Temporal variation in flight activity, foraging activity and social interactions by bats around a suburban pond

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

Keywords: Chiroptera, flight activity, foraging activity, social calls.

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 partially feed on fish (Levin et al. 2006). In temperate regions, insect eating bats face ecological constraints such cold temperatures in winter and associated food shortages. Because most temperate bats hibernate, they devote a limited amount of time to breeding and fat accumulation (Ransome 1990). Monitoring bat activity during the active season can thus provide insights into bat behaviour and requirements during this critical period. For insectivorous species, activity patterns, i.e. changes in flight or foraging activities, may vary on a daily or seasonal basis in response to many factors, such as 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 the activity patterns of different bat species over the night and the season (Gaisler et al. 1998, Bartonička & Zukal 2003), and these have generally focused on species distribution in different habitats. Analyses of temporal variations of bat communities at 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 are likely to represent a plentiful and predictable supply of prey and calm water provide a suitable

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drinking site (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 of finding 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 suburban pond based upon data collected in a standardised way. We determined the occurrence, flying and foraging activity patterns of different identified bat species. Because these parameters may be affected by reproductive status (Audet 1990, Barclay 1991), we analysed the data with regard to three reproductive periods: pregnancy, lactation and post-lactation. We also studied for any variations of social calls by common pipistrelles (*Pipistrellus pipistrellus*, Schreber, 1774) on both a nightly and seasonal basis.

Material and methods

Study area and sampling

Our study was conducted between April and September 2003 around the Silex pond, located in the south-east of Brussels, Belgium. This 1 ha pond is located 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, including wet meadows, a pasture with a few hedgerows, and a few apple trees, on the other side.

We recorded bat activity over 50 nights ($\overline{x}$ ± SD: 8.7 ± 2.7 nights per month). Recordings were performed during the first hours following sunset, the time when bats display the highest activity (Anthony & Kunz 1977). Each night, bat activity was sampled 45, 90, and 135 minutes after sunset: these points in time are referred to as Round 1 (R1), Round 2 (R2) and Round 3 (R3), respectively. On each of these nightly sampling rounds, two-minute recordings were randomly taken at six points on the bank of the pond, separated by at least 50 m. Overall, our survey involved taking 870 two-minute recordings. Recordings were made during warm (t° > 10°C at starting point), calm and dry nights to minimize the influence of temperature, wind and rain on bat activity.

To determine the effect of reproductive status on activity patterns, data were separated into three periods: April to mid-June, mid-June to the 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 (Swift 1980, Bogdanowicz 1994, Bartonicka & Zukal 2003). Occasional captures by mist-netting Daubenton's bats (*Myotis daubentonii*, Kuhl, 1817) over the pond confirmed that the selected periods were consistent with the 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 means of 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 in which 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. These were recognised by the 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 lapse of time.

Emission of social calls

Social calls are signals with low-frequency components that can occur between echolocation calls for the purpose of communication (Fenton 2003). Because the common pipistrelle was the most abundant in the study area, we focused our analysis of social calls solely on this species. Emission of social calls was assessed by counting the number of vocalisations registered per two-minute interval, through simultaneous recordings in time expansion and frequency division.

Statistical analysis

Data were compared by using nonparametric Kruskall-Wallis, Mann-Whitney and Dunn's post hoc tests using Statistica 6.0. For comparisons of activity levels, records where no bats were registered were excluded from the analyses, to move the median value from zero and to obtain clearer graphs.

