii* and *P. nathusii* exhibited a stable activity for each round, independently to the period considered (**P**:  $H=0.6$ ,  $P=0.72$ ; **L**:  $H=0.6$ ,  $P=0.76$ ; **PL**:  $H=5.2$ ,  $P=0.07$ ; **P**:  $H=2.1$ ,  $P=0.34$ ; **L**:  $H=1.7$ ,  $P=0.41$ ; **PL**:  $H=0.4$ ,  $P=0.83$  respectively, table 1).

**Table 1:** Overall flight and foraging activity medians (in brackets) and capture time (in italic) in each Round and reproductive period for *P. pipistrellus*, *P. nathusii* and *M. daubentonii*

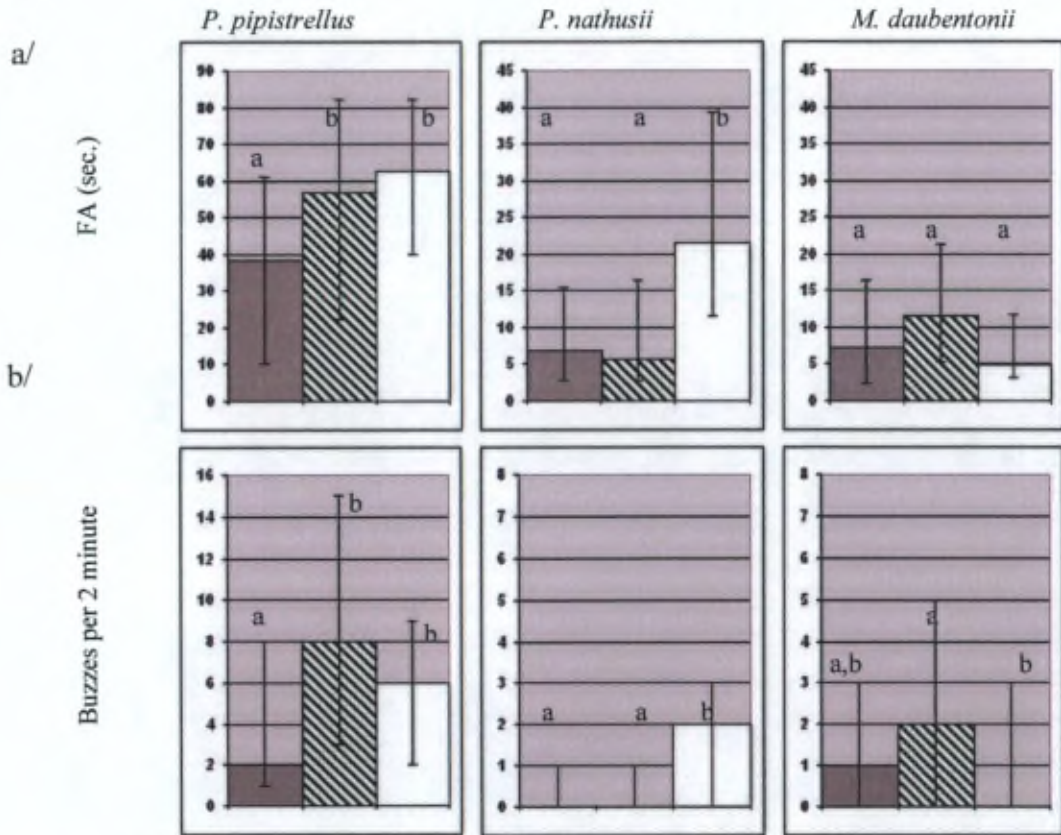
	Pregnancy			Lactation			Post-lactation		
	R1	R2	R3	R1	R2	R3	R1	R2	R3
<i>P. pipistrellus</i>	38.4	18.0	17.4	56.7	53.0	37.6	62.7	49.6	42.9
	(2)	(1)	(1)	(8)	(5)	(3)	(6)	(2)	(1)
	<i>7.8</i>	<i>11.3</i>	<i>15.2</i>	<i>6.0</i>	<i>9.4</i>	<i>11.3</i>	<i>10.2</i>	<i>20.2</i>	<i>25.0</i>
<i>P. nathusii</i>	6.9	5.5	4.0	5.6	10.2	8.2	21.6	25.1	26.9
	(0)	(0)	(0)	(0)	(0)	(0)	(2)	(0)	(0)
	<i>15.3</i>	<i>39.2</i>	<i>27.6</i>	<i>18.2</i>	<i>13.1</i>	<i>16.1</i>	<i>13.2</i>	<i>29.8</i>	<i>49.6</i>
<i>M. daubentonii</i>	7.3	6.8	5.9	11.5	7.9	9.0	4.8	8.0	7.3
	(1)	(1)	(1)	(2)	(1)	(1)	(0)	(1)	(0)
	<i>4.8</i>	<i>5.8</i>	<i>5.3</i>	<i>4.7</i>	<i>6.6</i>	<i>7.7</i>	<i>6.1</i>	<i>8.8</i>	<i>7.2</i>

Consistent with flight activities, there was a significant difference in the number of feeding buzzes recorded between the three rounds and for each period in *P. pipistrellus* (**P**:  $H=19.8$ ,  $P<0.001$ ; **L**:  $H=32.5$ ,  $P<0.001$ ; **PL**:  $H=61.0$ ,  $P<0.001$ ; table 1). This species showed a decrease in foraging activity between R1 and R3 for each reproductive period considered ( $P<0.01$ ). In *P. nathusii*, foraging activity after sunset did not vary during pregnancy and lactation (**P**:  $H=1.1$ ,  $P=0.57$ ; **L**:  $H=1.3$ ,  $P=0.522$ ; table 1); more feeding buzzes were however recorded in R1 during post-lactation ( $H=22.6$ ,  $P<0.001$ ; Dunn's test,  $P<0.01$ ). Foraging activity remained constant during the three nightly intervals and for all

three periods considered (P:  $H= 1.6$ ,  $P= 0.45$ ; L:  $H= 5.3$ ,  $P= 0.071$ ; PL:  $H= 0.7$ ,  $P= 0.69$ ) in *M. daubentonii*, with medians being generally higher than in *P. nathusii* (table 1).

### Seasonal variations in flight and foraging activities

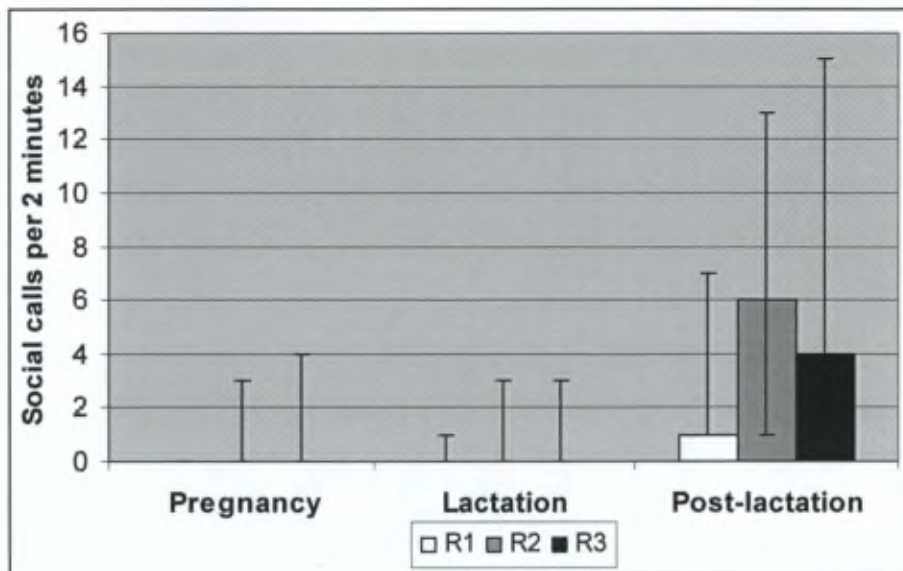
Comparisons of flight and foraging activities between the periods of pregnancy, lactation and post-lactation were based on the data from round R1. As shown above, recordings during R1 revealed the highest overall activity values. Moreover, differences in activity between R1, R2 and R3 were independent of the season. Flight activity varied significantly with the reproductive period for the three species studied ( $H= 25.9$ ,  $P< 0.001$  for *P. pipistrellus*;  $H= 24.5$ ,  $P< 0.001$  for *P. nathusii* and  $H= 6.6$ ,  $P< 0.04$  for *M. daubentonii*; figure 2a). In *P. pipistrellus*, flight activity was significantly lower during pregnancy than during lactation and post-lactation ( $P< 0.01$ ). *P. nathusii* was more active during post-lactation than during the two other reproductive periods ( $P< 0.01$ ). In *M. daubentonii*, a lower but non significant flight activity occurred during post-lactation ( $P> 0.05$ ). Foraging activity levels followed the same trend as flight activity ( $H= 24.6$ ,  $P< 0.001$ ; *P. nathusii*  $H= 17.9$ ,  $P< 0.001$ ; *M. daubentonii*  $H= 9.5$ ,  $P< 0.009$ ; figure 2b). In *P. pipistrellus* and *M. daubentonii*, foraging activity was, however, significantly higher during lactation than during pregnancy and post-lactation ( $P< 0.01$ ).



**Figure 2:** Flight activity (FA) and foraging activity (buzzes) (median, percentile 25% and 75%) of *P. pipistrellus*, *P. nathusii* and *M. daubentonii* during R1, according to three reproductive periods: pregnancy, lactation and post-lactation (respectively grey, striped and white bars). Treatments with the same lowercase letters did not differed significantly (Dunn's tests,  $P<0.05$ ).

### Emission of social calls

The number of social calls emitted by *P. pipistrellus* varied significantly between the three nightly sampling rounds (R1, R2 and R3) during the periods of pregnancy ( $H= 7.9$ ,  $P< 0.02$ ) and post-lactation ( $H= 16.0$ ,  $P< 0.001$ ). In both periods bats produced less social calls during R1 than R2 and R3 ( $P< 0.05$ ). The number of social calls produced also varied between reproductive periods ( $H= 121.1$ ,  $P< 0.001$ ), with higher numbers recorded during post-lactation ( $P< 0.001$ ) (figure 3).



**Figure 3:** Social calls sampled per round (median, percentile 25% and 75%) as a function of the reproductive period in *P. pipistrellus*.

### Discussion

The genus *Pipistrellus* is represented by three species in our study area, *P. pipistrellus*, *P. nathusii*, and *P. pygmaeus*. Activity levels, and presumably total numbers of individuals of each species over the pond, are however very different. *P. pipistrellus* was recorded persistently around the pond and our estimates of activity levels also show that it is the most dominant species. *P. nathusii* is the second most abundant species. This result must be considered against the background of a differential presence of the sexes for the two species in spring and summer. In Belgium, groups of *P. pipistrellus* are composed of both sexes whereas groups of *P. nathusii* in spring and at early summer consist mainly of males. At this period of the year, females of *P. nathusii* indeed move to the eastern part of their range and join harems on their migration routes to hibernation sites at the end of summer (Lina 1990; Kapteyn & Lina 1994). *P. pygmaeus* occurs less regularly and activity levels remain very low. This species has been described for the first time in the Brussels Region in 2002 and is not widespread in Belgium (Kapfer et al., 2007). *M. daubentonii* was also commonly recorded over the pond and made capture attempts very often, which demonstrates that the species is particularly efficient in catching prey in this environment. Finally, *E. serotinus*, *N. noctula*, and *N. leisleri* are recorded with a relatively low frequency and activity levels. The results

suggest that these species used the area as a feeding ground occasionally and for brief periods only.

Our data also show a decrease in flight and foraging activities throughout the hours following sunset for *P. pipistrellus*. This might stem from the quick drop in the number of flying insects due to the rapid decline of temperature after sunset (Anthony & Kunz 1977). When insect density rapidly decreases, aerial hawking bats stop hunting as the cost associated with prey detection may become too high (Rydell et al. 1996). Whether decrease in activity recorded over the night results from bats returning to their roost with filled stomach or from animals leaving the pond to move to other more rewarding hunting areas remains however unknown. Flight and foraging activities in *M. daubentonii* remain relatively constant for at least the first hours after sunset. Similar data were documented for this species in other study areas (i.e., Dietz, 1993; Bartonicka & Zukal 2003). Daubenton's bats usually fly 10 – 30 cm above the water surface and prey on insects emerging from or standing on the water (Jones & Rayner, 1988), or occasionally on small fishes (Brosset & Delmare 1966, Siemers et al. 2001). Emergence of aquatic insects follows a diurnal rhythm closely linked with illumination levels and water temperature, but it does not correlate with air temperature (Morgan & Waddell 1961). Our results are consistent with this hypothesis since *M. daubentonii* continues to hunt with a constant and high capture rate, when *Pipistrellus* species hunt less efficiently.

Variation in flight activity throughout summer may be explained by bats hunting more or less over the pond according to their biological requirements (e.g., induced by the endogen cycle), or by bats coming to or leaving the area for more rewarding places. Our study area was not located in a confined space. Previous studies (unpublished data) suggest that food is not a limited resource in that area, at least for the time we conducted the experiments. Moreover, Kapfer et al. (*in press*) recently showed recently that female and juvenile *M. daubentonii* are faithful to the same hunting places. This strongly supports that fluctuations in flight activity are associated with the reproductive periods. Indeed, arrival of juvenile *P. pipistrellus* that start to fly at the end of June, beginning of July (Swift 1980; Whitaker 1998) and the higher activity of males during post-lactation (Gerell-Lundberg & Gerell 1994) may explain the increase in activity around the pond during lactation and post-lactation. Our results reveal a decrease in foraging activity associated with an increase in flight activity during post-lactation. This is consistent with the mating system of *Pipistrellus*, best characterised as a resource defence polygyny with males defending the roost where they constitute harems (Gerell-Lundberg & Gerell 1994). Males probably reduce foraging activity and spend considerable time flying in the immediate vicinity of their day roosts (Gerell & Lundberg 1985, Lundberg & Gerell 1986). As mentioned above, flight activity in *P. nathusii* is relatively low from spring to mid-summer, but increases during the post-lactation period, which can be related primarily to a higher flying activity of males but also to an influx in additional individuals (e.g. migrating females) visiting the area (Kapteyn & Lina 1994, Peterson 2004). Low flight activity of *M. daubentonii* recorded in August and September might result from change in activity patterns, with males resting in the day roost to establish mating roosts (Encarnação et al. 2004). This period also corresponds to the timing of

movement towards winter roosts (*i.e.*, caves, forts) (Klawitter 1980, Lesiński 1986, Dietz & Fitzenräuter 1996).

Our data suggest that the emission of social calls by *P. pipistrellus* varies in relation to the course of the night and the reproductive period. Emission of social calls increased during the first hours after sunset, probably resulting from dropping of insect availability, and thus increasing a territorial behaviour. By using play-back experiments, Barlow & Jones (1997) showed that social calls are used to warn off and drive away other pipistrelles of the same species when insect densities decrease. These advertisements are often joined with chases. Our investigations also reveal that the species emit more social calls during post-lactation than the two former reproductive periods. At the end of summer, males produce "songflights" supposedly to remove male intruders but also to attract females to their roost (Gerell-Lundberg & Gerell 1994). Preliminary works suggest that social calls of pipistrelle species emitted before and during the reproductive periods might have different structures (De Smet 2004). Further studies should be carried out to test this hypothesis and to investigate if both sexes emit social calls and/or if the message associated with the social call varies according to the reproductive status, the emission rate or associated behaviours.

The general picture on the behaviour of bat assemblages over a pond is shared by many field workers (*pers. com.*). However, to the best of our knowledge, field experiments on bat temporal flight and foraging activities performed in a standardised manner are lacking. The present study confirms that urban ponds are particular habitats for bats and may show a high species richness. Apart from being an important drinking site, such ponds are also used as foraging and mating ground, in relation to the reproductive period and the species considered.

