

Seasonal activity patterns of seven vespertilionid bat species in Polish lowlands

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Data on seasonal dynamics of bat activity in central Europe are scarce, mostly restricted to either summer period or autumn swarming. Few studies provide extensive interspecific comparisons of temporal activity patterns. Through broadband ultrasound detection, temporal variation of flight activity was studied in seven insectivorous bat species in N Poland for the first time. Seasonal activity pattern of *Myotis daubentonii* (Kuhl, 1817) was clearly bimodal with the higher peak of activity in April and the second, smaller peak in August–September. The first peak is possibly associated with post-hibernal restoration of fat reserves, while the second one might result either from pre-hibernal fat accumulation, increase in energy demands of males during spermatogenesis or from dispersal of newly weaned juveniles. The highest flight activity of *Nyctalus*, *Eptesicus* and *Pipistrellus* bats was noted in summer months, reflecting mainly an increase in energy demands between pregnancy and lactation. However, a distinct, second peak in activity of *N. noctula* appeared at the end of September, probably matching the late migration wave of individuals from E Europe. The cluster analysis of species' activity patterns reflected division on different hunting tactics, but not migratory behaviour.

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Introduction

Temperate zone bats are small heterotherms with clearly patterned annual life cycles (Speakman and Thomas 2004). Their flight activity reveals significant seasonal variation (Rachwald 1992, Hayes 1997, Russ *et al.* 2003) and some descriptive studies have tried to interpret its re-

current patterns as effects of annual life cycle. Different energy demands during pregnancy and lactation (Racey and Speakman 1987) result in different time spent outside the roost by female bats (Rydell 1993) and might be expected to result in different levels of bat activity recorded in foraging areas. Harsh winters force bats to migrate different distances or to hibernate (Fleming and Eby 2004, Speakman and

Thomas 2004), thus the strategy of winter survival might be the other factor determining the seasonal dynamics of bat activity.

In many locations, ensembles of insectivorous bats are composed of several species, revealing clear resource partitioning patterns, manifested in differential morphology, echolocation, flight style and hunting tactics (Baagøe 1987, Schnitzler *et al.* 2003, Siemers and Schnitzler 2004). The co-occurring species forage in different microhabitats (Baagøe 1987) but may prefer similar macrohabitats (eg water bodies – Vaughan *et al.* 1997a) thus the activity of several taxa can be monitored in the same sites. Temperate insectivorous bats are therefore likely to be a valuable model to examine if different life histories cause interspecific differences in seasonal patterns of animal activity, although no such study has ever been conducted.

Seasonal dynamics of chiropteran activity is only unsatisfactorily recognised. Most studies conducted in the Palearctic have been restricted to the summer period and frequently devoted only to single species (Rachwald 1992, Furmankiewicz 2003, Bartonička and Řehák 2004), thus they do not provide any interspecific comparisons. For many Central European species (including the commonest ones, eg *Myotis daubentonii*), almost no data on activity have been collected from foraging sites in early spring or late autumn (Encarnação *et al.* 2004a, Dietz and Kalko 2005, Encarnação and Dietz 2006). The only exception was the study of Furmankiewicz and Kucharska (2009) who recorded directionality of migratory movements in five species above a large lowland river of S Poland. Some observations that durated from March–April until October have also been conducted in urban environments (Gaisler *et al.* 1998) and in the agricultural landscape of The British Isles (Russ *et al.* 2003). Hayes (1997) performed year-round automatic bat recording over two forest streams in the Nearctic, although he did not distinguish species and the recorded material was treated as general bat activity. There were also attempts to monitor bat activity year-round in the entrances of underground sites (Parsons *et al.* 2003, Berková and Zukal 2006), however these movements are supposed to be associated primarily not with for-

aging or commuting but with social contacts or assessment of suitable hibernacula (Kerth *et al.* 2003, Piksa 2008). Results obtained in mild, oceanic climates cannot be directly extrapolated to bat populations inhabiting a harsher, continental environment. Bats with large migratory ranges exhibit seasonally varying distribution patterns (Cryan 2003), thus may be expected to reveal geographically varying seasonal patterns of activity.

The aim of this study was to examine if co-occurring insectivorous bats, differing in hunting tactics and migratory behaviour, reveal different patterns of temporal variation in flight activity. We expected that long-distance migrants would start their activity later and finish earlier than sedentary species, and that they would reveal peaks of echolocation activity in spring and autumn, reflecting their migratory movements. We also assumed that activity patterns, subjected to cluster analysis, would group together, reflecting classification of species' based on either seasonal migrations (migratory vs sedentary) or hunting tactics (aerial hawkers vs water-surface foragers). The paper provides, for the first time, data on timing and dynamics of activity of seven vespertilionid species from N Poland that underlay already published multivariate analyses of relationships between environmental factors and spatio-temporal activity of bats (Ciechanowski *et al.* 2007b).

Study area and bat species

The study was conducted in Reda river valley (Baltic Sea Coast region, N Poland; 54°36'N, 18°13'E). The bottom of the valley is covered by pastures, meadows, orchards, willow shrubs, stands of *Alnus glutinosa*, water courses, small ponds and adjacent buildings of the Wejherowo city. The forests of *Fagus sylvatica*, *Quercus robur*, *Carpinus betulus* and planted *Pinus sylvestris* predominate at the valley's slope. Climate is temperate with mean annual temperature 7°C and annual amplitude of monthly temperatures 18–19°C.

Among 12 vespertilionid bat species occurring in the area, only seven were recorded regularly with ultrasound detectors that their dynamics in flight and vocal activity could be analysed. These were: Daubenton's bat *Myotis daubentonii* (Kuhl, 1817), serotine *Eptesicus serotinus* (Schreber, 1774), common pipistrelle *Pipistrellus pipistrellus* (Schreber, 1774), soprano pipistrelle *Pipistrellus pygmaeus*

Table 1. Hunting tactics and migratory behaviour of the studied bat species. WS – water-surface forager (hawking insects less than 0.5 m above the water or gaffing them directly from the surface); AH – exclusive aerial hawkler: 1 – slow but manoeuvrable flyers, hunting at distance 2–10 m from the ground and vertical obstacles, 2 – fast flyers with poor manoeuvring abilities, hunting at height 10–20 m and at distance > 8 m from the vegetation; Se – sedentary, Re – regional, facultative migrants, covering moderate distances (up to 500 km), Lo – long-distance migrants (seasonal, bird-like, movements > 1000 km), ^a under name *P. pipistrellus mediterraneus*.