Results

Occurrence, overall flight activity and foraging rate

The recordings allowed identification of seven species (figure 1): common pipistrelle, Nathusius' pipistrelle (*Pipistrellus nathusii*, Keyserling & Blasius, 1839), soprano pipistrelle (*Pipistrellus pygmaeus*, Leach, 1825), Dauben-

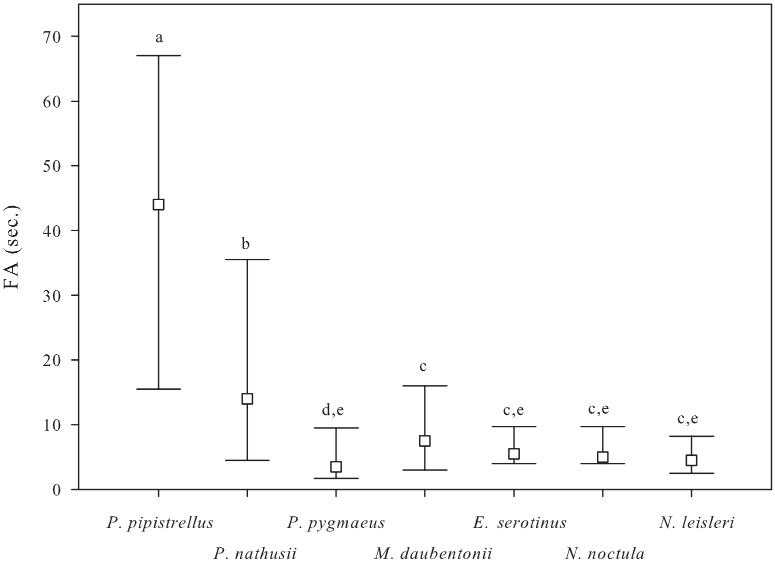

Figure 1. Overall flight activity (FA) (median, percentiles 25%, 75%), measured as the duration of bat passes per two-minute period, for the seven species identified around the pond. Equal lowercase letters indicate absence of significant differences (Dunn's tests, P<0.05).

Table 1. Overall flight and foraging activity medians (in brackets) and capture time (in italic) in each reproductive period and round for *Pipistrellus pipistrellus, Pipistrellus nathusii* and *Myotis daubentonii*.

	Pregnancy			Lactation			Post-lactation		
	R1	R2	R3	R1	R2	R3	R1	R2	R3
Pipistrellus pipistrellus	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)
	7.8	*11.3*	*15.2*	*6.0*	*9.4*	*11.3*	*10.2*	*20.2*	*25.0*
Pipistrellus nathusii	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)
	15.3	*39.2*	*27.6*	*18.2*	*13.1*	*16.1*	*13.2*	*29.8*	*49.6*
Myotis daubentonii	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)
	4.8	*5.8*	*5.3*	*4.7*	*6.6*	*7.7*	*6.1*	*8.8*	*7.2*

ton's bat, noctule (*Nyctalus noctula,* Schreber, 1774), Leisler's bat (*Nyctalus leisleri,* Kuhl, 1817) and serotine (*Eptesicus serotinus,* Schreber, 1774).

Flight activity levels differed significantly between species (Kruskall-Wallis test, H= 517.2, P<0.001; figure 1). Overall activity was higher among common pipistrelles (P<0.001); which was identified in 100% of the nightly samplings. Nathusius' pipistrelles were more active than Daubenton's bats (P<0.001), primarily because of the higher flight activity of Nathusius' pipistrelles during post-lactation (see below). However, whereas Nathusius' pipistrelles were identified on 76% of our recording nights, this value reached 96% for Daubenton's bats, indicating that this species regularly visits the study area. There were no significant differences in the activity levels of Soprano pipistrelles, serotines, Leisler's bats and noctules (P>0.05) and these species were excluded from further analyses due to their low activity levels and/or occurrence.

Capture time also varied according to the species (H=18.38, P< 0.001). Daubenton's bats captured insects more rapidly, with their feeding attempts occurring approximately every six seconds. By comparison common pipistrelles and Nathusius' pipistrelles captured insects every 13 and 24 seconds, respectively (P<0.05; table 1).

Flight and foraging activities after sunset during each reproductive period

The flight activity of common pipistrelles decreased after sunset throughout the successive reproductive periods **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). Activity in round R1 was significantly higher than in R3 (P<0.05). By contrast, the flight activities of Daubenton's bats and Nathusius' pipistrelles were relatively stable between these three rounds throughout all three periods (**P**: H=0.6, P=0.72; **L**: H=0.6, P=0.76; **PL**: H=5.2, P=0.07; and **P**: H=2.1, P=0.34; **L**: H=1.7, P=0.41; **PL**: H=0.4, P=0.83 respectively, table 1).