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## References

- Aguirre, L. 2002. Resource partitioning and community structure of bats (Chiroptera) in a neotropical savanna. PhD thesis, University of Antwerp, Belgium.
- Anthony, E. L. P. & T. H. Kunz 1977. Feeding strategies of the little brown bat, *Myotis lucifugus*, in southern New Hampshire. *Ecology* 58: 775-786.
- Anthony, E. L. P., M. H. Stack & T. H. Kunz 1981. Night roosting and the Nocturnal Time Budget of the Little Brown bat, *Myotis lucifugus*: Effects of reproductive Status, Prey Density and environmental Conditions. *Oecologia* 51: 151-156.
- Audet, D. 1990. Foraging behavior and habitat use by a gleaning bat *Myotis myotis* (Chiroptera: Vespertilionidae). *Journal of Mammalogy* 71 (3): 420-427.
- Avery, M. I. 1985. Winter activity of pipistrelle bats. *Journal of Animal Ecology*, 54: 721-738.
- Barataud, M. 1996. Balades dans l'in audible. Edition Sittelle, France.
- Barclay, R. M. R. 1991. Population structure of temperate zone insectivorous bats in relation to foraging behaviour and energy demand. *Journal of Animal Ecology* 60: 165-178.
- Barlow, K. E. & G. Jones 1997. Function of pipistrelle social calls: field data and playback experiment. *Animal Behaviour* 53: 991-999.
- Bartonička, T. 2002. Habitat use of four bat species in Jablonec n. N. revealed by bat detector. *Przyroda Sudetów Zachodnich*, Suppl. 2: 79-87.
- Bartonička, T. & J. Zukal 2003. Flight activity and habitat use of four bat species in a small town revealed by bat detectors. *Folia Zoologica* 52 (2): 155-166.
- Brigham, R. M., H. D. J. N. Aldridge & R. L. Mackey 1992. Variation in habitat use and prey selection by yuma bats, *Myotis yumanensis*. *Journal of Mammalogy* 73 (3): 640-645.
- Brosset, A., & D. Delmare 1966. Le régime alimentaire du vespertilion de daubenton *Myotis daubentonii*. *Mammalia* 30: 247-251.
- Catto, C. M. C., P. A. Racey & P. J. Stephenson 1995. Activity patterns of the serotine bat (*Eptesicus serotinus*) at a roost in southern England. *Journal of Zoology*, London 235: 635-644.
- De Jong, J. & I. Ahlén 1991. Factors affecting the distribution pattern of bats in Uppland, central Sweden. *Holarctic Ecology*, 14: 92-96.
- De Smet, P. 2004. Contribution à l'étude de la communication acoustique chez deux espèces de pipistrelles: *Pipistrellus pipistrellus* et *Pipistrellus nathusius*. MSc thesis. Université libre de Bruxelles, Belgium.
- Dietz, M. & B. Fitzenrütter 1996. Zur Flugroutennutzung einer Wasserfledermauspopulation (*Myotis daubentonii* Kuhl, 1819) im Stadtbereich von Giessen. *Säugetierkundliche Informationen* 20 (4): 107-116.
- Dietz, M. 1993. Beobachtungen zur Lebensraumnutzung der Wasserfledermaus (*Myotis daubentonii* KUHL, 1819) in einem urbanen Untersuchungsgebiet in Mittelhessen. Thesis, Justus-Liebig-Universität Gießen, Germany.
- Encarnação, J. A., M. Dietz & U. Kierdorf 2004. Reproductive condition and activity pattern of male Daubenton's bats (*Myotis daubentonii*) in the summer habitat. *Mammalian biology* 69 (3): 163-172.
- Entwistle, A. C., P. A. Racey & J. R. Speakman 1996. Habitat exploitation by a gleaner bat, *Plecotus auritus*. *Philosophical Transactions Royal Society London B* 351: 921-931.
- Fenton M. B. 2003. Eavesdropping on the echolocation and social calls of bats. *Mammal Review* 33 (3): 193-204.
- Gaisler, J., J. Zukal, Z. Řehák & M. Homolka 1998. Habitat preference and flight activity of bats in a city. *Journal of Zoology*, London 244 (3): 439-445.
- Geggie, J. F. & M. B. Fenton 1985. A comparison of foraging by *Eptesicus fuscus* (Chiroptera: Vespertilionidae) in urban and rural environments. *Canadian Journal of Zoology* 63: 263-267.
- Gerell, R. & K. Lundberg 1985. Social organization in the bat *Pipistrellus pipistrellus*. *Behavioral Ecology Sociobiology* 16 (2): 177-184.

- Gerell-Lundberg, K. & R. Gerell 1994. The mating behaviour of the Pipistrelle and the Nathusius' Pipistrelle (Chiroptera) - A comparison. *Folia Zoologica* 43 (4): 315-324.
- Griffin, D. R. 1958. Listening in the dark. Yale University Press, New Haven. Connecticut, USA
- Grindal, S. D., J. L. Morissette & R. M. Brigham 1999. Concentration of bat activity in riparian habitats over an elevational gradient. *Canadian Journal of Zoology* 77: 972-977.
- Jones, G. & J. M. V. Rayner 1988. Flight performance, foraging tactics and echolocation in free-living Daubenton's bats *Myotis daubentonii* (Chiroptera: Vespertilionidae). *Journal of Zoology*, London 215: 113-132.
- Kapfer G., T., Rigot, Holsbeek, L. & S. Aron. *in press*. Roost and hunting site fidelity of female and juvenile Daubenton's bat *Myotis daubentonii* (Kuhl, 1817) (Chiroptera: Vespertilionidae). *Mammalian Biology*
- Kapfer G., M. Van de Sijpe, B. Van der Wijden, W. Willems, B. Vandendriessche & B. Mulken, 2007. First recordings of the soprano pipistrelle *Pipistrellus pygmaeus* (Leach, 1825) in Belgium. *Belgian Journal of Zoology*, 137: 111-113.
- Kapteyn, K. & P. H. C. Lina. 1994. Eerste vondst van een kraamkolonie van Nathusius dwergvleermuis *Pipistrellus nathusii* in Nederland. *Lutra* 37 (2): 106-109.
- Klawitter, J. 1980. Spätsommerliche Einflüge und Überwinterungsbeginn der Wasserfledermaus (*Myotis daubentonii*) in der Spandauer Zitadelle. *Nyctalus* (N.F.) 227 - 234.
- Lesiński, G. 1986. Ecology of bats hibernating underground in central Poland. *Acta Theriologica* 31: 507-521.
- Levin, E., A. Barnea, Y. Yovel & Y. Yom-Tov 2006. Have introduced fish initiated piscivory among the long-fingered bat? *Mammalian biology* 71 (3): 139-143.
- Lina, P. H. C. 1990. Verre terugmeldingen van Nathusius' dwergvleermuisen «*Pipistrellus nathusii*» gevonden of geringd in Nederland. *Lutra* 33 (1): 45-48.
- Lundberg, K. & R. Gerell 1986. Territorial advertisement and mate attraction in the bat *Pipistrellus pipistrellus*. *Ethology* 71: 115-124
- Morgan, N. C. & A. B. Waddell 1961. Diurnal variation in the emergence of some aquatic insects. *Transactions of the Royal Entomological Society*, London 113: 123-137.
- O'Farrell, M. J. & W. G. Bradley 1970. Activity patterns of bats over a desert spring. *Journal of Mammalogy* 51 (1): 18-26.
- Peterson G. 2004. Seasonal migration of north-eastern populations of Nathusius' bat *Pipistrellus nathusii* (Chiroptera). *Myotis* 40-41: 29-56.
- Ransome, R. D. 1990. The Natural History of Hibernating Bats. Christopher Helm. London, UK.
- Rautenbach, I. L., M. B. Fenton & M. J. Whiting 1996. Bats in riverine forests and woodlands: a latitudinal transect in southern Africa. *Canadian Journal of Zoology* 74: 312-322.
- Ruedi, M. 1993. Variations de la fréquentation de gîtes nocturnes par *Myotis daubentonii* pendant la période de reproduction. Rôle des précipitations et de la température. *Mammalia* 57 (3): 307-315.
- Rydell, J., A. Entwistle & P. A. Racey 1996. Timing of foraging flights of three species of bats in relation to insect activity and predation risk. *Oikos* 76 (2): 243-252.
- Siemers, B. M., C. Dietz, D. Nill, & H.-U. Schnitzler 2001. *Myotis daubentonii* is able to catch small fish. *Acta Chiropterologica* 3 (1): 71-75.
- Swift, S. M. S. 1980. Activity patterns of Pipistrelle bats (*Pipistrellus pipistrellus*) in north-east Scotland. *Journal of Zoology*, London 190: 285-295.
- Verboom, B. & K. Spoelstra 1999. Effects of food abundance and wind on the use of tree lines by an insectivorous bat, *Pipistrellus pipistrellus*. *Canadian Journal of Zoology* 77: 1393-1401.
- Whitaker, J. O., Jr. 1998. Life history and roost switching in six summer colonies of eastern pipistrelles in buildings. *Journal of Mammalogy* 79 (2): 651-659.
- Wilkinson, L. C. & R. M. R. Barclay 1997. Differences in the foraging behaviour of male and female big brown bats (*Eptesicus fuscus*) during the reproductive period. *Ecoscience* 4 (3): 279-285.

## Chapter 3

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# Sampling protocol for assessment of insect availability in a riparian habitat

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## Abstract

In this short note, we present experiments aimed at selecting a convenient device for sampling prey availability for bats in a riparian habitat. For this purpose, we assessed insect availability at a pond, by comparing insect trapping between emergence traps and sticky traps. Our results show a lack of association in the number of prey captured between emergence and sticky traps.

## Introduction

Insects originating from lakes and ponds are an important food source for a number of flying vertebrates, including bats (Furlonger et al., 1987; Seidman & Zabel, 2001), swallows (Robertson et al., 1992) or swifts (Lack & Owen, 1955). In bats, the study of diet or food selection relies on the use of traps to identify insects and their abundance in the environment (Bell, 1980; Hickey & Fenton, 1990; Johnston & Fenton, 2001). Traps differ primarily in the way insects are captured, with some devices using sensory stimuli (attractant traps) whereas others do not (non-attractant traps). Among attractant devices, *light traps* have been the most frequently used in bat studies (Swift, 1980; Thomas, 1988; Sample & Whitmore, 1993). They are well indicated in the study of bats specialised on some food items like Lepidoptera (Sample & Whitmore, 1993; Sierro & Arlettaz, 1997), since moths are positively phototactic (Borror et al., 1981). However, light traps must be used with caution to estimate insect abundance in the field (Kunz, 1988), because of inherent bias due to attraction of some insect taxa according to light quality (UV, mercury vapour, tungsten incandescent filament) (Mikkola, 1972). Among non-attractant traps, *sweep nets* have been rarely used for monitoring insect availability (Entwistle et al., 1996; Warren et al., 2000; Kapfer, 2001), most likely because insecticides are required to avoid flying insects escape after sweeps. *Suction traps* offer several advantages since they measure absolute insect density for a certain volume of air sucked (Anthony & Kunz, 1977; Racey & Swift, 1985; Barlow & Jones, 1997; Park & Cristinacce, 2006). Nonetheless, this method is noisy and relatively expensive. *Malaise traps* have been used in a few studies on insect distribution and prey selection by bats (Barclay, 1985, 1991; Fukui et al., 2006). This method is not very accurate because it allows capture of very few insects per day, resulting in a large variance in estimates of insect abundance (Juillet, 1963). *Sticky traps* are impaction trap on which insects adhere to sticky substances upon contact. These traps are easy to set up. Yet, they are rarely chosen because removing specimens from the glue is difficult, time-consuming and frequently requires the use of toxic solvents (Bradbury & Verhencamp, 1977; Barclay, 1985; von Freckell & Barclay, 1987; Barclay, 1991).

Several studies have shown a positive relationship between activity of insectivorous bats and insect abundance (Swift & Racey, 1983; De Jong, 1994; Warren et al., 2000). To our knowledge, however, none of the works achieved in riparian habitats was based on the use of *emergence traps*, which sample insects that pass from an aquatic larval stage to the flying imago. Yet, such a device is useful to estimate the number of prey coming out of the water and, hence, to study how emerging insects contribute to bat foraging activity.

In this study, we carried out experiments aimed at selecting a convenient device for sampling insect availability in a riparian habitat and, more ultimately, to study variations of bat activity in relation to prey accessibility. For this purpose, we assessed prey availability for bats at a pond, by comparing insect trapping between emergence traps and sticky traps. Because of the non-synchronisation of insect emergence, no site can provide a constant and equal presence of resources over time. Whereas emergence traps reflect the effective productivity in insects of the pond, sticky traps give insight on the relative abundance of

flying insects emerging from the water and flying from around and/or nearby the pond. In addition, we studied how the number and diversity of insects captured by sticky traps varied among three habitats: in an open habitat located in the close vicinity of the pond, over the pond, and at the forest edge.

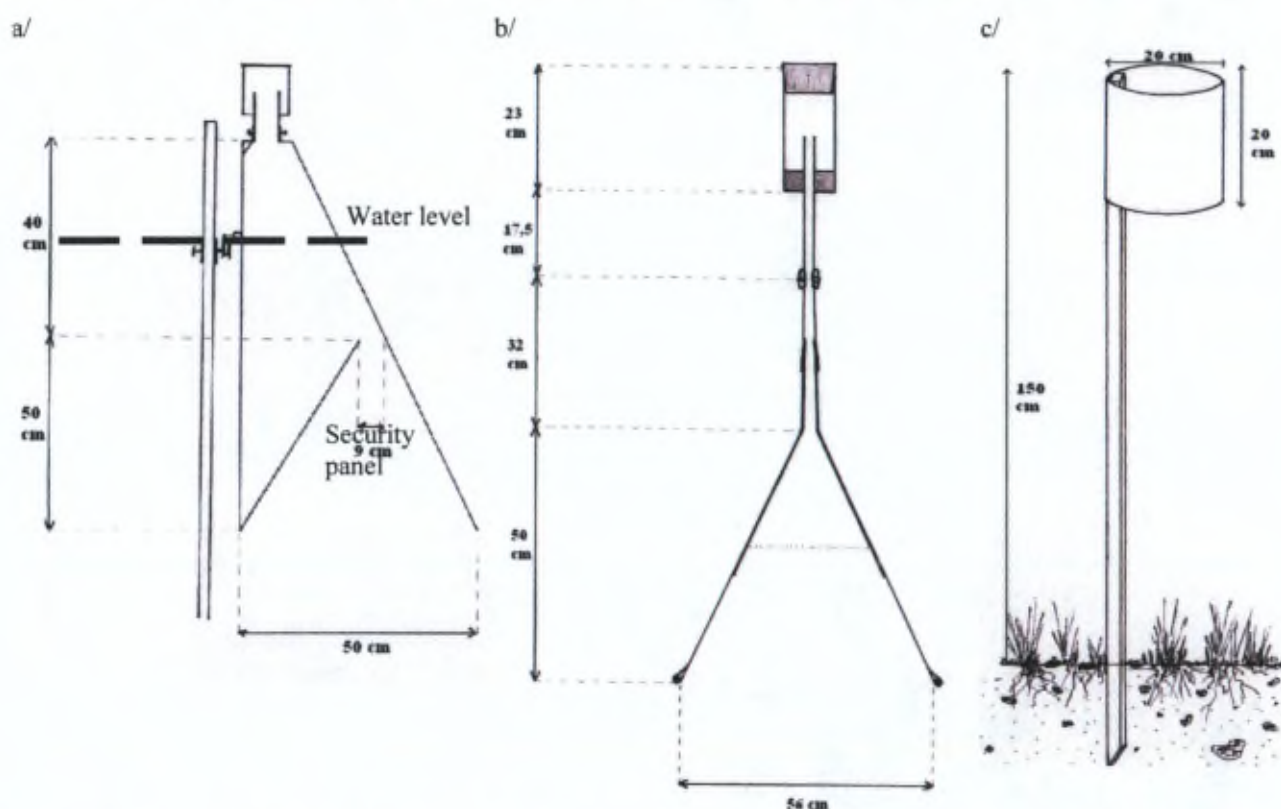
### Materials & Methods

We conducted our experiments at the Silex pond, located in the south-east of Brussels (Belgium). The pond covers an area of 1 ha, and stands 100 m from the nearest house and 150 m from the nearest illuminated road. It is surrounded by the Forêt de Soignes on one side and by wet meadows, a pasture with a few hedgerows, and a small orchard (figure 1). It is enclosed in a natural reserve with limited access, which prevented our material from degradation.



**Figure 1:** Study area and location of the traps in and around the pond.

Two emergence traps (pyramidal and funnel) and one sticky trap were designed, constructed and tested for insect captures (figure 2). The pyramidal trap was positioned in the middle of the pond and partially immersed in the water in order to collect emerging imagos. This emergence trap was modified after Mundie (1975). Its basis was placed 1 m above the bottom of the pond and covered a square of 0.25 m<sup>2</sup>. The skeleton was made of aluminium square tubes on which were fixed wood and mosquito-net veil (0.3 mm mesh). A small and removable container with formaldehyde (4%) was positioned at the top of the trap to collect emerging adults. A fixed veil (security panel) was stretched in order to collect imagos that did not reach the container (figure 2a). The funnel trap was fully immersed in the water and collected drowned adults about to emerge. It was made of a circular basis of 0.25 m<sup>2</sup> positioned at 10 cm from the bottom of the pond. It looked like a reverse funnel extended with a plastic pipe (container) at the end of which animals were collected (figure 2b).



**Figure 2:** a) Pyramidal trap, b) funnel trap, and c) sticky trap used in the study of insect availability around the Silex pond. See text for details.

Sticky traps allowed capture of flying insects. They were made of plastic bands (20x50 cm) covered by glue (Oecos, UK) and positioned 1.5 m above ground or water around PVC pipes (Heathcote, 1957) (figure 2c). This height is convenient for practical reasons, but also because many bat species hunt 0-3 m above ground (Anthony & Kunz, 1977; Bradbury & Verhencamp, 1976; Thomas, 1988; Barclay, 1991). The glue used offers the advantage of being transparent, odourless, easy to spread, long lasting, and it shows little or no oxidation.

Trapping experiments were carried out during eight nights between July 4 and 19 2002. Sampling was performed during calm and dry nights to minimize the influence of airstreams and rain on the number of insects captured by sticky traps. Nine sticky traps were

used: three were placed in an open habitat near a small orchard (A), three were placed in the middle of the pond (B), and three at the forest edge (C) (figure 1). They were placed at dusk and removed at dawn so that diurnal insects were not captured. Glued bands were removed by using a thin plastic film (cellophane) apposed on the sticky side. Instead of extracting insects by mean of a solvent to dissolve the glue (Murphie, 1985), we punched small plastic pastilles to isolate each insect from the band and put them in ethanol (70%) for subsequent identification and measurements (figure 3). Emergence traps (one pyramidal and one funnel) were placed in the pond at dusk and left for 24h periods, since emergence peaks generally occur at dusk and dawn (Lewis & Taylor, 1965; Swift, 1980; Racey & Swift, 1985). Each evening, insects were collected from the containers; for the pyramidal trap, insects were also gathered from the 'security panel'.