Species	Hunting tactics	Source	Migratory behaviour	Source
<i>M. daubentonii</i>	WS	Jones and Rayner 1988	Se Re	Strelkov 1969 Fleming and Eby 2004
<i>E. serotinus</i>	AH-1	Baagøe 1987	Se	Fleming and Eby 2004
<i>P. pipistrellus</i>	AH-1	Kalko 1995	Se (W Europe) Lo (E Europe) Lo?	Dietz <i>et al.</i> 2009 Strelkov 1969 Bryja <i>et al.</i> 2009
<i>P. pygmaeus</i>	AH-1	Kalko 1995 ^a	Lo?	Dietz <i>et al.</i> 2009, Bryja <i>et al.</i> 2009
<i>P. nathusii</i>	AH-1	Kalko 1995	Lo	Fleming and Eby 2004
<i>N. noctula</i>	AH-2	Baagøe 1987	Lo	Fleming and Eby 2004
<i>N. leisleri</i>	AH-2	Baagøe 1987	Lo	Fleming and Eby 2004

(Leach, 1825), Nathusius' pipistrelle *Pipistrellus nathusii* (Keyserling et Blasius, 1839), noctule *Nyctalus noctula* (Schreber, 1774) and Leisler's bat *Nyctalus leisleri* (Kuhl, 1817). Captures of lactating females or juveniles indicated that all these species were breeding in the study area. Six species belong to the aerial hawkers and one to the water-surface foragers (Table 1).

The studied taxa were formerly divided into two groups by Strelkov (1969), according to their migratory behaviour. *Myotis* and *Eptesicus* are considered to be sedentary species, hibernating in harsh winter conditions of E Europe, while *Pipistrellus* and *Nyctalus* are generally described as migratory species, performing long-distance movements from breeding areas to hibernacula in W part of the continent. This division, however, does not seem to reflect the complexity of interspecific and geographic differences (Table 1). All studied species give birth mostly in June and wean their young until August (Dietz *et al.* 2009).

Material and methods

The field data

In 2002–2004 bat calls were recorded with broadband ultrasound detectors Pettersson D-980 (in frequency division and time expansion modes) and Pettersson D-230 (in frequency division mode) working with SONY WMD-6C stereophonic tape recorders. Frequency divider in both detectors was able to retain not only call shape but also amplitude data, thus preserving information about peak frequency, commonly used as diagnostic feature for species determination (eg Vaughan *et al.* 1997b). Only frequency-divided calls were used for estimation of bat activity and time-expanded calls (stored on the second stereo channel) improved the accuracy of species identification. Recording was performed in six sites, located in 200–500 metres from each other: (1)

river, 4–5 metres wide, flowing along the ecotone of forest and orchards; (2) pond (0.11 ha) surrounded by pasture; (3) pond (0.12 ha) surrounded by forest; (4) pond (0.22 ha, created in March 2003, after the first study yr), located on pasture-forest edge; (5) canopy gap in deciduous forest; and (6) dense mixed forest.

We divided the sites into two groups (1–2–3 and 4–5–6) that were visited simultaneously by two research teams each night. The division was done because the three last sites were added to the scheme not before 2003 and data from six nights for that sites are missing due to failure of equipment. Detectors D-980 or D-230 were used alternately for the first or the second group of sites, except 2002 when only the first group was visited. Detectors were changed between groups of sites to minimize effects of different microphone sensitivities and we could not sample all six sites with one set of equipment because then each of the four recording sessions (see below) would lasted much longer than recommended one hr (Rachwald 1992). We recorded bat calls between April and November (23 times per season, approximately every 10 days). Every night, the recordings were made during four equally-spaced sessions, with the first session starting 30 minutes after sunset and the fourth session ending 30 minutes before sunrise. During each session, three recordings (each lasting 5 minutes) were performed in every site. The sites were visited in sequence 1·2·3 (4·5·6) or alternately 3·2·1 (6·5·4). We switched between these two schemes every second night.

Recordings were digitised and analysed with BatSound 3.3 software (Pettersson Elektronik AB, Sweden). Bat species were determined based on call shape, peak frequency (= frequency containing most energy), length of pulses and inter-pulse intervals (Ahlén 1990, Vaughan *et al.* 1997b). We identified to the species level 98% of sequences belonging to the *Vespertilio-Nyctalus-Eptesicus* group and 95% of sequences belonging to the genus *Pipistrellus*. Echolocation calls of various *Myotis* species are similar in structure, thus hard to identify reliably. However 98.5% of all *Myotis* net-

ted in the study area ($n = 197$) belonged to *M. daubentonii* (Ciechanowski *et al.* 2007b) and identification of recorded individuals was in most cases confirmed by observations of a specific flight style (circling repeatedly just few centimetres above the water-surface: Ahlén 1990). Both *Myotis mystacinus* and *Myotis brandtii* are extremely rare species in the region and no breeding has been confirmed there for the latter (Sachanowicz *et al.* 2006). The remaining two congeners, *M. nattereri* and *Myotis dasycneme*, appeared only once in mistnetted sample (Ciechanowski 2003, Ciechanowski *et al.* 2007a). We have never recorded the exceptional broadband signals of *Myotis nattereri*, which may be considered diagnostic (mean bandwidth 119 kHz; Siemers and Schnitzler 2004). Therefore, for simplification, we classified all recordings of *Myotis* bats as *M. daubentonii* and considered the occurrence of its congeners negligible in the area. About 1.1% of calls remained indeterminate or classified only to *Myotis-Pipistrellus* group – these were excluded from further analysis. To estimate flight activity of bats at particular night, we summed up durations of search call sequences measured on spectrograms (with accuracy of 0.1 s). In total, we analysed 322 hrs of recordings, containing 129 640 s of echolocation call sequences.