Consistent with flight activities, the pipistrelles showed a significant difference in the number of feeding buzzes recorded between the three rounds and for each period (**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 in each reproductive period (P<0.01). The after sunset foraging activity of Nathusius' pipistrelles did not vary during pregnancy and lactation (**P**: H=1.1, P=0.57; **L**: H=1.3, P=0.522; table 1); although more feeding buzzes were recorded in R1 during post-lactation (H=22.6, P<0.001; Dunn's test, P<0.01). Among Daubenton's bats, foraging activity remained constant during the three nightly intervals and for all three periods consid-

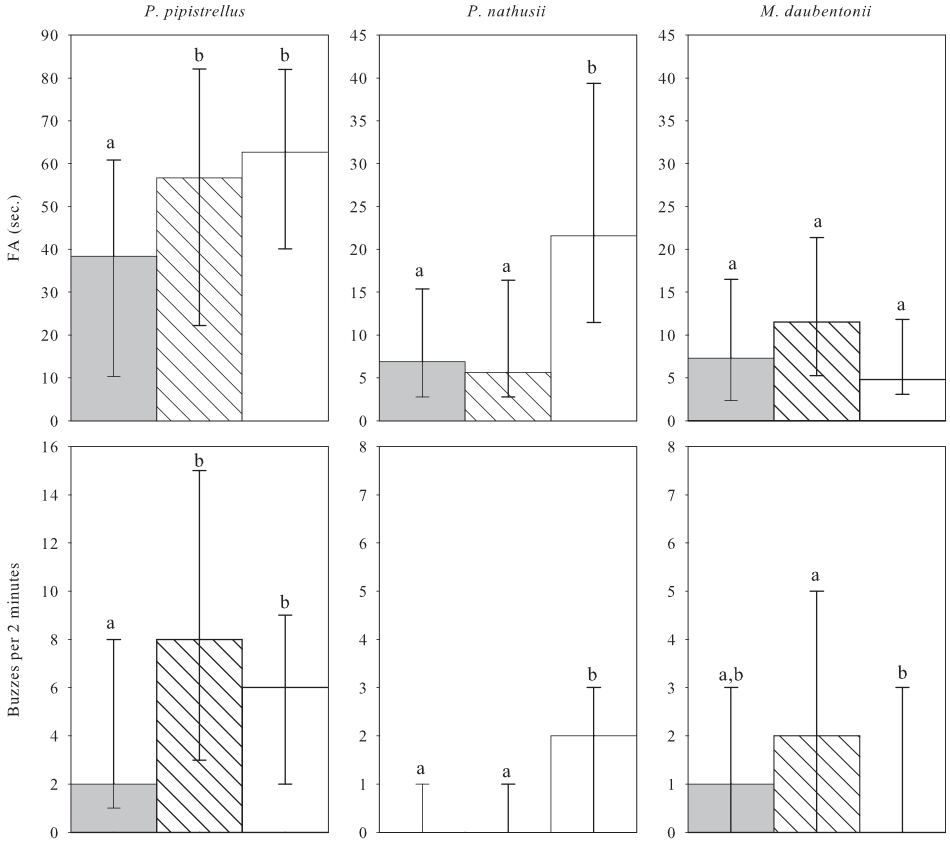

Figure 2. Flight activity (FA) and foraging activity (buzzes) (median, percentile 25% and 75%) of *Pipistrellus pipistrellus, Pipistrellus nathusii* and *Myotis daubentonii* during R1, according to three reproductive periods: pregnancy, lactation and post-lactation (respectively grey, hatched and white bars). Equal lowercase letters indicate absence of significant differences (Dunn's tests, $P<0.05$).