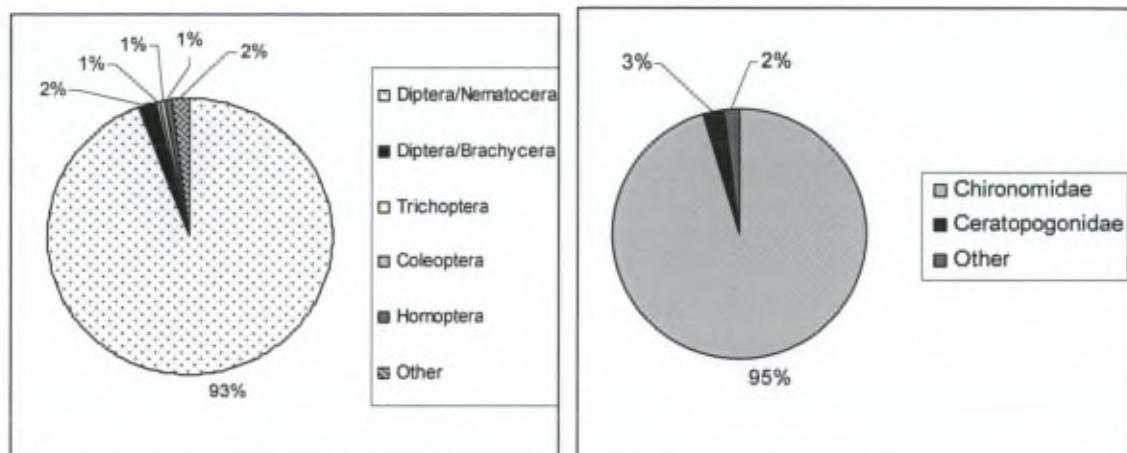


**Figure 3:** Nematoceran insects (Diptera) glued on sticky traps and magnified with the binocular. The first individual belongs to the family: Cecidiomyiidae, the second: Psychodidae, and the third: Chironomidae.

The insects trapped by each type of device were counted and identified to family level using a Leika NZ6 stereo-microscope at a magnification of  $\times 10$ . We tested if the number of insects captured differed between the three sticky traps within each habitat (A, B or C) and compared the number of insect captured with the three devices (pyramidal trap, funnel trap and sticky trap placed in the pond (habitat B), figure 1) using a one-way ANOVA. The association between numbers of emerging vs. flying insects was analysed using Pearson correlation tests. To assess the effect of spatial heterogeneity on insect availability, we compared the number and diversity of flying insects captured by sticky traps between the three habitats A, B, C using Kruskal-Wallis test and one-way ANOVA, respectively.

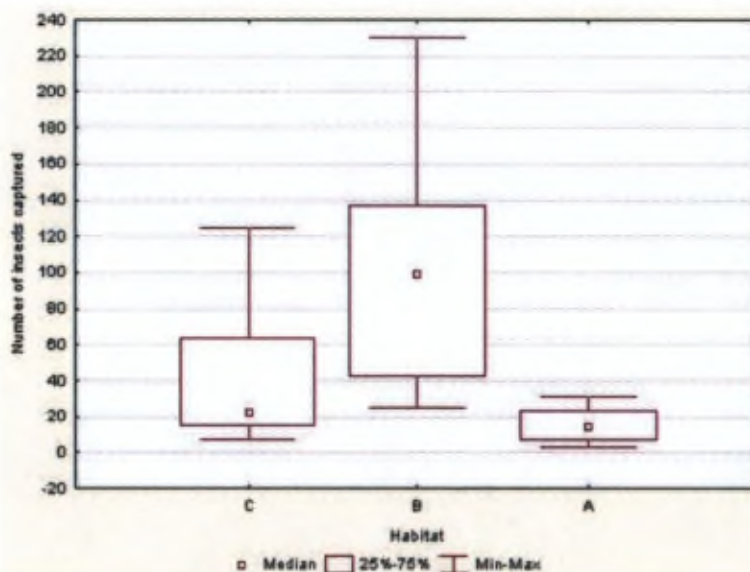
## Results

Overall, we captured 6567 insects with the three trapping devices. Insects collected with emergence traps all belonged to Chironomids (Diptera, Nematocera) and a few Trichoptera. Similarly, 95% of the insects collected on sticky traps were Chironomids, but other groups were found including Coleoptera, Homoptera, Lepidoptera, Hymenoptera, Psocoptera, Neuroptera, Heteroptera and Spiders (figure 4).



**Figure 4:** Proportion of a/ Insect Orders and b/ Nematocera among insects sampled by means of sticky traps.

Within each habitat (A, B, and C, figure 1), no difference occurred in the number of insects captured by the sticky traps between the three replicates (one-way ANOVA,  $F \leq 0.092$ ,  $p > 0.91$  for all comparisons). We therefore pooled the data from the three trapping sessions in each habitat, and considered the mean number of insects captured for subsequent analyses. The number of insects captured over the pond with the three trapping devices differed significantly (one-way ANOVA,  $F = 19.4$ ,  $p < 0.001$ ); it decreased following the sequence: pyramidal, funnel and sticky trap (Tukey post-hoc tests,  $p < 0.05$  for all comparisons). There was a strong positive correlation between the number of insects caught by both types of emergence traps (Pearson correlation,  $r = 0.84$ ,  $p < 0.005$ ). By contrast, no association occurred in the number of insects captured between sticky traps and emergence traps (pyramidal or funnel) ( $r = 0.23$  and  $r = -0.24$ , respectively,  $p > 0.59$  for both comparisons).



**Figure 5:** Number of insects captured in the different habitats (A: small orchard, B: middle of the pond, C: forest edge) by means of sticky traps.

The mean number of flying insects on sticky traps was statistically different between the three habitats (Kruskal-Wallis test,  $H = 32.9$ ;  $p < 0.001$ ), and decreased following the

sequence: middle of the pond (habitat B), forest edge (C), and open (A) (Dunn's multiple comparisons:  $p < 0.05$ ; figure 5). Furthermore, insect diversity varied among habitats (one-way ANOVA  $F = 5.0$ ,  $p < 0.03$ ), with the number of insect families being higher along the forest edge (C) than over the pond (B) (Tukey post-hoc test,  $p < 0.05$ ).

## Discussion

The comparison of the three trapping devices showed that Chironomids are the most abundant insect group in the study area. Similar results have been reported for other ponds in the Brussels' Region (Goddeeris, 2003). An interesting result of our study is the absence of association in the number of insect sampled between emergence and sticky traps. This difference may stem from the fact that one trap type collects only insects emerging from water, whereas the other also captures flying insects from all around the pond. For instance, adult Chironomids are not long dispersers but they remain and fly in the close vicinity of their natal site (Seguy, 1951; Bertrand, 1954). The density of flying and emerging insects is known to fluctuate in time and space (Johnsson, 1957). Flying insects are primarily influenced by weather conditions, like air temperature (Taylor, 1963; Black, 1974) or wind speed (Blake et al., 1994). On the other hand, emergence of aquatic insects is largely conditioned by factors such as water temperature (Mackey, 1977), wind (Blake et al., 1994), light exposure (Morgan & Waddell, 1961; Sweeney et al., 1986), mud and water quality (Kashian & Burton, 2000, Connolly et al., 2004; Irving et al., 2004) or predation (Hanson & Riggs, 1995).

Our data also indicate a strong correlation in capture rates between pyramidal and funnel traps. However, these devices greatly differed in the number of insects captured. Several hypotheses may account for this difference. (i) It may result from micro-geographic variations in the density of insect larvae at the bottom of the pond. (ii) The design of traps and their use may also be involved. Indeed, the funnel was positioned close to the bottom of the pond (see methods), so that some insect larvae not fixed to the substrate (*e.g.*, Chironomidae, Tanypodinae) may have escaped trapping (Armitage et al., 1995). (iii) Luminosity could also influence collection efficiency. Nymphs of Chironomids about to emerge are guided by a positive phototaxis (Lellak, 1968). Because the funnel trap was more opaque than the pyramidal one, the latter might have captured more insects.

Sticky traps reveal environmental variations in insect densities, with higher numbers sampled above water surface. As mentioned previously, these traps allow the sampling of insects both flying around and emerging from the pond. Comparatively, less insect numbers were captured at the edge of the forest. This site benefits from the forest a windbreak effect, which acts like a barrier for airborne plankton (Lewis, 1969; Whitaker et al., 2000). Insect diversity in this ecotone between an aquatic habitat and a forest was also greater, since we sampled insects associated with the presence of dense foliage as aphids, bugs and moths. Fewer insects were sampled in the third habitat located in a meadow close to the small orchard.

In conclusion, our results show a lack of association in the number of prey captured between emergence and sticky traps. Future work aimed at estimating bat activity in relation to prey availability in a riparian habitat should test whether bat activity is primarily affected

by insect emergences from the water, by the overall flying insect abundance or by both sources.

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## References

- Anthony, E. L. P. & T. H., Kunz, 1977. Feeding strategies of the little brown bat, *Myotis lucifugus*, in southern New Hampshire. *Ecology*, 58: 775-786.
- Armittage, P. D., Cranston, P. S. & L. C. V., Pinder, 1995. The Chironomidae: the biology and ecology of nonbiting midges. Chapman and Hall, London, 572p.
- Barclay, R. M. R., 1985. Long versus short-range foraging strategies of hoary (*Lasiurus cinereus*) and silver-haired (*Lasionycteris noctivagans*) bats and the consequences for prey selection. *Can. J. Zool.*, 63: 2507-2515.
- Barclay, R. M. R., 1991. Population structure of temperate zone insectivorous bats in relation to foraging behaviour and energy demand. *J. Anim. Ecol.*, 60: 165-178.
- Barlow, K. & G., Jones, 1997. Function of pipistrelle social calls: field data and playback experiment. *Anim. Behav.*, 53: 991-999.
- Bell, G. P., 1980. Habitat use and response to patches of prey by desert insectivorous bats. *Can. J. Zool.*, 58: 1876-1883.
- Bertrand, H., 1954. Encyclopédie Entomologique, Série A, Tome XXXI, Les Insectes Aquatiques d'Europe (Genres: Larves, Nymphes, Imagos), Volume II – Trichoptères, Lépidoptères, Diptères, Hyménoptères, Ed. Paul Lechevalier, 547p.
- Black H. L., 1974. A north temperate bat community: structure and prey populations. *J. Mamm.*, 55: 138-157.
- Blake, D., Hutson, A. M., Racey, P. A., Rydell, J. & J. R., Speakman, 1994. Use of lampits roads by foraging bats in southern England. *J. Zool., Lond.*, 234: 453-462.
- Borror, D. J., Delong, D. M. & C. A., Triplejorn, 1981. An introduction to the study of insects. Saunders College Publishing, Philadelphia, 827p.
- Bradbury, J. W. & S. L., Vehrencamp, 1976. Social Organization and Foraging in Emballonurid Bats. *Behav. Ecol. Sociobiol.*, 1: 337-381.
- Connolly, N. M., Crossland, M. R. & R. G. Pearson, 2004. Effect of low dissolved oxygen on survival, emergence, and drift of tropical stream macroinvertebrates. *J. N. Am. Benthol. Soc.*, 23: 251-270
- De Jong, J., 1994. Habitat use, home range and activity pattern of the northern bat, *Eptesicus nilssoni*, in a hemiboreal coniferous forest. *Mammalia*, 58: 535-548.
- Entwistle, A. C., Racey, P. A. & J. R., Speakman, 1996. Habitat exploitation by a gleaning bat, *Plecotus auritus*. *Phil. Trans. R. Soc. Lond., B*. 351: 921-931.
- Frenckell, von B. & R. M. R., Barclay, 1987. Bat activity over calm and turbulent water. *Can. J. Zool.*, 65: 219-222.
- Fukui, D., Murakami, M., Nakano, S. & T., Aoi, 2006. Effect of emergent aquatic insect on bat foraging in a riparian forest. *J. Anim. Ecol.*, 75: 1252-1258.
- Furlonger, C. L., Dewar, H. J. & M. B., Fenton, 1987. Habitat use by foraging insectivorous bats. *Can. J. Zool.* 65: 284-288.
- Goddeeris, B., 2003. Benthische Macro-Invertebrated van de Brussels vijvers. In IBGE, 2003. Inrichting van Speciale Beschermingszones in het Brussels Hoofdstedelijk Gewest. Technisch rapport, 34-56 pp.
- Hanson, M. A. & M. R. Riggs, 1995. Potential effects of fish predation on wetland invertebrates: a comparison of wetlands with and without fathead minnows. *Wetlands*, 15:167-175.
- Heathcote, G. D., 1957. The optimal size of sticky aphid traps. *Plant Path.*, 6: 104 -107.
- Hickey, M. B. C. & M. B., Fenton, 1990. Foraging by bats (*Lasiurus borealis*): do specific chases mean territoriality? *Can. J. Zool.*, 68: 2477-2482.
- Irving, E. C., Liber, K. & J. M., Culp, 2004. Lethal and sublethal effects of low dissolved oxygen condition on two aquatic invertebrates, *Chironomus tentans* and *Hyalella azteca*. *Environ. Toxicol. Chem.*, 23: 1561-1566.
- Johnston, D. S. & M. B., Fenton, 2001. The diet of pallid bats (*Antrozous pallidus*): variability at individual and population levels. *J. Mamm.*, 82: 362-373.

- Johnsson, C. G., 1957. The distribution of insects in the air and the empirical relation of density to height. *J. Anim. Ecol.*, 26: 479-494.
- Juillet, J. A., 1963. A comparison of four types of traps used for capturing insects. *Can. J. Zool.*, 41: 219-223.
- Kapfer, G., 2001. Inventaire des Chauves-souris des Z.S.C. de la Région Bruxelles-Capitale. Rapport de stage, DESS GRNR Lille, 94p.
- Kashian, D. R. & T. M., Burton, 2000. A Comparison of Macroinvertebrates of two great lakes. Coastal Wetlands: Testing potential metrics for an index of ecological integrity. *J. Gr. Lak. Res.*, 26: 460-481.
- Kunz, T. H., 1988. Ecological and behavioral methods for the study of bats. (T. H., Kunz, ed.) Smithsonian Institution Press, Washington D. C., 533p.
- Lack, D. & D. F., Owen, 1955. The food of the swift. *J. Anim. Ecol.*, 24: 120-136.
- Lellak, J., 1968. Positive Phototaxis der Chironomiden-Larvulae als regulierender Faktor ihrer Verteilung in stehenden Gewasser. *Ann. Zool. Fenn.*, 5: 84-87.
- Lewis, T. & L. R., Taylor, 1965. Diurnal periodicity of flight by insects. *Trans. R. Ent. Soc. Lond.*, 116: 393-435
- Lewis, T., 1969. The diversity of the insect fauna in a hedgerow and neighbouring fields. *J. App. Ecol.*, 6: 453-458.
- Mackey, A. P., 1977. Growth and development of larval Chironomidae. *Oikos* 28: 270-275.
- Mikkola, K., 1972. Behavioural and electrophysiological response of night-flying insects, especially Lepidoptera, to nearultraviolet visible light. *Ann. Zool. Fenn.*, 9: 225-254.
- Morgan, N. C. & A. B., Waddell, 1961. Diurnal variation in the emergence of some aquatic insects. *Trans. R. Ent. Soc., Lond.*, 113: 123-37.
- Mundie, J. H., 1975. Techniques for sampling emerging aquatic insects. *In: A manual on Methods for the Assessment of Secondary Productivity in Fresh Waters*, Edmonson, W. T. & G. G., Wingberg (Eds.). Blackwell Scientific Publications, Oxford, 80-108 pp.
- Murphie, W. L., 1985. Procedures for the removal of Insect Specimen from Sticky trap Material. *Ann. Ent. Soc. Am.*, 58: 881.
- Park, K. J. & A., Cristinacce, 2006. Use of sewage treatment works as foraging sites by insectivorous bats. *Anim. Cons.*, 9: 259-268.
- Racey, P. A. & S. M., Swift, 1985. Feeding ecology of *Pipistrellus pipistrellus* (Chiroptera: Vespertilionidae) during pregnancy and lactation. I. Foraging behaviour. *J. Anim. Ecol.*, 54: 205-215.
- Robertson, J., Stutchbury, B. J. & R. R., Cohen, 1992. Tree swallow. *In The birds of North America* 11. Poole, A., Stettenheim, P. & F., Gill (Eds). Academy of Natural Sciences, Philadelphia, and American Ornithologists' Union, Washington, D.C.
- Sample, B. E. & R. C., Whitmore, 1993. Food habits of the endangered Virginia big-eared bat in West Virginia. *J. Mamm.*, 74: 428-428.
- Seguy, E., 1951. Atlas des Diptères de France – Belgique – Suisse I, Introduction et caractères généraux Nématocères – Brachycères I, Editions N. Boubée & C<sup>ie</sup>, 185p.
- Seidman, V. M. & C. J., Zabel, 2001. Bat activity along intermittent streams in northwestern California. *J. Mamm.*, 82: 738-747.
- Sierro, A. & R., Arlettaz, 1997. Barbastelle bats (*Barbastella* sp.) specialize in the predation on moths: implications for foraging tactics and conservation. *Acta Oecol.*, 18: 91-106.
- Sweeney BW, Vannote R. L. & P. J., Dodds, 1986. Effects of temperature and food quality on growth and development of a mayfly, *Leptophlebia intermedia*. *Can. J. Fish. Aqua. Sc.*, 43: 12-18.
- Swift, S. M. S., 1980. Activity patterns of Pipistrelle bats (*Pipistrellus pipistrellus*) in north-east Scotland. *J. Zool., Lond.*, 190: 285-295.
- Swift, S. M. & P. A., Racey, 1983. Resource partitioning in two species of vespertilionid bats (Chiroptera) occupying the same roost. *J. Zool., Lond.*, 200: 249-259.
- Taylor, J. R., 1963. An analysis of the effects of temperature on insects in flight. *J. Anim. Ecol.*, 32: 99-117.