Data analysis

Statistical analyses were conducted with Statistica 6.0 and Excel 2000. Totals of flight activity values were calculated for every visit at all three sites from the first group (1, 2, 3) and – since 2003 – all three sites from the second group (4, 5, 6). These totals were used as single data points (five for each visit). Because of extremely right-skewed distributions of the studied variables, a non-parametric test (Kruskal-Wallis ANOVA) was applied to reveal if bat activity varied significantly within the season. As absolute values of activity index (total nightly duration of echolocation calls) varied significantly among yrs (all species in total: $H = 28.79$, $df = 2$, $n = 327$, $p < 0.0001$), for further analyses we converted them to percentages of annual maximum values. To test *post hoc* differences between particular half months, we applied non-parametric Dunn test (Zar 1996). Seasonal patterns of flight activity were compared among species with cluster analysis, using complete linkage method (see Kaczensky *et al.* 2006 for similar approach). For that purpose, we attributed to each species medians of percentage values for every of 23 visits (shown on Figs 1–3) as one of 23 parameters included in the analysis. Euclidean distance was used as measure of similarity.

Results

The flight activity revealed significant variation between half months in all species (Kruskal-Wallis test: $df = 14$, $n = 109$; *M. daubentonii*: $H = 54.17$, $p < 0.0001$; *E. serotinus*: $H = 63.91$, $p < 0.0001$; *P. pipistrellus*: $H = 41.17$, $p = 0.002$; *P. pygmaeus*: $H = 54.36$, $p = 0.0003$; *P. nathusii*:

$H = 63.12$, $p < 0.0001$; *N. noctula*: $H = 64.81$, $p < 0.0001$; *N. leisleri*: $H = 53.81$, $p = 0.0001$).

Seasonal activity pattern of *M. daubentonii* was clearly bimodal in each year with the highest activity in April and the second, significantly smaller peak in August–September (Fig. 1) (IV_1 – IX_1 : $Q = 3.88$, $p < 0.01$). After a spring peak, activity decreased towards early summer (IV_1 – V_1 : $Q = 5.39$, $p < 0.0001$; IV_2 – V_1 : $Q = 5.39$, $p < 0.0001$; IV_1 – VI_1 : $Q = 5.15$, $p < 0.0001$; IV_1 – VII_1 : $Q = 5.76$, $p < 0.0001$; IV_1 – $VIII_1$: $Q = 6.48$, $p < 0.0001$; V_2 – VI_1 : $Q = 3.73$, $p = 0.02$; V_2 – VII_1 : $Q = 4.34$, $p = 0.001$). After reaching minimum level, it increased again towards late summer (VI_2 – $VIII_1$: $Q = 3.93$, $p = 0.009$; VII_1 – $VIII_2$: $Q = 3.52$, $p = 0.004$; $VIII_1$ – $VIII_2$: $Q = 3.54$, $p = 0.04$). In October and November it declined ($VIII_2$ – X_1 : $Q = 4.95$, $p < 0.0001$; $VIII_2$ – XI_1 : $Q = 6.77$, $p < 0.0001$; $VIII_2$ – XI_1 : $Q = 6.77$, $p < 0.0001$; IX_1 – XI_1 : $Q = 3.67$, $p < 0.0001$), but single passes were recorded until the end of the season.

Activity of *E. serotinus* concentrated in late spring and summer (Fig. 1). Only single passes were noted in the first third of April but between early spring and early summer its activity increased significantly (IV_1 – VI_2 : $Q = 4.52$, $p = 0.0007$; IV_1 – VII_2 : $Q = 4.50$, $p = 0.0007$; V_1 – VI_2 : $Q = 3.88$, $p = 0.01$; V_1 – VII_2 : $Q = 3.86$, $p = 0.01$; VI_2 – VII_1 : $Q = 3.96$, $p = 0.008$). After reaching a peak in July, it declined rapidly and no calls were recorded in October–November (VII_2 – $VIII_1$: $Q = 7.04$, $p < 0.0001$; VII_2 – IX_2 : $Q = 6.20$, $p < 0.0001$).

Flights of *P. pipistrellus* were recorded since April and ceased at the end of October (Fig. 2). The seasonal distribution of its activity revealed no clear pattern and no significant differences between half-months during spring, although particularly low median values were noted in the beginning of April and some decrease was observed in July (VI_2 – VII_1 : $Q = 4.25$, $p = 0.002$). In some half months of late summer, the activity of *P. pipistrellus* was even modestly higher than in June (VI_2 – $VIII_1$: $Q = 4.55$, $p = 0.0006$; VI_2 – IX_1 : $Q = 4.37$, $p = 0.001$). It declined significantly towards the end of the season ($VIII_2$ – X_1 : $Q = 5.38$, $p < 0.0001$; $VIII_2$ – XI_1 : $Q = 5.88$, $p < 0.0001$).