ered (**P**: $H=1.6$, $P=0.45$; **L**: $H=5.3$, $P=0.071$; **PL**: $H=0.7$, $P=0.69$), with medians being generally higher than for Nathusius' pipistrelles (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 derived from round R1, which showed the highest overall activity values. Differences in activity between R1, R2 and R3 were independent of the season. Flight activity varied significantly with the reproductive period for all the three species studied ($H=25.9$, $P<0.001$ for common pipistrelles; $H=24.5$, $P<0.001$ for Nathusius' pipistrelles and $H=6.6$, $P<0.04$ for Daubenton's bats; figure 2a). The flight activity of common pipistrelles was significantly lower during pregnancy than during lactation and post-lactation ($P<0.01$). Nathusius' pipistrelles were more active during post-lactation than during the two other reproductive periods ($P<0.01$). Daubenton's bats showed lower, but non-significant levels, of flight activity during post-lactation ($P>0.05$). Foraging activity levels followed the same trend as flight activity among all three species (common pipistrelles $H=24.6$, $P<0.001$; Nathusius' pipistrelles $H=17.9$, $P<0.001$; Daubenton's bats $H=9.5$, *P*<0.009; figure 2b). In common pipistrelles and Daubenton's bats, foraging activity was significantly higher during lactation than during pregnancy and post-lactation (*P*<0.01).

Emission of social calls

The number of social calls emitted by common pipistrelles 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 these periods bats produced less social calls during R1 than during R2 and R3 (*P*<0.05). The number of social calls also varied between reproductive periods (*H*=121.1, *P*<0.001), with more calls recorded during post-lactation (*P*<0.001; figure 3).

Discussion

Three species of the genus *Pipistrellus* are represented in our study area: common pipistrelles, Nathusius' pipistrelles and the soprano pipistrelles. However, their activity levels and presumably the total numbers of individuals of each species over the pond, varies considerably. Common pipistrelles are the most dominant species, being recorded on all the sampling occasions and having higher estimated levels of activity. The Nathusius' pipistrelle 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 common pipistrelles consist of both sexes, whereas groups of Nathusius' pipistrelles in spring and early summer consist mainly of males. At this period of the year, female Nathusius' pipistrelles move to the eastern part of their range and join harems on their migration routes to their hibernation sites (Lina 1990, Kapteyn & Lina 1994). The soprano pipistrelle occurs less regularly and activity levels are very low. This species was described for the first time in the Brussels Region in 2002 and is not widespread in Belgium (Kapfer, Van de Sijpe et al., in press). The Daubenton's bat was also commonly recorded over the pond and made very frequent capture attempts, demonstrating that the species is particularly efficient in catching prey in this environment. Finally, serotines, noctules and Leisler's bats were 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.

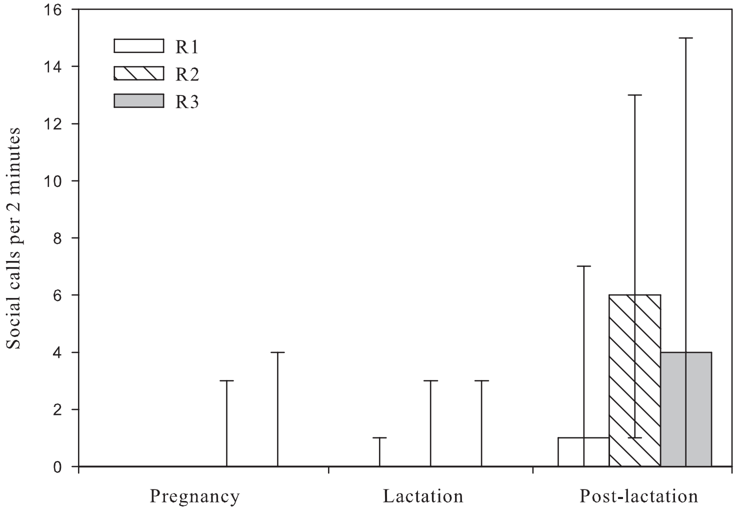

Figure 3. Social calls sampled per round (median, percentile 25% and 75%) as a function of the reproductive period in *Pipistrellus pipistrellus*.