- Thomas, D. W., 1988. The distribution of bats in different ages of Douglas-fir-forests. *J. Wildl. Manag.*, 52: 619-626.
- Warren, R. D., Waters, D. A., Altringham, J. D. & D. J., Bullock, 2000. The distribution of Daubenton's bats (*Myotis daubentonii*) and pipistrelle bats (*Pipistrellus pipistrellus*) (Vespertilionidae) in relation to small-scale variation in riverine habitat. *Biol. Cons.*, 92: 85-91.
- Whitaker, D. M., Carroll, A. L. & W. A., Montevecchi, 2000. Elevated numbers of flying insects and insectivorous birds in riparian buffer strips. *Can. J. Zool.*, 78: 740-747.

# Relationship between bat activity and insect availability around a sub urban pond

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## Abstract

In this paper, we studied the influence of the relative flying insect abundance and the size of potential prey on the flying activity of the three most common bat species in a sub urban pond. Our results did not show any influence of neither insect abundance nor insect body size on overall bat activity for all the three species studied. The majority of insects captured by sticky traps on the two consecutive years were Chironomidae. We did not find any relationship between air temperature and flying insect abundance because sampling was performed during warm nights only, and temperatures probably always exceeded the threshold of insect inactivity. A surprising result of this study was that bat activity decreased noticeably between 2003 and 2004, which was neither linked with air temperature variations, nor with bat survival. Finally, flight activity of *Pipistrellus* was greatly influenced by air temperature with *P. pipistrellus* and *P. nathusii* being less active during warmer nights. Daubenton's bat activity was not affected by air temperature.

## Introduction

Bat hunting behaviour is closely associated with prey distribution, predictability and mobility (Entwistle et al., 1996). A close relationship between foraging activity of insectivorous bats and prey availability has been documented in various conditions and environments, such as forests (Thomas, 1988; Rautenbach et al., 1996), rural and urban habitats (Geggie & Fenton, 1985) or water bodies (Swif & Racey, 1983; de Jong & Ahlen, 1991; Warren et al., 2000). Several studies have shown that bat activity and insect densities reach the highest levels in lacustrine and riverine habitats (Brigham et al., 1992; Vaughan et al., 1997). However, few examined how temporal variations in insect density and diversity affect the occurrence and hunting activity of bats in riparian habitats (Fukui et al., 2006). Such a study requires sustained and simultaneous monitoring of bat and flying insect activities. It may be complicated by the fact that bat activity is very likely related with insects emerging from water surface, with the overall flying insect abundance or with both these sources. More importantly, prey availability is not only characterised by their quantity (abundance or biomass), but also by their quality (energetic or nutrient content) and/or diversity (species richness) (Grindal & Brigham, 1999). For example, prey size influences bat activity, with some species selecting bigger insects than others (Black, 1974; Jones, 1990; Barclay & Brigham, 1994; Siemers & Schnitzler, 2000). In *Pipistrellus*, it has been suggested that the common pipistrelle *P. pipistrellus* selects bigger insects than the soprano pipistrelles *P. pygmaeus* (Barlow, 1997; Barlow et al., 1997). The skull morphology of a bat represents a historical record of the diet it has become adapted to over its evolutionary history (Bogdanowicz et al., 1999; Schoeman & Jacobs, 2003). Ultrasound shapes and frequencies may also differ according to the prey hunted; bats using high frequencies (short wavelengths) can detect smaller prey than bats using low-frequency calls (long wavelengths) (Kingston & Rossiter, 2004).

In this work, we studied the influence of (i) the relative flying insect abundance, (ii) the size of potential prey, and (iii) air temperature on the flying activity of bats in a sub urban pond.

## Material & Methods

Bat activity monitoring and insect sampling was performed in 2003 and 2004 from May to July, around Silex pond (Belgium). Experiments ended on mid-July to avoid monitoring bats at the reproductive period of pipistrelles, this period corresponding to a change in the behaviour of males that start flying actively to attract females and defend mating roosts rather than to forage (see Chapter 2.2). Each evening, we measured air temperature by means of a data logger (Testo 175-H1) before starting bat call recordings.

### *Insect sampling*

To assess insect availability and diversity, sticky traps were used. Glued bands were placed daily on traps at dusk and removed at dawn. Insect sampling was performed as described in

chapter 3.1. The number of insects captured was counted. All insects trapped were determined to the family level using a Leika NZ6 stereomicroscope at a magnification of x10. We also measured body length from head to abdomen to the nearest 0.5 mm.

*Bat activity monitoring*

To estimate activity, bat calls were sampled using a Pettersson D-980 (Pettersson Elektronik AB, Sweden) set on frequency division mode (division factor: 10) and recorded on a DAT-Sony recorder. Signals were then analysed with “Bat Sound” software (Pettersson Elektronik AB, Sweden). Recordings were carried out at six contact points located on the bank of the pond and separated 50 m from each other. Two-minute recordings were performed 45 min. and 90 min. after sunset. Flight activity was estimated with the activity duration (AD) per unit of time, defined as the time (in seconds) during which bats were detected (see Chapter 2.1). All our experiments were carried out during dry and still nights.

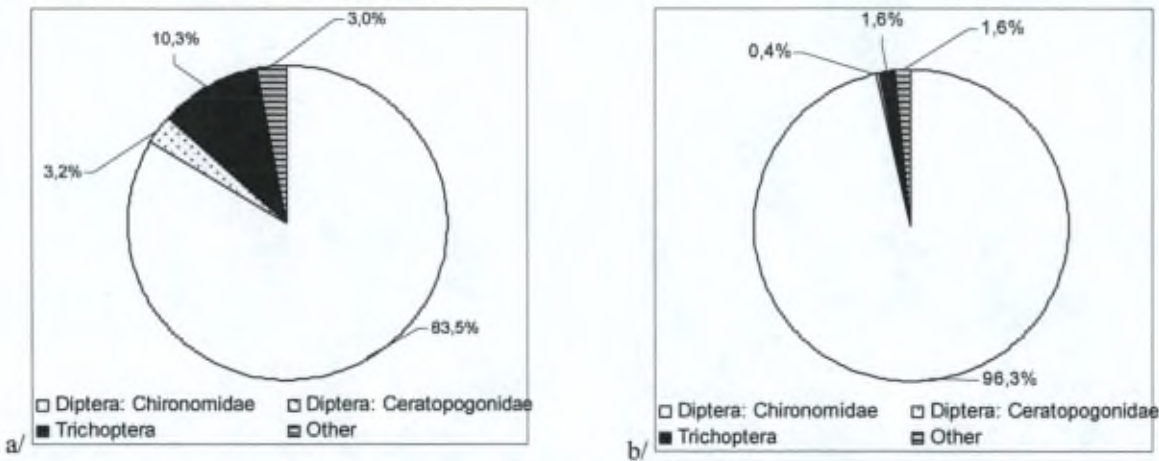
*Statistics*

We tested for a possible difference in insect abundance, insect size, bat activity and air temperature between the two consecutive years, by using the appropriate non-parametric (Mann-Whitney) or parametric (Student-*t*) test, after having controlled for the normal distribution of the data. To test for a possible association between temperature and insect abundance, between temperature and bat activity, and between insect availability and bat flight activity, we used Spearman rank correlation analyses.

**Results**

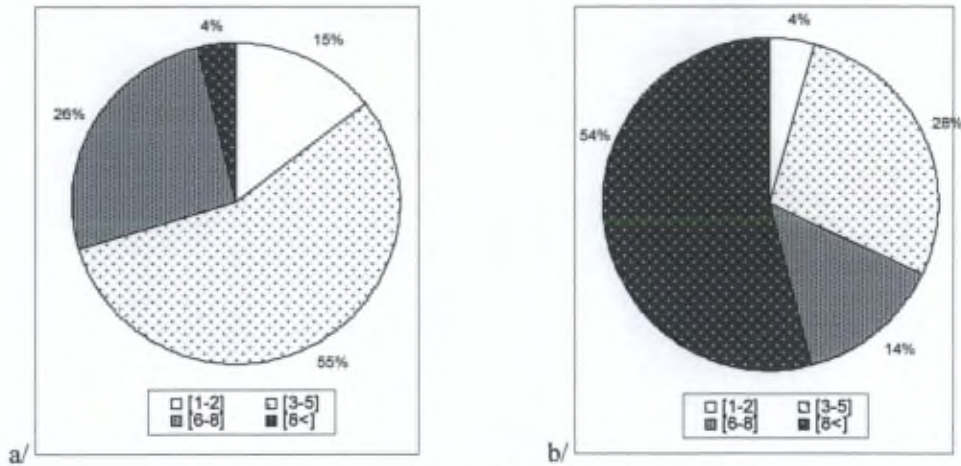
*Insect availability*

The mean number of insects captured did not differ between 2003 and 2004 (Mann-Whitney *U*-test:  $U= 257, p> 0.05$ ). Also, insect diversity was not different between both study years, even though the Trichoptera were slightly more abundant in 2003. As shown figure 1, most insects captured over the pond belonged to the Chironomidae (Diptera, Nematocera) (83.5% and 96.3% in 2003 and 2004, respectively).



**Figure 1:** Insects captured by sticky traps from May to July in a/ 2003 and b/ 2004, around the Silex pond (South-East of the Brussels Region, Belgium).

By contrast, insect body length differed markedly between both study years (figure 2). Insects ranging in the class [1-2 mm] ( $U= 6.5, p< 0.001$ ), [3-5 mm] (Student  $t$ -test:  $t= 4.3, p< 0.001$ ) and [6-8 mm] ( $t=2.4, p< 0.03$ ) were significantly more abundant in 2003 than in 2004. In addition, we sampled more insects exceeding 8 mm in 2004 than 2003 ( $U= 4.0, p< 0.001$ ).

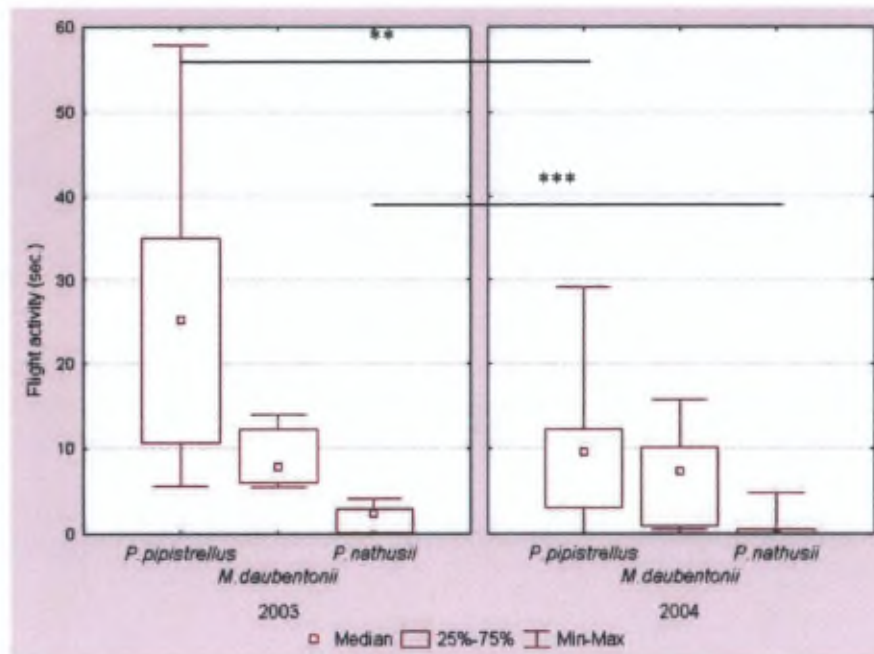


**Figure 2:** Body size of the insects trapped in a/ 2003 and b/ 2004 around the Silex pond (South-East of the Brussels Region, Belgium).

Mean air temperature did not differ between 2003 ( $\bar{x} \pm \text{SD} = 17.4 \pm 2.38$ ) and 2004 ( $\bar{x} \pm \text{SD} = 14.7 \pm 1.86$ ) (range for both years: [10-22 °C];  $t = 1.44, p > 0.05$ ). Moreover, insect availability was not associated with air temperature (Spearman rank correlation,  $r = 0.05, p = 0.91$  and  $r = 0.29, p = 0.24$ , respectively in 2003 and 2004).

#### Bat activity

Recordings allowed to identify seven species (figure 1): common pipistrelle *Pipistrellus pipistrellus* (Schreber, 1774), Nathusius' pipistrelle *P. nathusii* Keyserling & Blasius, 1839, soprano pipistrelle *P. pygmaeus* (Leach, 1825), Daubenton's bat *Myotis daubentonii* (Kuhl, 1817), noctule *Nyctalus noctula* (Schreber, 1774), Leisler's bat *N. leisleri* (Kuhl, 1817) and serotine *Eptesicus serotinus* (Schreber, 1774). *P. pipistrellus*, *P. nathusii* and *Myotis daubentonii* were the most recurrent species over the pond (see also Chapter 2). Overall bat activity decreased significantly between 2003 and 2004 ( $U = 4372, p < 0.001$ ). Whereas the median of the AD index reached 29.9 sec. in 2003, it decreased to 12.5 sec. in 2004. This trend was obvious in *P. pipistrellus* ( $U = 1520, p < 0.003$ ) and *P. nathusii* ( $U = 3846, p < 0.001$ ), but not in *M. daubentonii* ( $U = 5583, p = 0.85$ ) (figure 3).



**Figure 3:** Flight activity duration (AD) of the three most frequent bat species sampled around the Silex pond from May to July 2003 and 2004.

In 2003 and 2004, flight activity of *P. pipistrellus* was negatively associated with air temperature (2003:  $r = -0.31$ ,  $p < 0.05$ ; 2004:  $r = -0.35$ ,  $p < 0.05$ ). A similar result was found for *P. nathusii* in 2004 ( $r = -0.38$ ,  $p < 0.05$ ), but not in 2003 ( $r = 0.10$ ,  $p > 0.05$ ). In *M. daubentonii*, flight activity was never associated with air temperature ( $r > 0.19$ ,  $p > 0.05$  for both years).

#### *Comparison between bat activity and insect availability*

No association was found between bat activity and insect abundance or prey size for the three most common bat species encountered in the study area (*P. pipistrellus*, *P. nathusii* and *M. daubentonii*), neither in 2003 nor in 2004 (activity vs. total number of insects, vs. number of small insects [1-5 mm], or vs. number of big insects [ $> 6$  mm];  $-0.47 < r < 0.67$ ,  $p > 0.05$  for all comparisons).

### **Discussion**

Our results show no influence of insect abundance on bat flight activity. This contrasts with other studies reporting a positive association between bat activity and insect abundance (Rautenbach et al., 1996; Kusch et al., 2003). Two hypotheses, non-mutually exclusive, may account for such a discrepancy. First, it may stem from our estimate of prey availability to bats. Sticky traps capture flying insects but give only a poor estimate of the rate of emerging ones (see chapter 3.1). By examining the effect of aquatic prey subsidies in riparian zones on bat foraging behaviour, Fukui et al. (2006) recently showed that activity of insectivorous bats is directly affected by prey coming out from water in spring, when emergent insects are the most abundant. Using an insect-proof cover supported by aluminium frames over 1.2 km of a stream, they suppressed the movement of emerging aquatic insects from water. By the way, they were able to discriminate between the influence of flying insects emerging from water

and of other insects present in the environment on bat flight activity. Their results clearly showed that bat activity was primarily determined by the density of emergent adult aquatic insects. This is consistent with our previous study (Chapter 3.1), in which we advised to sample both flying and emerging insects to assess insect availability. Unlike Fukui et al. (2006), we could not distinguish in the present work between the effect of the movement of aquatic insects and that of insects that did not emerge from water. Second, insect availability may not be the single limiting factor to bat activity in our study area at the time experiments were conducted. Eutrophic lakes are among the highest insect productive grounds (Bertrand, 1954) and most likely fill the energy requirements of bats. Rather, bat activity could be affected by other factors, including competition, predation or abiotic conditions (local climatic fluctuations).

We did not find any association between insect body size and overall bat activity for all three species studied. In insectivorous bats, aerial foragers usually hunt in a range of prey-size depending of the species. They forage optimally and maximise energy intake, prey too large being distinguished from edible-sized targets (Bell, 1982; Barclay & Brigham, 1994). A positive association between prey size and bat size was reported in several species. In the Natterer's bat *Myotis nattereri*, foragers prefer medium-sized and large Diptera (Gregor & Bauerová, 1987; Siemers & Schnitzler, 2000). Also the common pipistrelle *Pipistrellus pipistrellus* selects bigger insects than the small soprano pipistrelles *P. pygmaeus* (Barlow, 1997; Barlow et al, 1997).

Consistent with our previous studies (Chapter 3.1), the vast majority of insects captured by sticky traps on the two consecutive years were Chironomidae. De Jong & Ahlen (1991) showed that bat abundance and species richness are greater in the ecotone between open deciduous forest and adjacent shallow eutrophic lakes corresponding with the high Chironomid abundance in this habitat. This Diptera Family is known to represent an important part of bats' diet (Swift & Racey, 1983; Sullivan et al., 1993). We did not find any relationship between air temperature and flying insect abundance. This seems surprising, since many studies reported a positive association between both these factors, low temperatures resulting in a diminution of insect metabolism and of their flight activity (Mellanby, 1939). It should be noted, however, that our sampling was performed during warm nights only, and temperatures probably always exceeded the threshold of insect inactivity (around 10°C; Cockbain, 1961). Finally, our results showed that the proportion of large insects trapped was higher in 2004 than 2003. At least two explanations may account for this difference. First, the number and species of insect larvae in the benthos may greatly vary from year to year. Such variations may stem from variation in water or mud quality (amount of organic mater, oxygen, etc...). Second, many fish species prey on insect larvae or on imagoes about to emerge. The predation rate may vary with time, because of human activities (maintenance of ponds, fishing, etc...).