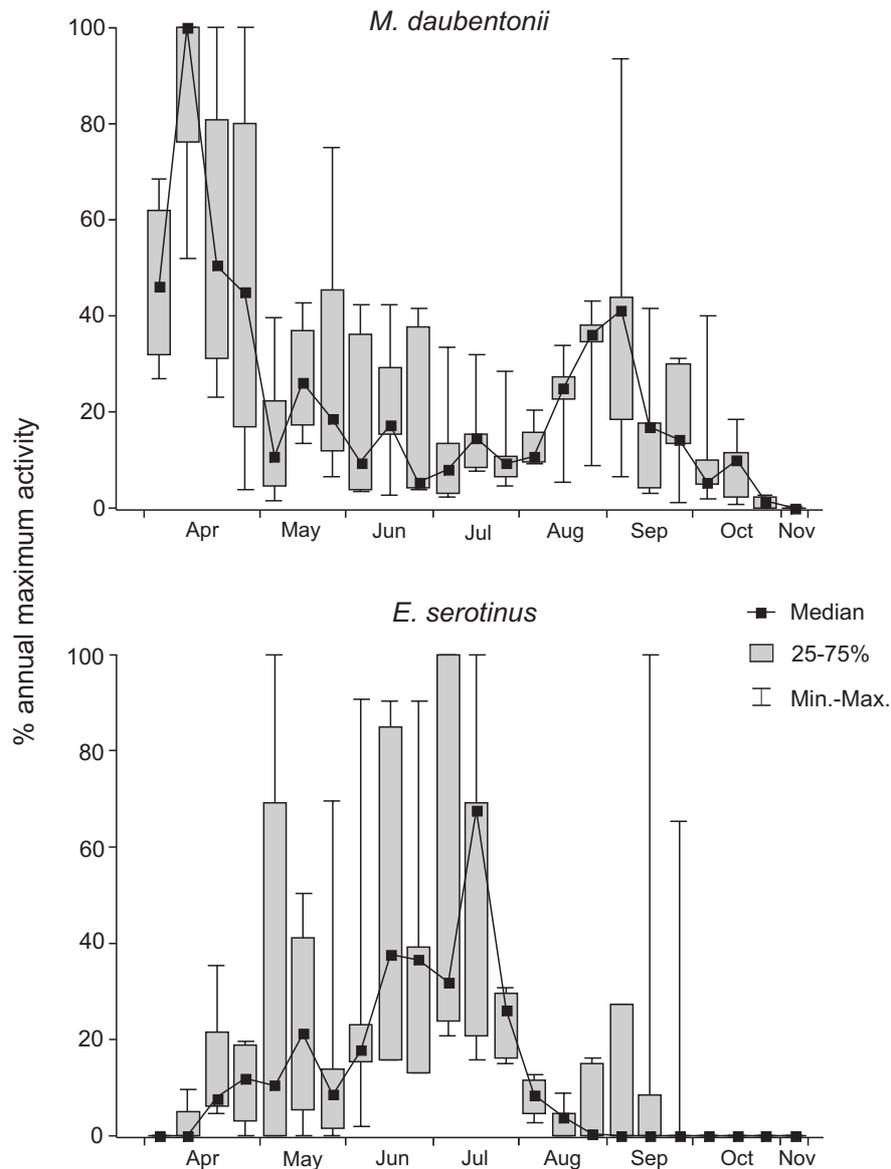


Fig. 1. Seasonal dynamics of the flight activity of *Myotis daubentonii* and *Eptesicus serotinus* bats in the Reda valley, N Poland.

The highest median values of activity in *P. pygmaeus* was noted in summer, particularly in late June and August (Fig. 2). Its passes appeared first in April and their number increased towards summer (IV_1-V_2 : $Q = 3.53$, $p = 0.04$; IV_1-VI_2 : $Q = 3.93$, $p = 0.009$; IV_2-VIII_2 : $Q = 3.62$, $p = 0.03$). After June peak, activity of *P. pygmaeus* decreased in July (VI_2-VII_1 : $Q = 3.88$, $p = 0.01$), although remained relatively high in late summer. It declined towards autumn ($VIII_2-IX_1$:

$Q = 5.70$, $p < 0.0001$; $VIII_2-X_1$: $Q = 6.30$, $p < 0.0001$; IX_2-X_1 : $Q = 3.83$, $p = 0.0002$) and ceased at the end of October.

General pattern of activity of *P. nathusii* resembled that recorded in *P. pipistrellus* and *P. pygmaeus*, with the highest median values in late June and August (Fig. 2). Activity of Nathusius' pipistrelles, very low in April, increased significantly towards early summer (IV_1-VI_2 : $Q = 4.29$, $p = 0.002$), but then decreased on the