Our data also show that the flight and foraging activities of common pipistrelles decrease throughout the hours following sunset. This might be due to a rapid fall in the number of flying insects, bought about by rapidly declining temperature after sunset (Anthony & Kunz 1977). When insect density rapidly decreases, aerial hawking bats stop hunting as the cost of prey detection may become too high (Rydell et al. 1996). We do not know whether the decrease in activity recorded over the night results from bats returning to their roost with a full stomachs, or from animals leaving the pond to move to other more rewarding hunting areas. The flight and foraging activities of Daubenton's bats remain relatively constant over at least the first hours after sunset. Similar data have been 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). The emergence of aquatic insects follows a diurnal rhythm, closely linked with illumination levels and water temperature, but not correlated with air temperature (Morgan & Waddell 1961). Our results are consistent with this observation since Daubenton's bats continue to hunt with a constant and high capture rate, even when *Pipistrellus* species hunt less efficiently.

Variation in flight activity throughout the summer might 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 the site, or leaving it for better ones. Our study area was not a confined space, so all these explanations are possibilities. Previous studies (Kapfer, in prep.) suggest that food is not a limited resource in the area, at least during the time that we conducted the experiments. Kapfer, Rigot et al. (in press) have recently shown that female and juvenile Daubenton's bats are faithful to the same hunting places. This strongly supports the idea that fluctuations in flight activity are associated with the reproductive periods. Indeed, the arrival of juvenile common pipistrelles that start to fly around the end of June and 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 containing their harems (Gerell-Lundberg & Gerell 1994). Males probably reduce their foraging activity and spend considerably more time flying in the immediate vicinity of their day roosts (Gerell & Lundberg 1985, Lundberg & Gerell 1986). As mentioned above, flight activity among Nathusius' pipistrelles is relatively low from spring to mid-summer, but increases during the post-lactation period. This may be primarily related to a higher flying activity of males but is also partly due to an influx of new individuals (e.g. migrating females) visiting the area (Kapteyn & Lina 1994, Peterson 2004). The low flight activity of Daubenton's bats recorded in August and September might be a result of changes in activity patterns, with males resting in the day roost to establish mating roosts (Encarnaçao 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 common pipistrelles varies in both during the course of the night and between different reproductive periods. Social calls are higher during the first hours after sunset, probably as a result of a decline in insect availability leading to increasingly territorial behaviour. Barlow & Jones (1997) used play-back experiments to demonstrate that social calls are used to warn off and drive away other pipistrelles of the same species when insect densities decrease. These calls are often combined with chases. Our investigations also reveal that the species emits more social calls during post-lactation than during the two former reproductive periods. At the end of summer, males produce “songflights” apparently to deter male intruders but also to attract females to their roost (Gerell-Lundberg & Gerell 1994). Preliminary work suggests that the 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 behaviour.

Many studies have built up general pictures of the behaviour of bat assemblages over a pond. However, to the best of our knowledge, there is a shortage of field experiments, performed in a standardised manner, on temporal patterns of bat flights and foraging activities. The present study confirms that urban ponds are important habitats for bats, and can show a high species richness. Apart from being important as drinking sites, they are also used as foraging and mating grounds during different reproductive periods of the species considered.

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Samenvatting

Temporele variatie in vliegactiviteit, jachtactiviteit en sociale interacties van vleermuizen boven een vijver in een buitengebied

Ons onderzoek spitste 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, Pipistrellus nathusii* en *Myotis daubentonii*) dominant wat betreft voorkomen en/of vliegactiviteit. De vliegactiviteit van *Pipistrellus pipistrellus* fluctueerde sterk in tijd, met een piek net na zonsondergang. De activiteit van *Pipistrellus nathusii* en *Myotis daubentonii* bleef vrij constant gedurende minstens twee uur na zonsondergang. De vlieg- en jachtactiviteit varieerden met het voortplantingsseizoen. Waar de vliegactiviteit toenam van drachtperiode tot de post-lactatieperiode bij het genus *Pipistrellus*, nam deze af gedurende de post-lactatie bij *Myotis daubentonii*. Een toename van sociale roepen werd aangetoond bij *Pipistrellus 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.

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