A surprising result of this study was that bat activity decreased noticeably between 2003 and 2004. This drop was particularly obvious in *Pipistrellus* species. It seems unlikely that this decrease was linked to a change in climatic conditions since air temperature did not vary between years. In addition, temperature always exceeded the critical value of 10°C often

described as the lowest temperature below which bats greatly limit their flying and foraging activities (Fenton et al., 1983; Catto et al., 1995). Also, it seems unlikely that the severe decrease observed in 2004 might have resulted from a drop in the number of bats in the area due to high bat mortality during rigorous winter or sudden frost in spring. Indeed, high bat activities were recorded over other ponds close to our study area (unpublished data). Finally, the diminution in bat activity might have resulted from a reduction in the site's attractiveness, the Silex pond being left for another more productive area in 2004. For instance, the rate of insect emergence in the Silex pond may have been high in 2003, but reduced in 2004 compared with adjacent ponds.

Finally, we found that flight activity of *Pipistrellus* was greatly influenced by air temperature with *P. pipistrellus* and *P. nathusii* being less active during warmer nights. Daubenton's bat activity was not affected by air temperature. This difference may be linked to the respective hunting strategies of the species. Pipistrelles are aerial hawking bats depending on flying insect abundance. As temperature increases, activity of flying insects increases in all habitats (Anthony & Kunz, 1977), which could explain why pipistrelles leave open water habitats for protected areas in the forest or in other cluttered environments (personal observation). On the other hand, Daubenton's bats catch their prey upon water surface and are less dependent on air temperature for the presence of insects. Nyholm (1965) observed in Finland that when temperatures cooled less than 10°C in summer, *Myotis mystacinus* and *M. daubentonii* hunted closer to water bodies because insect availability was greater than that in the forest. As mentioned above, temperature never went below this critical threshold in our study area, what may explain the lack of decreasing activity in Daubenton's bat.

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## References

- Anthony, E. L. P. & T. H., Kunz, 1977. Feeding strategies of the little brown bat, *Myotis lucifugus*, in southern New Hampshire. *Ecology*, 58: 775-786.
- Bell, G. P., 1982. Behavioral and ecological aspects of gleaning by a desert insectivorous bat *Antrozous pallidus* (Chiroptera: Vespertilionidae). *Behav. Ecol. Sociobiol.*, 10: 217-223.
- Black, H. L., 1974. A north temperate bat community: structure and prey populations. *J. Mamm.*, 55(1): 138-157.
- Barclay, R. M. R. & R. M., Brigham, 1994. Constraints on optimal foraging: a field test of prey discrimination by echolocating insectivorous bats. *Anim. Behav.*, 48: 1013-1021.
- Barlow, K. E., 1997. The diets of two phonic types of the bat *Pipistrellus pipistrellus* in Britain. *J. Zool., Lond.*, 243: 597-609.
- Barlow, K. E., Jones, G. & E. M., Barratt, 1997. Can skull morphology be used to predict ecological relationships between bat species? A test using two cryptic species of pipistrelle. *Proc. R. Soc. Lond. B.*, 264: 1695-1700.
- Bertrand H., 1954. Encyclopédie Entomologique, Série A, Tome XXXI, Les Insectes Aquatiques d'Europe (Genres : Larves, Nymphes, Imagos), Volume II – Trichoptères, Lépidoptères, Diptères, Hyménoptères, Editions Paul Lechevalier, 547p.
- Bogdanowicz, W., Fenton, M. B. & K., Daleszczyk, 1999. The relationships between echolocation calls, morphology and diet in insectivorous bats. *J. Zool., Lond.*, 247: 381-393.
- Brigham, R. M., Aldridge, H. D. J. N. & R. L., Mackey, 1992. Variation in habitat use and prey selection by yuma bats, *Myotis yumanensis*. *J. Mamm.*, 73: 640-645.
- Catto, C. M. C., Racey, P. A. & P. J., Stephenson, 1995. Activity patterns of the serotine bat (*Eptesicus serotinus*) at a roost in southern England. *J. Zool., Lond.*, 235: 635-644.
- Cockbain, A. J., 1961. Low temperature thresholds for flight in *Apis fabae* Slop. *Ent. Exp. Appl.*, 4: 211-219.
- Entwistle, A. C., Racey, P. A. & J. R., Speakman, 1996. Habitat exploitation by a gleaning bat, *Plecotus auritus*. *Phil. Trans. R. Soc. Lond. B.*, 351: 921-931.
- Fenton, M. B., Merriam, H. G. & G. L., Holroyd, 1983. Bats of Kootenay, Glacier, and Mount Revelstoke national parks in Canada: identification by echolocation calls, distribution, and biology. *Can. J. Zool.*, 61: 2503-2508.
- Fukui, D., Murakami, M., Nakano, S. & T., Aoi, 2006. Effect of emergent aquatic insect on bat foraging in a riparian forest. *J. Anim. Ecol.*, 75: 1252-1258.
- Geggie, J. F. & M. B., Fenton, 1985. A comparison of foraging by *Eptesicus fuscus* (Chiroptera: Vespertilionidae) in urban and rural environments. *Can. J. Zool.*, 63: 263-267.
- Gregor, F. & Z., Bauerová, 1987. The role of diptera in the diet of Natterer's bat, *Myotis nattereri*. *Folia Zool.*, 36: 18-19.
- Grindal, S. D. & R. M., Brigham, 1999. Impacts of forest harvesting on habitat use by foraging insectivorous bats at different spatial scales. *Ecoscience*, 6: 25-34.
- Jones, G., 1990. Prey selection by the Greater horseshoe bat (*Rhinolophus ferrumequinum*): optimal foraging by echolocation? *J. Anim. Ecol.*, 59: 587-602.
- Jong (de), J. & I., Ahlen, 1991. Factors affecting the distribution pattern of bats in Upland, Central Sweden. *Holarct. Ecol.*, 14: 92-96.
- Kingston, T. & S. J., Rossiter, 2004. Harmonic-hopping in Wallacea's bats. *Nature*, 429: 654-657.
- Kusch, J., Weber, C., Idelberger, S. & T., Koob, 2003. Foraging habitat preferences of bats in relation to food supply and spatial vegetation structures in a western European low mountain range forest. *Folia Zool.*, 53: 113-128.
- Mellanby, K., 1939. Low temperature and insect activity. *Proc. Roy. Soc. Lond. B.*, 127: 473-487.

- Nyholm, E. S., 1965. Zur Ökologie von *Myotis mystacinus* (Leisl.) und *M. daubentoni* (Leisl.) (Chiroptera). Ann. Zool. Fenn., 2: 77-123.
- Rautenbach, I. L., Fenton, M. B. & M. J., Whiting, 1996. Bats in riverine forests and woodlands: a latitudinal transect in southern Africa. Can. J. Zool., 74: 312-322.
- Siemers, B. M. & H.-U. Schnitzler, 2000. Natterer's bat (*Myotis nattereri* Kuhl, 1918) hawks for prey close to vegetation using echolocation signals of very broad bandwidth. Behav. Ecol. Sociobiol., 47: 400-412.
- Schoeman, M. C. & D. S., Jacobs, 2003. Support for the allotonic frequency hypothesis in an insectivorous community. Oecologia, 134: 154-162.
- Sullivan C. M., Shiel C. B., McAney C. M. & J. S. Fairley, 1993. Analysis of the diets of Leisler's *Nyctalus leisleri*, Daubenton's *Myotis daubentoni* and pipistrelle *Pipistrellus pipistrellus* bats in Ireland. J. Zool. Lond., 231: 656-663.
- Swift, S. M. & P. A., Racey, 1983. Resource partitioning in two species of vespertilionid bats (Chiroptera) occupying the same roost. J. Zool., Lond., 200: 249-259.
- Thomas, D. W., 1988. The distribution of bats in different ages of Douglas-fir-forests. J. Wildl. Manag., 52: 619-626.
- Vaughan, N., Jones, G. & S., Harris, 1997. Habitat use by bats (Chiroptera) assessed by means of a broad-band acoustic method. J. App. Ecol., 34: 716-730.
- Warren, R. D., Waters, D. A., Altringham, J. D. & D. J., Bullock, 2000. The distribution of Daubenton's bats (*Myotis daubentonii*) and pipistrelle bats (*Pipistrellus pipistrellus*) (Vespertilionidae) in relation to small-scale variation in riverine habitat. Biol. Cons., 92: 85-91.

## Chapter 4

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## Roost and hunting site fidelity of female and juvenile Daubenton's bat

### *Myotis daubentonii* (Kuhl, 1817) (Chiroptera: Vespertilionidae).

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#### Abstract

We investigated roosting and hunting site fidelity of Daubenton's bats *Myotis daubentonii* (Kuhl, 1817) in the Forêt de Soignes, an old-stand forest dominated by 150-200 year-old beeches, during the summers of 2003 and 2004. Roosting behaviour and hunting activity over ponds of adult females and juveniles were monitored using radio-telemetry. Eighteen roosts were located, all in natural cavities. The bats occupied a limited number of trees located in a specific and small roosting area. This roost aggregation was not linked to the distribution of hollow trees. Furthermore, whereas all eleven ponds in the study area were exploited by Daubenton's bats, monitored individuals were limited to two ponds to which they showed high fidelity. These two ponds were not the closest to the roosting area. Overall, these results show that, at least for the time we conducted our experiment, female and juvenile Daubenton's bats are highly faithful to specific roosting and hunting grounds.

**Keywords:** *Myotis daubentonii*, site fidelity

#### Zusammenfassung

Wir haben die Tagesquartier- und Jagdgebietstreue von Wasserfledermäusen im Forêt de Soignes, einem alten Wald mit 150 bis 200 Jahre alten Buchen, während der Sommer 2003 und 2004 beobachtet. Das Tagesquartier-Verhalten und die Jagdaktivität von Weibchen und Jungtieren über Teichen wurden mittels Telemetrie aufgezeichnet. Achtzehn Tagesquartiere wurden geortet, alle befanden sich in natürlichen Hohlräumen. Die Fledermäuse belegten eine begrenzte Anzahl von Bäumen, die in einem bestimmten und kleinen Tagesquartier-Gebiet lagen. Es bestand kein Bezug zwischen diesen Tagesquartieren und der Streuung hohler Bäume. Weiterhin wurde festgestellt, dass, obwohl alle elf Teiche in dem observierten Gebiet von Wasserfledermäusen besucht wurden, die überwachten Tiere sich auf zwei Teiche beschränkten, für die sie eine große Treue zeigten. Diese beiden Teiche waren nicht immer die dem Tagesquartier-Gebiet am nächsten gelegenen. Allgemein zeigen die Ergebnisse, dass - zumindest während der Zeit unserer Studie - die Weibchen und die juvenilen Wasserfledermäuse bestimmten Tagesquartier- und Jagdgebieten sehr treu sind.

**Mammalian Biology, in press**

## Introduction

Bat populations are probably limited by the availability of sites with high and constant insect productivity for foraging, sufficient suitable roosts and high connectivity (Limpens and Kapteyn 1991; De Jong 1995; Jenkins et al. 1998). This is particularly marked in temperate regions, where bats have only a limited time to give birth, raise their young and deposit fat reserves before winter (Ransome 1990). Site fidelity and territoriality may have been selected for increasing roosting and hunting efficiency. Site fidelity might indeed facilitate prior access to resources and territorial behaviour might have evolved to defend it. Hunting site fidelity has been reported in some temperate bat species, with individual bats showing strong loyalty to foraging areas on consecutive nights, such as the common pipistrelle *Pipistrellus pipistrellus*, the large mouse-eared bat *Myotis myotis*, the notch-eared bat *M. emarginatus*, the brown long-eared bat *Plecotus auritus* or the Bechstein's bat *M. bechsteinii*, (Racey and Swift 1985; Audet 1990; Krull et al. 1991; Entwistle et al. 1996; Kerth et al. 2001). On the other hand, roost fidelity seems closely associated with site permanency and availability. Species roosting in relatively short-lived but abundant roosts (as trees) tend to switch roost more often than species selecting more stable, predictable but rarer structures like buildings or caves (Lewis 1995). Roost fidelity has been described in various bat species (Lewis 1995), including the common pipistrelle, the serotine bat *Eptesicus serotinus*, the brown long-eared bat, the Natterer's bat *M. nattereri*, or the yuma bats *M. yumanensis* (Gerell and Lundberg 1985; Catto et al. 1996; Park et al. 1998; Entwistle et al. 2000; Evelyn et al. 2004). In a few species, fidelity was closely associated with a territorial behaviour, whereby foreigners to the colony are chased through fights or repelled by agonistic advertisement calls emitted in flight or while perched (Gerell and Lundberg 1985; Leonard and Fenton 1984). Some studies suggested that tree-dwelling bat species might not exhibit roost fidelity and not form colonies in individual trees but remain loyal year after year to a definite area enclosing many potential roost trees (Vonhof and Barclay 1996; O'Donnell and Sedgely 1999; Cryan et al. 2001; Willis and Brigham 2004; Russo et al. 2005). Colonies might then spread among those trees forming fission-fusion societies (Kerth and König 1999; Willis and Brigham 2004).

Daubenton's bat *Myotis daubentonii* (Kuhl, 1817) is among the most common bats in Europe (Mitchell-Jones et al. 1999). During the breeding season, it is a tree dwelling species occupying hollow branches, woodpecker holes, crevices, or finding sometimes shelter behind loose bark (Ebenau 1995; Rieger 1996a, 1996b; Kapfer et al. 2006). It hunts over water surfaces, feeding mainly on Chironomidae (Diptera, Nematocera) and Trichoptera, caught either by aerial hawking or by gaffing from the water (Jones and Rayner 1988; Sullivan et al. 1993; Flavin et al. 2001). Ponds are often very productive habitats, but are limited in number. The close dependence of Daubenton's bats on water bodies severely limits the habitat use and distribution of this species (Dietz et al. 2006). One should therefore expect populations of Daubenton's bats to show hunting site fidelity, and to defend sites against conspecifics. Chases over water bodies were documented (Wallin 1961; Rieger et al. 1992; Encarnação et al. 2005) and could reflect agonistic intentions. To date, most studies on roosting and/or hunting behaviour in the Daubenton's bat have explored roost selection (Rieger 1996a,

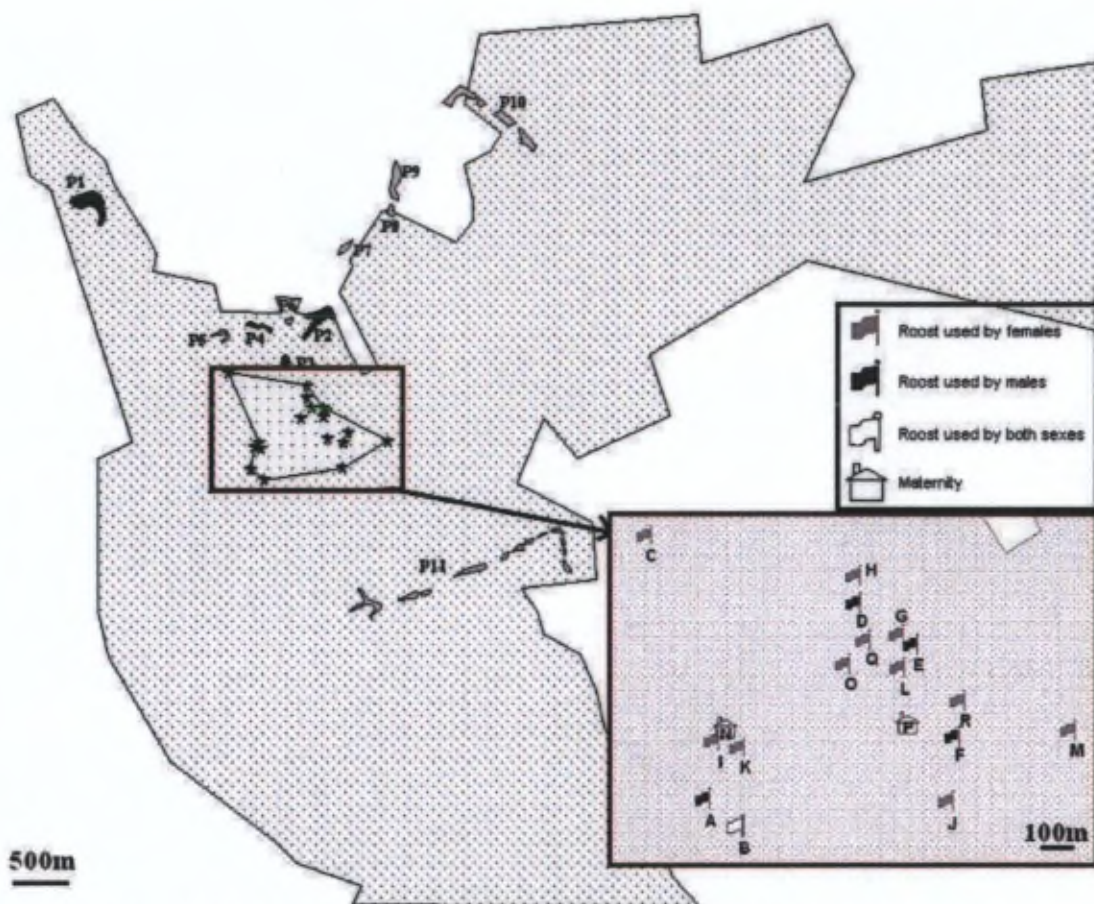
1996b; Boonman 2000), activity patterns (Rieger 1996c; Encarnação et al. 2004), use of linear landscape elements (Rieger et al. 1990; Dietz and Fitzenräter 1996), habitat use (Zahn and Maier 1997; Warren et al. 2000) or resource partitioning (Swift and Racey 1983). A limited diffusion in specific zones over several years of 'resident' males Daubenton's bats has been reported (Encarnação et al. 2002). Recently, two studies have documented an unequal distribution of adult female and male Daubenton's bats linked to the presence of water bodies, insect productivity, presence of roosting sites and climatic conditions (Encarnação et al. 2005; Dietz et al. 2006). It has been shown that energy demand and food intake is higher during the reproductive period (Encarnação and Dietz 2006), which may explain why females use energy-rich hunting sites during pregnancy and lactation (Encarnação et al. 2005). Moreover, juvenile Daubenton's bats often experience high mortality during their first winter and they might need good feeding places to fatten up before hibernation (Boyd and Stebbings 1989; O'Donnell, 2002). Therefore, whether female and juvenile Daubenton's bats exhibit roost and/or hunting site fidelity deserves further studies.