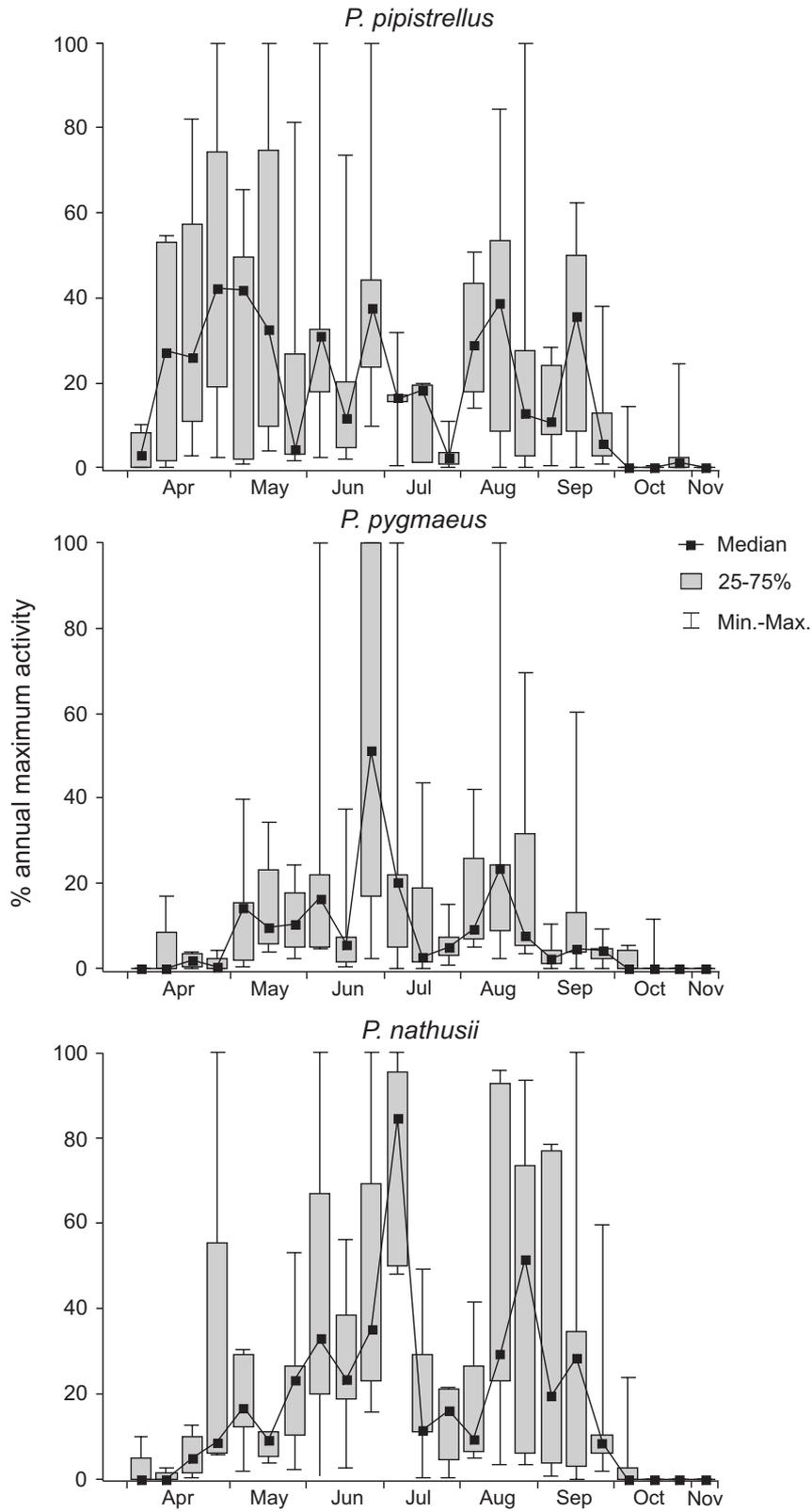


Fig. 2. Seasonal dynamics of the flight activity of three *Pipistrellus* bat species (separately) in the Reda valley, N Poland.

turn of July (VI₂–VIII₁: $Q = 6.02$, $p < 0.0001$; VII₂–VIII₁: $Q = 3.91$, $p = 0.009$). It increased again in late summer (VIII₁–VIII₂: $Q = 3.78$, $p = 0.02$) and then declined again in autumn (VIII₂–IX₁: $Q = 4.40$, $p = 0.001$; VIII₂–X₁: $Q = 6.27$, $p < 0.0001$; IX₂–X₁: $Q = 4.47$, $p = 0.0008$). Flying *P. nathusii* disappeared from the study area about three weeks earlier than the remaining two *Pipistrellus* species (Fig. 2). Although the activity of all three members of this genus

appear to reveal some bimodality (with significant decrease in July), its levels subjected to high interannual variability, manifesting in very broad interquartile ranges.

N. noctula had a clear bimodal pattern of seasonal activity each yr, but with peaks in different periods than *M. daubentonii* (Fig. 3). The activity of *N. noctula* increased since April, reaching its maximum level in June–July (IV₁–VI₂: $Q = 4.29$, $p = 0.002$; IV₁–VII₂: $Q = 5.35$,

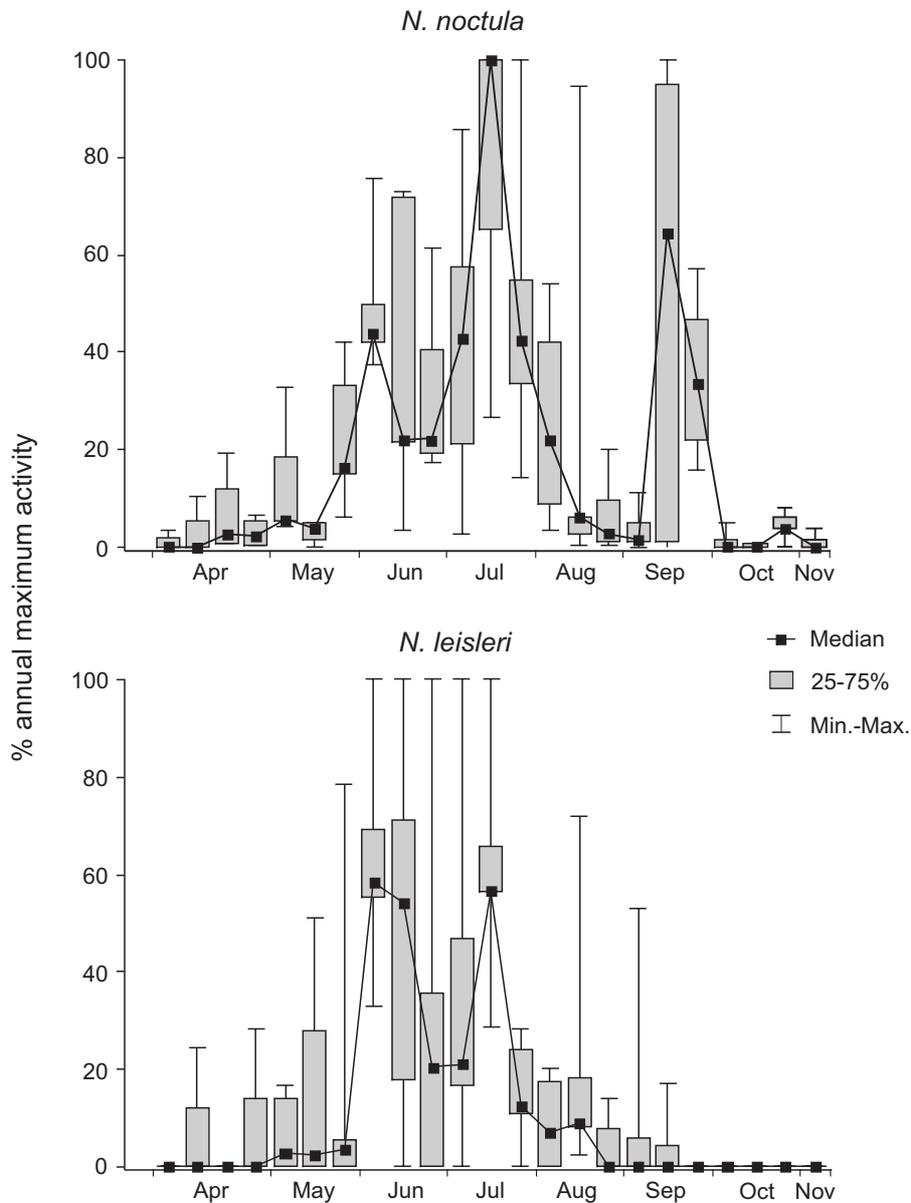


Fig. 3. Seasonal dynamics of the flight activity of two *Nyctalus* bat species (separately) in the Reda valley, N Poland.