In this paper, we investigated both roost and hunting site fidelity in a population of female and juvenile Daubenton's bats in a sub-urban deciduous forest, using radio-tracking. More specifically, we assessed whether bats stay loyal to a defined roosting area, occupy several trees within this roosting area and/or switch roost frequently. We also investigated if bats focused their hunts over a few number of ponds or if they spread equally over the different ponds available around their roosts.

## Material and methods

### *Study area*

The study was carried out in the Forêt de Soignes, Belgium (50°48'N, 4°24'E). The forest is an even-aged system of 4380 ha enclosing mostly hardwoods, with beeches (*Fagus sylvatica*) and oaks (*Quercus* spp.) as dominant species. Sixty-five percent of the forest surface is covered with old (130-200 years) and tall beeches. This old forest has an overall low biodiversity but seems to shelter many species of bats (Devillers et al. 2004). Ponds are located in the north-western edge of the forest zone (figure 1). In three locations, closely contiguous ponds (P2, P10, and P11) were considered as single water bodies. All ponds were visited by various species of bats, including the Daubenton's bat (Devillers et al. 2004).



**Figure 1:** Map of the Forêt de Soignes showing ponds (P1: Cambre, P2: Moulin/Silex, P3: Vuilbeek, P4: Enfants noyés, P5: Fer à cheval, P6: Tournay-Solvay, P7: Leybeek, P8: Royale belge, P9: Ten Reuken, P10: Rouge-Cloître and P11: Groenendael), the roosting area and roosts' location. Ponds exploited by the studied population are shown in black; ponds used by other populations are shown in grey.

**Table 1:** Daubentons' bats equipped with transmitters, data on tracking period and qualitative use of roosts and hunting sites.

Nr.	Capture location	Date of capture	Age class	Sex	Reproductive class	Tracking days	Tracking interruption	Ponds used	Roost used	Weight (g)	Forearms (mm)
Mist netting over pond											
1	P 2	28/07/2003	Juvenile	Male	-	8	Transmitter fall	P2, P3	A, B	-	-
2	P 2	9/08/2003	Juvenile	Female	Non reproductive	2	Transmitter fall	P1, P2	C	9.5	-
3	P 2	12/08/2003	Juvenile	Male	-	14	Battery	P1, P2	D, E, F	8.5	-
4	P 2	9/09/2003	Juvenile	Female	Non reproductive	10	Battery	P2	G	10.5	34
5	P 2	12/04/2004	Adult	Female	Non reproductive	17	Battery	P1, P2	H, I, J, K	9	40
6	P 2	14/05/2004	Adult	Female	Pregnant	12	Battery	P1, P2	L, M, N, O	10	34
10	P 2	28/05/2004	Adult	Female	Pregnant	4	Battery	P1, P2, P3, P4	B, N	12	38
11	P 2	3/06/2004	Adult	Male	-	13	Battery	P2, P11	B	9	38
12	P 2	19/06/2004	Adult	Female	Lactating	7	Battery	P2	P	11	37
Harp trapping at roost											
7	N	20/05/2004	Adult	Female	Pregnant	9	Transmitter fall	P2, P3	N	11	37
8	N	20/05/2004	Adult	Female	Pregnant	7	Transmitter fall	P1, P4	N	12	37
9	N	20/05/2004	Adult	Female	Pregnant	7	Transmitter fall	P2	N	8.5	37
13	P	10/07/2004	Adult	Female	Lactating	7	Transmitter fall	P1, P2	P, Q	9.5	35
14	P	10/07/2004	Adult	Female	Lactating	13	Battery	P1, P2, P3	P, Q, R	11	39

### *Capture and monitoring*

Mist-netting was performed during summer 2003 and 2004 over pond P2 in the Silex Domain, a natural reserve that borders the forest on its north-eastern side (figure 1). Four mist-nets of 12 and 18 m long were placed over the pond. Nine bats were captured and were immediately tagged with radio-transmitters (table 1). In spring 2004, tracking of marked individuals allowed identification of tree roosts where an additional sample of five bats was captured by using bag traps placed at roost exits, and equipped with transmitters. Individuals were sexed, aged (adult vs. juvenile) (Richardson 1994), weighed to the nearest 0.5 g (115K, Pesola, Switzerland) and the length of their forearms was measured ( $\pm 1$  mm) (table 1). Females were separated into reproductive classes (non reproductive, pregnant, lactating) by palpating abdomens and examining nipples.

Either BD-2N (0.39-0.51 g, Holohil Systems Ltd., Canada) or Ag317 (0.55 g, Biotrack Ltd., U.K.) transmitters were fixed on the back of animals using surgical adhesive (Skinbond, Smith and Nephew, Largo, Florida) after clipping the fur. Transmitter weight was kept under 5% of the animal body weight ranging in our study between 8.5 and 12 g (Aldridge and Brigham 1988). Signals were detected using the 'homing in' method (White and Garrott 1990) by means of a TR-4 receiver (Telonics, US) fitted either with a three-element Yagi antenna or with an omni-directional antenna fixed on a car roof. Bats were monitored from the first night following their capture until loss of tag or battery failure. We considered a loss of tag either when a transmitter was found on the ground, or when the tracked animal was no longer found to leave the roost for two consecutive nights and days, indicating that the transmitter fell inside the roost or on the way between roosting and hunting sites. At most, five bats were followed simultaneously. Radio-tracking was performed over nightly activity periods to localise roosts and hunting sites. Bat movements from and to roosts and hunting grounds were monitored for a total of 62 nights (from sunset to sunrise) and 33 half-nights (from sunset to 1 am). Bats were tracked one at a time except during a week in May during which we monitored activity patterns of four bats roosting together to investigate if these females used the same hunting grounds. We measured the distance travelled by individuals between their roost and the middle of hunting grounds. We did not use the distance between roosts and minimum, innermost or outermost measurement point of the hunting area because animals hunted over the entire pond's surface but also because there were no large water bodies in our study area. To depict tracking data, in 2004, we measured contact time, here, reported as 'hunting activity', by counting the number of 20 minutes periods during which Daubenton's bats were detected over hunting grounds. In total, 714 periods of 20 minutes were recorded.

Statistica 6 was used for data analysis. With non parametrical Kruskal-Wallis ANOVA by ranks test we estimated if the panel of ponds was distributed at even distance from roosts or not. Dunn Multiple Comparison test were used to determine which ponds were situated the closest or farthest from roosts. We compared bat activities over the different ponds using Kruskal-Wallis ANOVA by ranks test. Student-t test or Mann-Whitney U-test helped us to assess whether bats were more likely found over specific ponds or groups of ponds. We also

tested whether bat activity was correlated to the distance from roosts to hunting grounds with Spearman Rank Correlation test.

MapInfo Professional 5.5 was used to draw maps, measure distances and areas.

## Results

Fourteen Daubenton's bats were captured and fitted with transmitters. Nine individuals were caught over P2: four adult females (bats 5, 6, 10, 12), one adult male (bat 11) and two juveniles of each sex (bats 1-4) (table 1). On May 2004, we captured by harp trap 33 adult females emerging from roost N and tagged three of them (bats 7-9). On July 2004, 19 adult females and 19 first season juveniles were caught from roost P; two adults were fitted with a transmitter (bats 13, 14) (table 1). The mean monitoring time  $\pm$  S.D. per individual was  $9.3 \pm 4.1$  days (range: 2-17 days). About half the transmitters stopped functioning due to progressive battery failure; in all other cases, the tracking stopped due to transmitter loss.

### Roost fidelity

Five females (bats 4, 12, 7, 8, 9) and the adult male (11) stayed loyal to the same roost during monitoring time (table 2). The remaining seven bats changed roost using two to four roosts. On average, these bats (six females and one juvenile male) stayed on the same roost  $3.18 \pm 2.84$  days (range: 1-10 days) before switching. Overall, individuals spent more than 50% of the monitoring time in a single roost (table 2). Three females initially trapped in roost N were found in roost P. These individuals were recognised thanks to a short fur area on their back occasioned by previous equipment with a radio-tag.

**Table 2:** Quantitative use of roost by Daubenton's bats.

Tracking days																		nr. days	% time in a roost	
Bat nr.	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17			18
Mist netting over pond																				
1	P2	-	A	A	A	A	A	B											6	83
2	P2	C																	1	-
3	P2	-	-	-	D	D	E	E	E	E	E	F	F	F					10	50
4	P2	-	-	G	G	G	G	G	G	G									7	100
5	P2	H	I	I	I	I	I	I	I	I	I	J	J	J	J	K	K		16	56.2
6	P2	L	M	N	N	N	N	-	N	O	N	N	N						12	72.7
10	P2	B	N	N															3	66.6
11	P2	B	B	B	B	B	B	B	B	B	B	B	B						12	100
12	P2	P	P	P	P	P	P												6	100
Harp trapping at roost																				
7	N	N	N	N	N	N	N	N	N										8	100
8	N	N	N	N	N	N	N												6	100
9	N	N	N	N	N	N	N												6	100
13	P	P	Q	Q	P	P	P												6	71.4
14	P	Q	P	P	P	P	P	P	P	P	P	P	R						12	85.7

### Roost site fidelity

Tagged bats were found to roost in 18 trees located in a restricted area of 1.12 km<sup>2</sup>, south of the majority of the ponds (figure 1). Juveniles and adults used roosts in the same limited forest area. Occupation of the roosts was not linked to the overall distribution of hollow trees. A survey carried out from 1999 to 2002 showed that trees with cavities or loose barks were equally distributed over the forest (Ben van der Wijden, unpublished data).

### Hunting site fidelity

Hunting grounds were located in the North, North-west (P1-P6), in the South (P11) or in the North-East (P7-P10) of the roosting area (figure 1). Adult females did not use ponds equally (Kruskal-Wallis ANOVA by ranks test,  $H(df=8, N=99)=48.4, p<0.001$ ). They hunted over four ponds (P1, P2, P3 and P4) north of their roosts, out of the eleven ponds available. Hunting activity was significantly higher over ponds P1-P2 (Mann-Whitney U test,  $U=6.5, df=8, p<0.003$ ) than any other, with overall 95% of total radio-tracking time registered over these ponds (table 3). We did not find any significant difference between hunting activity over P1 and P2 (Student-t test,  $t=0.15, df=16, p=0.88$ ). The single adult male was the only bat that visited a different pond (P11) (table 3).

**Table 3:** Use of hunting grounds by monitored Daubenton's bats in 2004. n: periods of 20 minutes during which we observed the bat over ponds P1, P2, P3, P4 and P11. %: proportion of time we observed the bat over the pond.

Bat nr.	Capture location	Age class	Sex	P1		P2		P3		P4		P11	
				n	%	n	%	n	%	n	%	n	%
Mist netting over pond													
5	P2	Ad	F	102	79	28	22	-	-	-	-	-	-
6	P2	Ad	F	95	100	-	-	-	-	-	-	-	-
10	P2	Ad	F	35	86	-	-	5	12	1	2	-	-
11	P2	Ad	M	-	-	12	41	-	-	-	-	17	59
12	P2	Ad	F	-	-	30	100	-	-	-	-	-	-
Harp trapping at roost													
7	N	Ad	F	-	-	84	92	7	8	-	-	-	-
8	N	Ad	F	46	98	-	-	-	-	1	2	-	-
9	N	Ad	F	-	-	86	100	-	-	-	-	-	-
13	P	Ad	F	11	33	22	67	-	-	-	-	-	-
14	P	Ad	F	32	24	96	73	4	3	-	-	-	-
Total				321	45	358	50	16	2	2	1	17	2

Ponds were not localised at equal distances from the roosting area (Kruskal-Wallis ANOVA on ranks,  $H(df=10, N=198)=173.5, p<0.001$ ): P2, P3, P4, P5, P6 and P11 were generally closer to roosts than P1, P7, P8, P9 and P10 (Dunn's Multiple Comparison tests,  $p<0.05$ ). Mean flight distance of bats between roost and foraging area was  $2.4 \pm 1.0$  km (range: 0.5-3.8 km). Bat activity and distances between hunting sites and roosts showed no association (Spearman Rank Correlation,  $r=-0.05, p=0.88$ ). Tagged individuals visited one to three different ponds each night, some bats returning to the same hunting site up to six times in a single night. Four females, roosting in the same site, monitored simultaneously were found to hunt over ponds P1 and P2: bats 8 and 10 were hunting predominantly over P1 and bats 7 and 9 over P2 (table 3).

## Discussion

### *Roost fidelity*

Roost fidelity in summer greatly varies according to bat species. Whereas some are faithful to a single roost site (e.g., horseshoe bat *Rhinolophus* sp., Rossiter et al. 2002; serotines bat, Catto et al. 1996; soprano pipistrelle *Pipistrellus pygmaeus*, Barlow & Jones 1999), others shift roost site regularly (e.g., common pipistrelle, Barlow and Jones 1999). Our data show that females Daubenton's bats do not display a strict pattern of roost fidelity: some bats changed roost frequently, whereas others did not. During monitoring time, half the bats switched roost after a stay of about three days, which is consistent with Rieger (1996a) and Senior et al. (2005). Roost availability and permanency have been suggested to affect roost fidelity (Kunz 1982). Daubenton's bats occupying spatially abundant roosts in a forest are more likely to change roost frequently. On the other hand, an adult male and five females did not switch roost during our study. Telemetry only allows a limited time of tracking because of transmitter loss or battery failure and except for the male, the five females were tracked at most for seven days, which could partly explain why these individuals did not exhibit roost changes. Roost lability, defined as changing roost locations at least once every ten days, could result from disturbance, predation, changes in micro-climate and roost structure, parasitism, avoiding guano accumulation, or teaching newly volant juveniles about site locations (Lewis 1995). Costs and benefits of site fidelity for females might also change with the reproductive cycle. During pregnancy and lactation, females might be more faithful to some roosts because of the energetic constraints associated with the carrying of offspring to new roosts (Lewis, 1995). As in Natterer's bats, it is possible that females Daubenton's bats shift roost sites frequently, but that they remain in specific roosts at certain periods of the year (Swift 1997).

### *Roost site fidelity*

Our data also reveal that Daubenton's bats occupy many roosts clumped in a restricted area of forest. Females and juveniles captured over a given pond during summer 2003 and 2004 were all found to roost in a specific number of trees, in a small section of the forest. When bats switched to a new roost, they remained in the same limited area. It is unlikely that the restricted dispersion of the roost range results from hollowed trees availability, since mature beeches rich in cavities and in which we found the roosts, cover most of the forest clumps. Our study also indicates that different roosts may be connected to each other, since some individuals captured in roost N during pregnancy were found in roost P during lactation. This supports that Daubenton's bats use a network of roosting sites within a single forest, as previously suggested by Rieger (1996a). However, in this latter study, the author called 'forests' small woods more or less isolated from each other. Our investigations provide new information and demonstrate that loyalty to small roosting areas is not influenced by the forest surface. They also agree with Willis and Brigham (2004), according to whom loyalty to defined roosting areas, occupation of multiple trees within a roosting area, and roost switching are consistent with the hypothesis that tree-roosting bats maintain stable social groups that are larger than the number of individuals occupying any given tree. In Bechstein's bats, females show little roost fidelity but exhibit an extreme degree of

philopatry to a specific home range in the forest (Kerth et al. 2002). Daubenton's bats could follow the same biological trait.

Several studies suggest that bat colonies using tree cavities are not restricted to individual trees, and that forest roosting bats are faithful to a defined area containing many potential roost trees (Vonhof and Barclay 1996; O'Donnell and Sedgely 1999; O'Donnell 2000; Cryan et al. 2001; Willis and Brigham 2004). Daubenton's bats that are loyal to small roosting area in the forest could learn and memorise the location and thermal characteristics of the different roosts and thus reduce time and energy invested in searching for suitable roosts and/or colony mates, reducing the risk of having to roost alone. Under the fission-fusion model, on a given night, the colony would consist of multiple roosting sub-groups spread among different trees within the roosting area (Kerth and König 1999; O'Donnell 2000; Kerth et al 2001). Repeated roost switching over time may eventually enable bats to share roosts and maintain long-term associations with other residents to their roosting area (O'Donnell 2000). Although it seems likely, whether fission-fusion occurs in Daubenton's bats await further study. Moreover, monitoring time in the present work never exceeded two weeks. It might be necessary to investigate whether roosting site fidelity remains over years.

#### *Hunting site fidelity*

Our findings are consistent with hunting ground fidelity in Daubenton's bats. Dietz et al. (2006) showed that female Daubenton's bats forage next to their nursery colonies along a river in Germany. In our study, foragers had access to eleven ponds but used only four of them, with two ponds being more intensively exploited. None of the females and juveniles tagged was recorded foraging on the remaining seven ponds of the study area, even though some were closer to the roosting area. More precisely, our bats foraged in the North, North-east whereas other ponds were available South or North-east to the roosting area. It seems unlikely that water quality and, hence, insect availability accounted for this pond selection. Macro-benthos samples revealed that other ponds (i.e. P9 and P10) do produce large amounts of insects (Unpublished data). Furthermore, all ponds of the study site were actively visited each night by several species, including Daubenton's bats indicating that they were prosperous foraging sites (Devillers et al. 2004).

Many studies agreed that foraging areas are limiting resources for Daubenton's bats populations with individuals competing and partitioning their home ranges according to food location (Encarnação et al. 2005; Senior et al. 2005). Sexual segregation was described in this species, females and males hunting at different elevation levels (Leuzinger and Brossard 1994; Russo 2002; Encarnação et al. 2005; Dietz et al. 2006). A shorter stay of males compared to females at foraging sites was also reported as an evidence for males being evicted from feeding sites by females defending rewarding places against males (Encarnação et al. 2005). Senior et al. (2005) also documented intra-sexual segregation in male population of Daubenton's bats along a river. Dominant males excluded other males from better foraging and roosting places near nursery colonies for prior access to food but also to females. These data and the occurrence of chases over water bodies (Wallin 1961; Rieger et al. 1992, Encarnação et al. 2005) denote the particular territorial trend of the species. Territoriality in bats occurs either individually or

collectively (Gerell and Lundberg 1985; Leonard and Fenton 1984). To date, group defence of maternity roost has been documented for Bechstein's bats, where individuals severely attack intruders to the colony (Kerth et al. 2002). Other studies in tropical regions described a group territorial behaviour with females actively defending foraging grounds against conspecifics (Bradbury and Verhecamp 1976; McCracken and Bradbury 1981). In Daubenton's bats competition occurs between males and females but also among males for access to hunting sites. As mentioned by Dietz et al (2006), such a competition might also occur between females, which might defend high quality water bodies against strangers to their colony, especially during cost intensive periods such as pregnancy and lactation. Whether groups of females display collective hunting and/or collective defence of resources awaits further investigation.

### *Management implications*

There is an urge to consider roosting areas, comprising all the roosts used by a sub-population of tree-dwelling bats, as distinct entities and to define their spatial boundaries. In Daubenton's bats, roosting entities seem also to be closely associated with discrete hunting grounds. The link between roosting and hunting sites in our study was exclusive, since individuals caught on a given ponds were found in a specific roosting area, and vice-versa. This particular resource selection and use implies very specific management actions. First, managers should avoid clear cutting in forest parcels where a roosting entity has been located. Total clearing of roosting trees could impair bat population badly, even if after some intensive search for new roosts, some bats were able to mix with other sub-groups or create a new roosting entity. Big brown bats, *Eptesicus fuscus*, are loyal to their roosts but after eviction from their roost, bats tend to produce fewer offspring in the newly discovered roosts (Brigham and Fenton 1986). Second, there should not be simultaneous water draining of all ponds used as main hunting grounds by a sub-population. Finally, connectivity between roosting entity and hunting grounds of each sub-group should be maintained because biological corridors are indispensable to Daubenton's bats for commuting flights between sites (Limpens et al. 1989).

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## References

- Aldridge, H. D. J. N.; Brigham, R. M. R. (1988): Load carrying and manoeuvrability in an insectivorous bat: a test of the 5% 'rule' of radio-telemetry. *J. Mamm.* **69**, 379-382.
- Audet, D. (1990): Foraging behavior and habitat use by a gleaning bat *Myotis myotis* (Chiroptera: Vespertilionidae). *J. Mamm.* **71**, 420-427.
- Barlow, K. E.; Jones, G. (1999): Roosts, echolocation calls and wing morphology of two phonic types of *Pipistrellus pipistrellus*. *Z. Säugetierk.* **64**, 257-268.
- Boyd, I. L.; Stebbings, R. E. (1989): Population changes of brown long-eared bats (*Plecotus auritus*) in bat boxes at Theford forest. *J. App. Ecol.* **26**, 101-112.
- Brigham, R. M.; Fenton, M. B. (1986): The influence of roost closure on the roosting and foraging behaviour of *Eptesicus fuscus* (Chiroptera: Vespertilionidae). *Can. J. Zool.* **64**, 1128-1133.
- Boonman, M. (2000): Roost selection by noctules (*Nyctalus noctula*) and Daubenton's bats (*Myotis daubentonii*). *J. Zool. Lond.* **251**, 385-389.
- Bradbury, J. W.; Vehrencamp, S. L. (1976): Social Organization and Foraging in Emballonurid Bats. *Behav. Ecol. Sociobiol.* **1**, 337-381.
- Catto, C.C.M.; Hutson, A.M.; Racey, P.A.; Stephenson, P. J. (1996): Foraging behaviour and habitat use of the serotine bat (*Eptesicus serotinus*) in southern England. *J. Zool. Lond.* **238**, 623-633.
- Cryan, P. M.; Bogan, M. A.; Yanega, G. M. (2001): Roosting habits of four bat species in the Black Hills of South Dakota. *Acta Chiropterol.* **3**, 43-52.
- De Jong J. (1995): Habitat use and species richness of bats in a patchy landscape. *Acta Theriol.*, **40**, 237-248.
- Devillers P.; Kapfer, G.; Devillers-Terschuren, J.; Lafontaine, R.-M.; Laurent, Y. (2004): Les Chauves-souris de la Région bruxelloise: Distribution et Habitats. *Nat. Belges*, **85**, 1-50.
- Dietz, M.; Encarnação, J. A.; Kalko, E. K. V. (2006): Small scale distribution patterns of female and male Daubenton's bats (*Myotis daubentonii*). *Acta Chiropterol.* **8**, 403-415.
- Dietz, M.; Fitzenräter, B. (1996): Zur Flugrouthenutzung einer Wasserfledermauspopulation (*Myotis daubentonii* Kuhl, 1819) im Stadtbereich von Giessen. *Säugetierk. Inf.*, **20**, 107-116.
- Ebenau, C. (1995): Ergebnisse telemetrischer Untersuchungen an Wasserfledermäusen (*Myotis daubentonii*) in Mulheim an der Ruhr. *Nyctalus* **5**, 379-394.
- Encarnação, J. A.; Dietz, M. (2006): Estimation of food intake and ingested energy in Daubenton's bats (*Myotis daubentonii*) during pregnancy and spermatogenesis. *Eur. J. Wildl. Res.* **52**, 221-227.
- Encarnação, J. A.; Dietz, M.; Kierdorf, U. (2002): Zur Mobilität männlicher Wasserfledermäuse (*Myotis daubentonii* Kuhl, 1819) im Sommer. *Myotis* **40**, 19-31.
- Encarnação, J. A.; Dietz, M.; Kierdorf, U. (2004): Reproductive condition and activity pattern of male Daubenton's bats (*Myotis daubentonii*) in the summer habitat. *Mamm. biol.* **69**, 163-172.
- Encarnação, J.A.; Holweg, D.; Jasnoch, U.; Kierdorf, U.; Wolters, V. (2005): Sex-related differences in roost-site selection of Daubenton's bats (*Myotis daubentonii*) during the nursery period. *Mamm. Rev.* **35**, 285-294.
- Entwistle, A. C.; Racey, P. A.; Speakman, J. R. (1996): Habitat exploitation by a gleaning bat, *Plecotus auritus*. *Phil. Trans. R. Soc. Lond. B.* **351**, 921-931.
- Entwistle, A. C.; Racey, P. A.; Speakman, J. R. (2000): Social and Population structure of a gleaning *Plecotus auritus*. *J. Zool. Lond.* **252**, 11-17.
- Evelyn, M. J.; Stiles, D. A.; Young, R. A. (2004): Conservation of bats in suburban landscapes: roost selection by *Myotis yumanensis* in a residential area in California. *Biol. Cons.* **115**, 463-473.
- Flavin, D. A.; Biggane, S. S.; Shiel, C. B.; Smiddy, P.; Fairley, J. M. (2001): Analysis of the diet of Daubenton's bat *Myotis daubentonii* in Ireland. *Acta Theriol.* **46**, 43-52.
- Gerell, R.; Lundberg, K. (1985): Social organization in the bat *Pipistrellus pipistrellus*. *Behav. Ecol. Sociobiol.* **16**, 177-184.

- Jenkins, E. V.; Laine, T.; Morgan, S. E.; Cole, K. R.; Speakman, J. R. (1998): Roost selection in the pipistrelle bat, *Pipistrellus pipistrellus* (Chiroptera: Vespertilionidae), in northeast Scotland. *Anim. Behav.* **56**, 909-917.
- Jones, G.; Rayner, M. V. (1988): Flight performance, foraging tactics and echolocation in free-living Daubenton's bats *Myotis daubentonii* (Chiroptera: Vespertilionidae). *J. Zool. Lond.* **215**, 113-132.
- Kapfer, G.; Rigot, T.; Devillers, P. (2006). Caractéristique des premiers gîtes arboricoles de Chiroptères identifiés en Forêt de Soignes. *Nat. Belges* **87**, 25-36.
- Kerth, G.; König, B. (1999): Fission, fusion and nonrandom associations in female Bechstein's bats (*Myotis bechsteinii*). *Behaviour* **163**, 1187-1202.
- Kerth, G.; Safi, K.; König, B. (2002): Mean colony relatedness is a poor predictor of colony structure and female philopatry in the communally breeding Bechstein's bat (*Myotis bechsteinii*). *Behav. Ecol. Sociobiol.* **52**, 203-210.
- Kerth, G.; Wagner, M.; König, B. (2001): Roosting together, foraging apart: information transfer about food is unlikely to explain sociality in female Bechstein's bats (*Myotis bechsteinii*). *Behav. Ecol. Sociobiol.* **50**, 283-291.
- Krull, D.; Schumm, A.; Metzner, W.; Neuweiler, G. (1991): Foraging areas and foraging behavior in the notch-eared bat, *Myotis emarginatus* (Vespertilionidae). *Behav. Ecol. Sociobiol.* **28**, 247-253.
- Kunz, T.H. (ed.) (1982): Ecology of bats. Plenum Press, New York.
- Leonard, M. L.; Fenton, M. B. (1984): Echolocation calls of *Euderma maculatum* (Vespertilionidae) use in orientation and communication. *J. Mamm.* **65**, 126-130.
- Leuzinger, Y.; Brossard, C. (1994): Répartition de *M. daubentoni* en fonction du sexe et de la période de l'année dans le Jura bernois : résultats préliminaires. *Mitt. natf. Ges. Schaffhausen* **39**, 135-143.
- Lewis, S. E. (1995): Roost fidelity of bats: a review. *J. Mamm.* **76**, 481-496.
- Limpens, H. J. G. A.; Helmer, W.; van Winden, A.; Mostert K. (1989): Vleermuizen (Chiroptera) en lintvormige landschapselementen. *Lutra* **32**, 1-20.
- Limpens, H. J. G. A.; Kapteyn, K. (1991): Bats, their behaviour and linear landscape elements. *Myotis* **29**, 39-48.
- McCracken, G. F.; Bradbury, J. W. (1981): Social organization and kinship in the polygynous bat *Phyllostomus hastatus*. *Behav. Ecol. Sociobiol.* **8**, 11-34.
- Mitchell-Jones, A. J.; Amori, G.; Bogdanowicz, W.; Krištufek, B.; Reijnders, P. J. H.; Spitzenberger F.; Stubbe, M.; Thissen, J. B. M.; Vohralik, V.; Zima, J. (eds.) (1999): The Atlas of European Mammals. Academic Press, London.
- Park, K. J.; Masters, E.; Altringham, J. D. (1998): Social structure of three sympatric bat species (Vespertilionidae). *J. Zool., Lond.* **244**, 379-389.
- O'Donnell, C. F. J. (2002): Timing of breeding, productivity and survival of long-tailed bats *Chalinolobus tuberculatus* (Chiroptera: Vespertilionidae) in cold-temperate rainforest in New Zealand. *J. Zool., Lond.* **257**, 311-323.
- O'Donnell, C. F. J. (2000): Cryptic local populations in a temperate rainforest bat *Chalinolobus tuberculatus* in New Zealand. *Animal Conservation* **3**, 287-297.
- O'Donnell, C. F. J.; Sedgeley, J. A. (1999): Use of roosts by the long-tailed bat, *Chalinolobus tuberculatus* in temperate rainforest in New Zealand. *J. Mamm.* **80**, 913-923.
- Racey, P. A.; Swift, S. M. (1985): Feeding ecology of *Pipistrellus pipistrellus* (Chiroptera: Vespertilionidae) during pregnancy and lactation. I. Foraging behaviour. *J. Anim. Ecol.* **54**, 205-215.
- Ransome, R. D. (1990): The Natural History of Hibernating Bats. Christopher Helm, Bromley, Kent, U.K.
- Richardson, P. W. (1994): A new method for distinguishing Daubenton's bats (*Myotis daubentonii*) up to one year old from adults. *J. Zool. Lond.* **233**, 307-309.
- Rieger, I.; Walzthöny, D.; Alder, H. (1990): Wasserfledermäuse, *Myotis daubentoni*, benutzen Flugstrassen. *Mitt. natf. Ges. Schaffhausen*, **35**, 37-68.
- Rieger, I.; Alder, H.; Walzthöny, D. (1992): Wasserfledermäuse, *Myotis daubentoni*, im Jagdhabitat über dem Rhein. *Mitt. natf. Ges. Schaffhausen* **37**, 1-34.

- Rieger, I., (1996a): Wie nützen Wasserfledermäuse, *Myotis daubentoni* (Kuhl, 1817), ihre Tagesquartiere? Z. Säugetierk. **61**, 202-214.
- Rieger, I. (1996b): Tagesquartiere von Wasserfledermäusen, *Myotis daubentoni* (Kuhl, 1819), in hohlen Bäumen. Z. Forstwes. **147**, 1-20.
- Rieger, I. (1996c): Aktivität von Wasserfledermäusen, *Myotis daubentonii*, über dem Rhein. Mitt. natf. Ges. Schaffhausen **41**, 27-58.
- Rossiter, S. J.; Jones, G.; Ransome, R. D.; Barratt, E. M. (2002): Relatedness structure and kin-biased foraging in the greater horseshoe bat (*Rhinolophus ferrumequinum*). Behav Ecol Sociobiol. **51**, 510-518.
- Russo, D. (2002): Elevation affects the distribution of the two sexes in Daubenton's bats *Myotis daubentonii* (Chiroptera: Vespertilionidae) from Italy. Mammalia **66**, 543-551.
- Russo, D.; Cistrone, L.; Jones, G. (2005): Spatial and temporal patterns of roost use by tree-dwelling barbastelle bats *Barbastella barbastellus*. Ecography **28**: 769-776.
- Senior, P.; Butlin, R. K.; Altringham, J. D. (2005): Sex and segregation in temperate bats. Proc. R. Soc. B. **272**, 2467-2473.
- Sullivan, C. M.; Shiel, C. B.; McAney, C. M.; Fairley, J. S. (1993): Analysis of the diet of Leisler's *Nyctalus leisleri*, Daubenton's *Myotis daubentonii* and pipistrelle *Pipistrellus pipistrellus* bats in Ireland. J. Zool. Lond. **231**, 656-663.
- Swift, S. M.; Racey, P. A. (1983): Resource partitioning in two species of vespertilionid bats (Chiroptera) occupying the same roost. J. Zool. Lond. **200**, 249-259.
- Swift, S. M. (1997): Roosting and foraging behaviour of Natterer's bats (*Myotis nattereri*) close to the northern border of their distribution. J. Zool. Lond. **242**, 375-384.
- Vonhof, M. J.; Barclay, R. M. R. (1996): Roost-site selection and roosting ecology of forest-dwelling bats in southern British Columbia. Can. J. Zool. **74**, 1797-1805.
- Wallin, L. (1961): Territorialism on the hunting ground of *Myotis daubentoni*. Säugetierk. Mitt. **9**, 156-159.
- Warren, R. D.; Waters, D. A.; Altringham, J. D.; Bullock, D. J. (2000): The distribution of Daubenton's bats (*Myotis daubentonii*) and pipistrelle bats (*Pipistrellus pipistrellus*) (Vespertilionidae) in relation to small-scale variation in riverine habitat. Biol. Cons. **92**, 85-91.
- White, G. C.; Garrott, R. A. (1990): Analysis of wildlife radio-tracking data. Academic Press, New York.
- Willis, C. K. R.; Brigham, R. M. (2004): Roost switching, roost sharing and social cohesion: forest-dwelling big brown bats, *Eptesicus fuscus*, conform to the fission-fusion model. Anim. Behav. **68**, 495-505.
- Zahn, A.; Maier, S. (1997): Jagdaktivität von Fledermäusen an Bächen und Teichen. Z. Säugetierk. **62**, 1-11.

## **Discussion générale**

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The main goal of this PhD thesis was to provide a comprehensive data set on the distribution and habitat use of different bat species along a string of ponds in the South-eastern part of the Brussels Region. In particular, this work addressed four complementary research topics. Firstly, we assessed the composition of assemblages along the Woluwe hydrographical network to evaluate bat species richness in the studied area. We also investigated the impact of various factors, including the distance to the forest or insect production of ponds on the distribution of bat species along the pond network. Secondly, to estimate the relative bat activity around a pond, we compared two methods based on acoustic sampling, namely Activity Duration and Bat Passes. Then, we determined variations in bat activity for different species throughout the activity season, using a standardized method. Thirdly, we compared the efficiency of different insect sampling devices to investigate how insect availability (*i.e.*, numbers, taxa and size) influences bat activity around ponds. Finally, we focused our effort on the study of roosting and hunting fidelity of one bat species strictly dependent on the presence of water bodies for foraging.