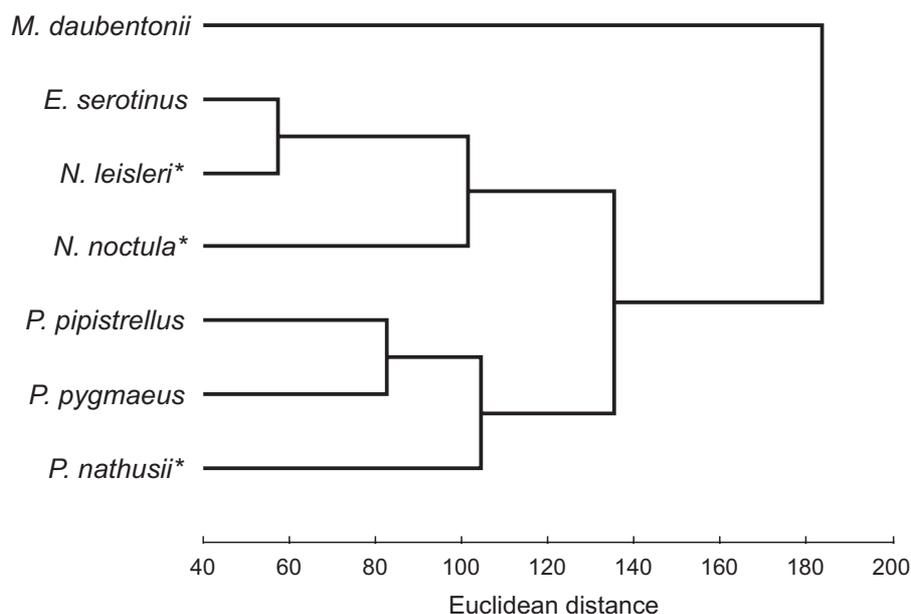


Fig. 4. Complete linkage tree of similarities among patterns of seasonal dynamics of six bat species in Reda valley. For each species, medians of percentage of maximum annual activity (total duration of recorded echolocation calls) were calculated for every 23 visits from April until November (shown as Fig. 1–3) and included in the analysis as succeeding 23 variables. Long-distance migrants were indicated with an asterisk (*).

$p < 0.0001$; IV_2 – VII_2 : $Q = 4.33$, $p = 0.002$; V_1 – VII_2 : $Q = 4.47$, $p = 0.0008$; VI_2 – VII_1 : $Q = 3.86$, $p = 0.01$; VII_1 – VII_2 : $Q = 3.78$, $p = 0.02$). Hunting individuals of that species almost disappeared at the end of August and only single flights were noted in late summer (VII_2 – $VIII_1$: $Q = 7.33$, $p < 0.0001$; VII_2 – IX_1 : $Q = 7.46$, $p < 0.0001$). The activity of *N. noctula* increased again rapidly in last week of September (IX_1 – IX_2 : $Q = 4.03$, $p = 0.006$), resulting in second peak, restricted to one or two visits. It declined rapidly in autumn (IX_2 – X_1 : $Q = 6.37$, $p < 0.0001$; IX_2 – XI_1 : $Q = 6.52$, $p < 0.0001$), although some noctules were recorded until November.

N. leisleri flew mostly in summer months, with maximum numbers in June–July. Only single observations of *N. leisleri* were made in spring and no flights were recorded in autumn (Fig. 3). Its activity increased between April and early summer (IV_2 – VII_2 : $Q = 3.79$, $p = 0.02$; V_1 – VII_2 : $Q = 3.99$, $p = 0.007$) and then decreased in late summer (VI_2 – IX_1 : $Q = 5.03$, $p < 0.0001$; VII_2 – IX_1 : $Q = 5.85$, $p < 0.0001$; VI_2 – IX_1 : $Q = 3.69$, $p = 0.02$).

Cluster analysis of flight activity patterns revealed a separate position of the only water-surface forager (*M. daubentonii*), while all the aerial hawkers clustered together. All the species considered as unambiguous long-distance migrants (*N. noctula*, *N. leisleri*, *P. nathusii*) appeared in the latter cluster, however jointly with sedentary species (*E. serotinus*, but also disputably *P. pipistrellus*). It formed two sub-clusters, the first grouping exclusively clutter-adapted hawkers, hunting close to obstacles, belonging to *Pipistrellus* genus (irrespective of their migratory behaviour) and the second, consisting of two open-air hawkers (*Nyctalus* spp.) and more clutter-adapted *E. serotinus* (Fig. 4).

Discussion

The highest flight activity of all the aerial hawkers (genus's *Eptesicus*, *Pipistrellus* and *Nyctalus*) appeared in the summer period after very low activity recorded at the beginning of

April. A similar phenomenon was observed in *Pipistrellus* spp. in Northern Ireland (Russ *et al.* 2003), in *P. pipistrellus* in England (Maier 1992) and in northern bat *Eptesicus nilssonii* in Sweden (Rydell 1993). It is usually explained by ca one-third increase of energy demands in females between pregnancy and lactation (Racey and Speakman 1987). Any traces of annual life-cycle in seasonal activity of *Pipistrellus* might be masked by changes in food abundance and air temperature, that – based on the same material – were the strongest correlates of spatiotemporal activity in the Reda valley pipistrelles (Ciechanowski *et al.* 2007b). Although similar in general patterns, observed phenologies of particular *Eptesicus*, *Pipistrellus* and *Nyctalus* species differ in some secondary features, that might be explained by their specific behaviour in transitional periods.

Activity of *E. serotinus* was restricted to spring-summer months, coming to an end during the period covering dispersion of nursery colonies (Catto *et al.* 1995). *E. serotinus* does not perform any long-distance migrations (Dietz *et al.* 2009), thus one may expect that termination of the species' activity would be in late autumn. Pattern of seasonal activity recorded in Reda valley resembles somewhat that observed in Czech Republic by Gaisler *et al.* (1998). Its maximum intensity appeared earlier than in Poland (second half of April), but later successively decreased to zero until the end of September. Such a decline can be associated with autumn switching of foraging areas, eg movements from waters and forest edges to the urban habitats (de Jong and Ahlén 1991).