### **Composition and distribution of bat species**

Our results confirmed the high species richness of bats in the south-east of the Brussels' Region, along the Woluwe hydrographical basin. One species, the soprano pipistrelle *Pipistrellus pygmaeus*, was described for the first time in the Brussels' Region and this occurrence also corresponds to the southern report of the species in the Benelux. The coexistence of several bat species requires the presence of convenient roosts and hunting sites that may greatly vary among species. All species roosting in the vicinity of riparian or riverine habitats may be surveyed in this particular environment either temporarily or more permanently during the night, because of the presence of water and insects. This is particularly true in urban environments, where drinking and food sources may be scarce. In agreement with this hypothesis, we found that water bodies situated close to the Forêt de Soignes were exploited by at least ten bat species. Many were observed occasionally and likely came to ponds for short periods to drink, before reaching the foraging habitats they were adapted to. Other species remained for longer periods and foraged actively in this habitat sometimes until dawn. We estimated that species richness over ponds decreased with increasing distance to the forest. Indeed, some species typically hunt exclusively inside woodland drives or clearings, and are usually absent from more anthropogenic areas (Nyholm, 1965; Devillers et al., 2004).

To date, most investigations on bat species richness in the Brussels' Region have been performed in parks, in the South-east, North, and the South-west of the Region (Devillers et al., 2004). Comparatively, few studies have been carried out in the Forêt de Soignes (Kapfer, 2001). Yet, it is probably the largest roosting spot in the area, and individuals or small populations belonging to others bat species than those identified in this study may still occupy the forest, more or less regularly throughout years. In the last decades, previous works reported sightings of the barbastelle *Barbastellus barbastella*, the great mouse-eared bat *Myotis myotis*, and more recently of the Bechstein's bat *Myotis bechsteini* (Devillers et al., 2004; van der Wijden pers. com.). Cryptic species from the whiskered bat *M. mystacinus* (*i.e.*, *Myotis brandtii*, *M. alcathoe*) might also be present according to their geographical distribution (Fairon, 1980; von Helversen

et al., 2001). During summer, intensive prospecting involving many field workers and including mist-netting sessions as well as monitoring of echolocation calls in clearings, forest drives and the canopy, could reveal the existence of these species, which are mostly encountered in deciduous forests. In winter, regular visits should also be encouraged in all possible or reported hibernation sites. Those surveys will be valuable tools to assess the status of bat populations in the area and provide feedbacks regarding the success of conservation management for bats.

### **Bat assemblages around ponds, does competition occurs?**

Belgian bat species are all insectivorous, but they do not necessarily prey on the same food items. Species have either specialised on different insect groups and/or adapt their hunting behaviour to a type habitat. For example, among gleaners some species select diurnal insect resting on the foliage by using echolocation (e.g., notch-eared bats *Myotis emarginatus*, Krull et al., 1991), or moths by using passive listening (long-eared bats *Plecotus* sp., Anderson & Racey, 1991). Other species hunt over water surface (e.g., Daubenton's bats *M. daubentonii*, Jones & Rayner, 1988) or in altitude (>10m) (e.g., serotines bats *Eptesicus serotinus*, Jensen & Miller, 1999). The common pipistrelles *Pipistrellus pipistrellus*, one of the most opportunistic European bat species (Vaughan et al., 1997), mostly hunts near vegetation in forests, lowland agricultural areas as well as near new housing estates (Racey & Swift, 1985; Gaisler et al., 1998). We assessed insect availability at a pond, by comparing insect trapping between emergence and sticky traps. Our results showed a lack of association in the number of prey captured between both trapping methods. Clearly, future work aimed at estimating bat activity in relation to prey availability in a riparian habitat should test whether bat activity is primarily affected by insect emerging from the water or by the overall flying insect abundance. Although this kind of experiment implies much effort, Fukui et al. (2006) clearly showed that both prey sources must be considered to decipher the relative contribution of both sources of preys on bat foraging activity.

Three pipistrelle species have been simultaneously recorded over the Silex pond, *P. pipistrellus*, Nathusius' pipistrelles *P. nathusii*, and soprano pipistrelles *P. pygmaeus*. The co-occurrence of these species is not surprising, since soprano pipistrelles and Nathusius' pipistrelles forage respectively in freshwater habitats in the vicinity of their roosts and in wooded areas (Oakley & Jones, 1998; Mitchell-Jones et al., 1999); both these types of habitats characterise our study area. According to the niche theory, the stable coexistence of species within a guild (here, aerial hawking insectivorous bats) should be associated with a mechanism of resource partitioning when resources are limited (Ricklefs, 1990). Arlettaz et al. (2000) suggested that the decrease of the lesser horseshoe bat *Rhinolophus hipposideros* might result from an increase in populations of common pipistrelles, which prey on the same insect items. Common pipistrelles often concentrate their foraging activity around lit areas, whereas lesser horseshoe bats usually avoid such anthropogenic zones (Rydell, 1992; Arlettaz et al., 2000). Other cases of competitive exclusion have been described by Baagøe (1986), with serotines bats evincing parti-coloured bats *Vespertilio murinus* from Danish islands. In Southern Switzerland, common pipistrelles are confined to the uplands as a result of competitive pressure from the larger and more aggressive pipistrelle *P. kuhlii* species (Haffner & Stutz, 1985-86). Dietary

segregation in morphologically similar species results from the use of distinct foraging habitats. Sympatric sibling species of mouse-eared bats *M. myotis* and *M. blythii* segregated spatially to an extent preventing competitive interference. They exploited highly distinct niches as predicted by niche theory, the former preying on ground- and grass-dwelling insect taxa, respectively (Arlettaz et al., 1997; Arlettaz, 1999). Whether species of the genus *Pipistrellus* partition their food resources on the basis of prey type or size and, if hunting on similar prey, how they share the hunting space, await further studies. To the best of our knowledge, few works have focused on comparisons of flight, hunting behaviour and diet between different *Pipistrellus* species hunting in the same environment (Gerell-Lundberg & Gerell, 1994; Barlow, 1997). The use of telemetry and/or reflecting tape, and a standardised protocol could help assessing variations for the different species in flight height, distance to the foliage, or flying patterns.

### **Ponds as foraging and mating grounds**

We tested two methods for the assessment of bat activity around ponds. The best estimator in a highly frequented habitat was Activity Duration (AD) instead of Bat Passes (BP), the latter being usually chosen in most studies on bat activity (Vaughan et al., 1996; Kalcounis et al., 1999; Karlsson et al., 2002). The use of BP is convenient when comparing bat activity between different environments or for continuous monitoring in areas with low bat records per unit of time. Conversely, AD is advised in case studies carried out in habitats showing high activity levels. This estimator gives more accurate views of activity fluctuations, especially when estimating changes in habitat use by bats around ponds in relation to the surroundings or throughout the season. Our data reveal contrasting results for two common species currently observed around ponds: the common pipistrelles and the Daubenton's bats. Foraging and flight activities of common pipistrelles changed markedly throughout the season. On the one hand, flight activity rose progressively from spring to late summer, whereas foraging activity followed the same trend until August-September, when the number of captures dropped significantly. These changes were most likely influenced by the reproductive cycle of the species. Arrival of juveniles that start to fly at the end of June - beginning of July (Swift, 1980; Whitaker, 1998), and the higher activity of males during post-lactation (Gerell-Lundberg & Gerell, 1994) may explain the increase in activity around the pond during lactation and post-lactation. The decrease in foraging activity during post-lactation is consistent with males reducing their foraging activity and spending considerable time to defend their day roosts where they constitute harems (Gerell & Lundberg, 1985, Lundberg & Gerell, 1986). The species also showed a decreased activity after sunset, associated with a drop in foraging behaviour and a rise in the time needed to capture insects. This may be linked to a significant drop of air temperature just after sunset, which is usually associated with a decrease in flying insect availability (Anthony & Kunz, 1977).

However, we also observed that during warm nights, pipistrelles were generally less active around ponds, which account for a displacement of individuals either back to their roost or to other more sheltered hunting places. In Daubenton's bats, changes in flight activity were not so obvious. However, we noticed a small increase during lactation and a decrease in late summer that could be related to the arrival of young and with individuals leaving the area for mating or

hibernation, respectively (Dietz & Fitzenr uter, 1996; Encarn ao et al., 2004). Capture time was very low and constant in Daubenton's bats, which shows that the species is well adapted to this habitat. Air temperature did not seem to affect the species activity over the pond. Indeed, if Daubenton's bats rely on emerging insects, their activity is expected to be more closely affected by water temperature that conditions insect emergence success, rather than by air temperature.

### **Roosting and hunting site fidelity**

Unequal prey distribution requires the use of cues allowing animals to find their food resource and help to minimise foraging costs. In Daubenton's bats, foraging grounds are limited to freshwater surfaces located in the vicinity of their tree-roosts (Helmer, 1983; Ebenau, 1995). In addition, the species usually exploit foraging areas that are connected with Linear Landscape Elements to their roost (Limpens et al., 1989). Using radio-telemetry of female and juvenile Daubenton's bats, we investigated the strategy used by this species to survive in a saturated and closed environment such as the Brussels' Capital Region. We found that bats occupied a limited number of trees located in a specific and small roosting area. This roost aggregation was not linked to the distribution of hollow trees. Furthermore, whereas other ponds were available in the study area and indeed exploited by other Daubenton's bats, monitored individuals showed high fidelity to two ponds. Overall, these results strongly suggest that female and juvenile Daubenton's bats are highly faithful to specific roosting and hunting grounds. There is need for more experimental studies to be carried out on the territorial behaviour of the species. Further investigation using telemetry and/or transponders could find out if females Daubenton's bats use the same zone over years, if changes occur from time to time, or if females keep territories chasing intruders. The demarcation of discreet roosting territories should not only be carried out in the For t de Soignes, but also along the Woluwe River. A map of different roosting aggregates and the associated ponds could then be drawn. Captures and monitoring with radio-tags should allow determining the differential repartition of sexes along the pond network – if any, the role of biological corridors on commuting hunting sites, or existence of roosting territories away from the forest in wooded areas and perhaps in human constructions. In the same vein, banding and genetics studies would be helpful to analyse if females roosting together during summer share roosts with the same individuals over years, if individuals are philopatric to their natal roost or if they adopt a dispersion pattern. Finally, it would be of particular interest to study in what extent roost mates hunt together and if they adopt a territorial behaviour against strangers to the colony or to the roosting zone.

## References

- Anderson, M. E. & P. A., Racey, 1991. Feeding behaviour of captive brown long-eared bats, *Plecotus auritus*. Anim. Behav., 42: 489-493.
- Anthony, E. L. P. & T. H., Kunz, 1977. Feeding strategies of the little brown bat, *Myotis lucifugus*, in southern New Hampshire. Ecology, 58: 775-786.
- Arlettaz, R., Perrin, N. & J., Hausser, 1997. Trophic resource partitioning and competition between the two sibling bat species *Myotis myotis* and *Myotis blythii*. J. Anim. Ecol., 66: 897-911.
- Arlettaz, R., 1999. Habitat selection as a major resource partitioning mechanism between the two sympatric sibling bat species *Myotis myotis* and *Myotis blythii*. Journal of Animal Ecology, 68: 460-471.
- Arlettaz, R., Godat, S. & H., Meyer, 2000. Competition for food by expanding pipistrelle bat populations (*Pipistrellus pipistrellus*) might contribute to the decline of lesser horseshoe bats (*Rhinolophus hipposideros*) Biol. Cons., 93: 55-60.
- Baagøe, H. J., 1986. Summer occurrence of *Vespertilio murinus* (Linné 1758) and *Eptesicus serotinus* (Schreber 1780) (Chiroptera, Mammalia) on Zealand, Denmark, based on records of roosts and registration with bat detectors. Annales Naturhistorisches Museum Wien, 88-99: 281-291.
- Barlow, K. E., 1997. The diets of two phonic types of the bat *Pipistrellus pipistrellus* in Britain. J. Zool., Lond., 243: 597-609.
- Devillers P., Kapfer G., Devillers-Terschuren J., Lafontaine R.-M. & Y., Laurent, 2004. Les Chauves-souris de la Région bruxelloise: Distribution et Habitats. Nat. Belg., 85: 1-50.
- Dietz, M. & B., Fitzenräter, 1996. Zur Flugroutennutzung einer Wasserfledermauspopulation (*Myotis daubentonii* Kuhl, 1819) im Stadtbereich von Giessen. Säugetierkd. Inf., 20: 107-116.
- Ebenau, C., 1995. Ergebnisse telemetrischer Untersuchungen an Wasserfledermausen (*Myotis daubentonii*) in Mulheim an der Ruhr. Nyctalus, 5: 379-394.
- Encarnação, J. A., Dietz, M. & U., Kierdorf, 2004. Reproductive condition and activity pattern of male Daubenton's bats (*Myotis daubentonii*) in the summer habitat. Mamm. Biol., 69: 163-172.
- Fairon, J., 1980. *Myotis brandti* en Belgique. Bull. Int. r. Sci. nat. Belg., 52: 1-8.
- Fukui, D., Murakami, M., Nakano, S. & T., Aoi, 2006. Effect of emergent aquatic insect on bat foraging in a riparian forest. J. Anim. Ecol., 75: 1252-1258.
- Gaisler, J., Zukal, J., Rehak, Z. & M., Homolka, 1998. Habitat preference and flight activity of bats in a city. J. Zool., Lond., 244: 439-445.
- Gerell, R. & K., Lundberg, 1985. Social organization in the bat *Pipistrellus pipistrellus*. Behav. Ecol. Sociobiol., 16: 177-184.
- Gerell-Lundberg, K. & R., Gerell, 1994. The mating behaviour of the Pipistrelle and the Nathusius' Pipistrelle (Chiroptera) - A comparison. Folia Zool., 43: 315-324.
- Haffner, M. & H. P., Stutz, 1985-86. Abundance of *Pipistrellus pipistrellus* and *Pipistrellus kuhlii* foraging at street lamps. Myotis, 23-24, 167-172.
- Helmer, W., 1983. Boombewonende watervleermuizen *Myotis daubentonii* (Kuhl, 1817) in het van nijmegen. Lutra, 26: 1-11.
- Helversen (von), O., Heller, K.-G., Mayer, F., Nemeth, A., Volleth, M. & P., Gombkötö, 2001. Cryptic mammalian species: a new species of whiskered bat (*Myotis alcathoe* n. sp.) in Europe. Naturwissenschaften, 88: 217-223.
- Jensen, M. E. & L. A., Miller, 1999. Echolocation signals of the bat *Eptesicus serotinus* recorded using a vertical microphone array: effect of flight altitude on searching signals. Behav. Ecol. Sociobiol., 47: 60-69.
- Jones, G. & M. V., Rayner, 1988. Flight performance, foraging tactics and echolocation in free-living Daubenton's bats *Myotis daubentonii* (Chiroptera: Vespertilionidae). J. Zool., Lond., 215: 113-132.
- Kalcounis, M. C., Hobson, K. A., Brigham, R. M. & K. R., Hecker, 1999. Bat activity in the boreal forest: importance of stand type and vertical strata. J. Mamm., 80: 673-682.
- Kapfer, G., 2001. Inventaire des Chauves-souris des Z.S.C. de la Région Bruxelles-Capitale. Rapport de stage de DESS GRNR, Lille, 94p.

- Karlsson, B.-L., Eklöf, J. & J., Rydell, 2002. No lunar phobia in swarming insectivorous bats (family Vespertilionidae). *J. Zool., Lond.*, 256: 473-477.
- Krull, D., Schumm, A., Metzner, W. & G., Neuweiler, 1991. Foraging areas and foraging behavior in the notch-eared bat, *Myotis emarginatus* (Vespertilionidae). *Behav. Ecol. Sociobiol.*, 28: 247-253.
- Limpens, H. J. G. A., Helmer, W., Van Winden, A. & K., Mostert, 1989. Vleermuizen (Chiroptera) en lintvormige landschapselementen. *Lutra*, 32: 1-20.
- Lundberg, K. & R., Gerell, 1986. Territorial advertisement and mate attraction in the bat *Pipistrellus pipistrellus*. *Ethology*, 71: 115-124.
- Mitchell-Jones, A. J., Amori, G., Bogdanowicz, W., Krystufek, B., Reinjnders, P. J. H., Spitzenberger, F., Stubbe, M., Thissen, J.B.M., Vohralik V. & J., Zima, 1999. *The Atlas of European Mammals*, 496p.
- Nyholm, E. S., 1965. Zur Ökologie von *Myotis mystacinus* (Leisl.) und *M. daubentoni* (Leisl.) (Chiroptera). *Ann. Zool. Fenn.*, 2: 77-123.
- Oakeley, S. F. & G., Jones, 1998. Habitat around maternity roosts of the 55 kHz phonic type of pipistrelle bats (*Pipistrellus pipistrellus*). *J. Zool., Lond.*, 245: 222-228.
- Racey, P. A. & Swift, S., 1985. Feeding ecology of *Pipistrellus pipistrellus* (Chiroptera: Vespertilionidae) during pregnancy and lactation. I. Foraging behaviour. *J. Anim. Ecol.*, 54: 205-215.
- Ricklefs, R. F., 1990. *Ecology*. W. H., Freeman, New York, USA.
- Rydell, J., 1992. Exploitation of insects around streetlamps by bats in Sweden. *Funct. Ecol.*, 6: 744-750.
- Swift, S. M. S., 1980. Activity patterns of Pipistrelle bats (*Pipistrellus pipistrellus*) in north-east Scotland. *J. Zool., Lond.*, 190: 285-295.
- Vaughan, N., Jones, G. & S., Harris, 1996. Effects of sewage effluent on the activity of bats (Chiroptera: vespertilionidae) foraging along rivers. *Biol. Cons.*, 78: 337-343.
- Vaughan, N., Jones, G. & S., Harris, 1997. Habitat use by bats (Chiroptera) assessed by means of a broad-band acoustic method. *J. App. Ecol.*, 34: 716-730.
- Whitaker, Jr., J. O., 1998. Life history and roost switching in six summer colonies of eastern pipistrelles in buildings. *J. Mamm.*, 79: 651-659.

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