As the studied species differed in migratory behaviour, it was expected that such differences would determine interspecific variation in patterns of activity. It was confirmed only in a minor extent, partially because the migratory status of some Central-European bats remains ambiguous. Based on banded individuals, Strelkov (1969) considered *P. pipistrellus* (*sensu lato*) as a long-distance migrant in Russia, what was uncritically related to the whole distribution range (Fleming and Eby 2004). Seasonal migrations of *P. pipistrellus* (*sensu lato*) were indicated by its spring and autumn concentrations

on the coasts of Sweden (Ahlén 1997) and genetic differentiation of European populations appeared very weak, suggesting long-distance movements in both sibling species of European pipistrelles (Bryja *et al.* 2009). However, *P. pipistrellus* is regarded a sedentary species in W Europe, where its local movements do not exceed 20 km (Dietz *et al.* 2009). There are several recent records of *P. pipistrellus* hibernating in W Poland (Sachanowicz *et al.* 2006), that suggest a significant part of the Polish population to be a sedentary one. On the contrary, *P. nathusii* is a typical long-distance migrant in almost its whole distribution range, moving to the S and W Europe for winter (Strelkov 1969, Dietz *et al.* 2009). In the recent study, its activity ceased at the end of September, suggesting departure of the local population. *P. pygmaeus*, restricted its activity to a shorter period than *P. pipistrellus*, resembling more that observed in *P. nathusii*. Some authors suggest the species might perform long-distance flights and few recoveries of banded individuals (up to 775 km) support such hypothesis (Dietz *et al.* 2009). Genetic structuring appeared more weakly expressed in *P. pygmaeus* than in *P. pipistrellus*, suggesting longer distances covered by seasonal movements of the first species (Racey *et al.* 2007).

There is little evidence for passing through the study area by *P. nathusii* from E Europe during their seasonal migration. Such an event would cause recurrent peaks of activity in May and August, similar to that assigned for spring and autumn migration of *P. nathusii* on nearby Vistula Spit (Jarzembowski 2003). Although river valleys can act as migration corridors by *P. nathusii* (Furmankiewicz and Kucharska 2009), in N Poland it may concentrate their movements along the Baltic Sea coast (Jarzembowski 2003, cf Ahlén *et al.* 2009), avoiding inland areas. Some significant decrease in activity of all three *Pipistrellus* species, observed during recent study in late July may reflect early dispersion of local nursery colonies (and departure of their members), while successive increase in August–September – appearance of migrating individuals, eg foraging here on stop-over and mating in nearby roosts. However, August increase in *Pipistrellus* activity is subjected to strong inter-

annual variation (large interquartile ranges) and extended in time, suggesting, at most, very prolonged and poorly expressed 'autumn' migration, especially when compared to *N. noctula* (cf Jarzembowski 2003, Furmankiewicz and Kucharska 2009). A strong peak of hunting activity of *P. pygmaeus* in August was detected in S Bohemia (Bartonička and Řehák 2004), explained there by the appearance of newly weaned juveniles. In S Poland, the number of echolocation calls of *P. nathusii* increased gradually from spring, reaching its maximum in August (Furmankiewicz 2003). In Germany *P. pipistrellus* revealed such peak even later, ie in September (Sachteleben and Helversen 2006). In the two last cases, maximum flight activity coincided with the highest intensity of advertisement vocalization. Territorial *Pipistrellus* males spend a significant portion of their time budget for display (Gerell-Lundberg and Gerell 1994), thus it is unlikely that they increase their use of foraging sites. However, females aggregating around territorial males may contribute to late-summer peak of flight activity.

Seasonal dynamics of the activity of *N. noctula* showed a recurrent pattern, possibly shaped by long-distance migrations. Only single passes were recorded in early spring, while more intensive activity of that species was noted at the beginning of June, which might indicate its late arrival at the Polish Baltic Sea Coast. At least some Polish populations of *N. noctula* are known to migrate S for winter (Sachanowicz *et al.* 2006). Even in the Czech Republic, the first active *N. noctula* appeared in tree holes in May, while nursery colonies formed in June (Červený and Bürger 1989). Recent colonization of well insulated anthropogenic roosts in Central Europe (Bihari 2004) may lead to much earlier aggregation of breeding females. In E Poland maximum hunting activity of *N. noctula* was recorded in July and decreased significantly in August, similar to Reda valley (Rachwald 1992, Rachwald *et al.* 2001). A strong late-summer decline in activity of *N. noctula* is probably caused by dispersal of maternal colonies (Červený and Bürger 1989) but mostly by departure of local populations to wintering areas, located up to 1600 km from summer roosts (Petit and Mayer 2000). In S Ger-

many, where *N. noctula* does not breed, its highest activity was registered in May and September, but no individuals were observed in June–July, suggesting that the species occurred there only when migrating through the region (Zahn *et al.* 1998).

Short periods of intensive flight activity of *N. noctula*, repeated every year at the end of September, might be associated with strongly synchronised migration wave of individuals belonging to the populations from N and NE Europe. On the Baltic coast of Sweden, *N. noctula* leaving land in S direction were observed from the end of August, but large concentrations of migrating individuals were noted even in October (Ahlén 1997). In the Oder River valley, southward migratory flights of noctules started to predominate in mid-September, peaking in the 1st half of October, quite similarly to our results (Furmankiewicz and Kucharska 2009). Surprisingly, in Reda valley no analogous peak of activity was ever noted in spring, although such peak would indicate migration of *N. noctula* from hibernacula to the breeding areas in NE Europe. A similar peak in May–June was associated with summer migration of nearctic silver-haired bat *Lasionycteris noctivagans* and red bat *Lasiurus borealis* in S Canada (Barclay 1984). We can only speculate that the migration strategy of noctules crossing N Poland resembles loop migrations known in some birds, which use different routes in spring and autumn (Meyburg *et al.* 2003). Observations of flying *N. noctula* until mid-November remain in conformity with known fact that some number of noctules regularly spends winter in N Poland (Sachanowicz *et al.* 2006).

Echolocation calls of *N. leisleri* were registered almost exclusively in spring and summer, with the highest flight activity in June–July. *N. leisleri* performs long-distance migrations to the wintering areas in S and W Europe (Dietz *et al.* 2009) thus the absence of species in autumn indicates that the local population leaves the study area for winter. The only research on seasonal dynamics of activity of *N. leisleri* was conducted in the mild climate of Northern Ireland where the species was observed between April and mid-October and the highest number of

passes appeared in May and July (Russ *et al.* 2003).

M. daubentonii, the only water-surface forager studied, revealed a bimodal pattern of activity with two peaks; April and August–September. Studies of that species by Kretschmer (2001) in Germany did not cover April and October, however its activity peaked there in May–June above the Rhine river and in July above nearby lake; no September activity occurred at the first site. The April peak of activity of *M. daubentonii* in the Reda valley may be associated with regeneration of energy reserves, exhausted during hibernation (Kokurewicz 2004). A respective pattern was described by Encarnaç o *et al.* (2004b), who found significant increase in body mass of male *M. daubentonii* between April and May. Much higher energy demands should be expected in females, which then became pregnant (Bogdanowicz 1994, Speakman and Thomas 2004). Later decline in activity of *M. daubentonii* may be a result of a foetus load and increasing costs of flight, resembling an effect observed in *E. nilssonii* (Rydell 1993) but not in aerial-hawking species in the present study. An early seasonal start of activity of *M. daubentonii* appeared to be very close to the period of departure from hibernacula, observed in the Polish underground roosts in the middle of March (Jurczyszyn and Bajaczyk 2001). Such proximity indicates its status as a sedentary species or regional (facultative) migrant (Strelkov 1969, Bogdanowicz 1994). Similarly, in the Oder River valley, S Poland, *M. daubentonii* started its activity in the second half of March and its directional movements peaked in April (Furmankiewicz and Kucharska 2009).

Contrary to the aerial-hawking species, no increase in activity of *M. daubentonii* was noted in early summer, although it might be expected, basing on energy demands of lactating females (Racey and Speakman 1987). However, the seasonal dynamics of energy intake and torpor use in *M. daubentonii* may partially explain patterns observed in our study. The females of that species are known to forage longer during pregnancy than during post-lactation period (Encarnaç o and Dietz 2006). They remain normothermic during both pregnancy and lac-

tation, as expected, however body temperature recorded in gravid females is slightly higher than in lactating females. After the young are weaned, the females decrease their daily temperatures further and remain torpid during the day (Dietz and Kalko 2005). This transition corresponds to high level of activity of *M. daubentonii* and its later decrease in summer. On the contrary, adult males reveal lower food intake (Encarnaç o and Dietz 2006), longer and deeper daily torpor (Dietz and Kalko 2005) and longer time spent in roosts in spring than in summer, thus they cannot contribute to the spring peak of activity in *M. daubentonii* (Encarnaç o *et al.* 2004a).

Doubts may be arisen around the function of the second peak of seasonal activity of *M. daubentonii*, occurring between late summer and early autumn. It could be associated with fat accumulation prior to hibernation (Kunz *et al.* 1998). Increase in body mass of Daubenton's bats, being a result of that process, appears just between the end of July and mid-September (Encarnaç o *et al.* 2004b). However, the high level of activity of *M. daubentonii* ended surprisingly early, when taking into account that maximum body weight were achieved by this species already in mid-October (Encarnaç o *et al.* 2004b), when the number of torpid Daubenton's bats increased rapidly in hibernacula (Lesiński 1990). Nevertheless, preparation for winter period may not demand any significant increase in hunting activity of bats, known to accumulate fat deposits by alterations in energy expenditure and periodical remaining in torpor (Speakman and Rowland 1999). The early second peak of flight activity (August) might be also associated with weaning of juvenile bats, increasing their number on hunting grounds. In N Bohemia, *M. daubentonii* significantly increased their activity in mid-July to mid-August just between lactation and post-lactation period (Bartonička and Zupal 2003). Moreover, an increase in body mass of juvenile males, recorded during late summer by Encarnaç o *et al.* (2004b) may be associated with not only pre-hibernal fat accumulation but also with the ongoing post-natal development. Also adult males increase their food intake and daily body temperature in June–August, as their

energy demands are higher during spermatogenesis (Dietz and Kalko 2005, Encarnaç o and Dietz 2006). However, adult males can contribute to the late-summer peak of activity only in its first part. During late August and September they stayed significantly longer in their day roosts than in early summer, being probably involved in mating (Encarnaç o *et al.* 2004a).

Although some elements of activity dynamics can be interpreted as a result of species' migratory behaviour, it appeared to explain clustering of activity patterns only in minor extent, while the most visible contribution was that of hunting tactics. The only water-surface forager occupied clearly separate position. All six aerial hawkers clustered together, irrespectively of their migratory behaviour. Moreover, the group divided into two sub-clusters, also associated with hunting mode. One consisted exclusively of species adapted to flight in moderate distance to obstacles and ground, ie members of *Pipistrellus* genus. Although *E. serotinus* is described as using hunting tactics similar to pipistrelles (Dietz *et al.* 2009), it clustered together with typical open-air aerial hawkers, belonging to *Nyctalus* genus. However, serotine is known to forage at much higher distances from obstacles than pipistrelles and appears to be much less clutter-adapted (Baag e 1987). The effect of species' hunting tactics on the general picture of seasonal activity may result from different abundance of prey used by the two groups (Ciechanowski *et al.* 2007b). It might force some aerial-hawkers to change frequently their foraging patches but allow water-surface foragers to maintain steadily high activity at the same sites for longer periods (Kusch and Idelberger 2005), responding only to different energy demands during particular stages of their annual life cycle. Interspecific differences in activity patterns can therefore be treated as a next ecological consequence of contrasting foraging modes, similarly to previously recognised effects on predation risk, energy expenditure, learning abilities and breeding parameters (Huey and Pianka 1981).

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