UNIVERSITAS LATVIENSIS

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AUTUMN SWARMING AND MIGRATION OF BATS IN LATVIA

LATVIJAS SIKSPĀRŅU RUDENS SPIETOŠANA UN MIGRĀCIJA

Doctoral Thesis

Submitted for the Degree of Doctor in Biology
Subfield: Zoology

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Rīga, 2014

Autumn swarming and migration of bats in Latvia

Jurģis Šuba

This thesis is based on the following articles:

I **J. Šuba**, Vintulis V., Pētersons G. 2008. Late summer and autumn swarming of bats at Sikspārņu caves in Gauja National Park. Acta Universitatis Latviensis, 745 (Biology): 43–52.

II J. Rydell, Bach L., Bach P., Diaz L.G., Furmankiewicz J., Hagner-Wahlsten N., Kyheröinen E.-M., Lilley T., Masing M., Meyer M.M., Pētersons G., **Šuba J.,** Vasko V., Vintulis V., Hedenström A. 2014. Phenology of migratory bat activity around the Baltic Sea and the south-eastern North Sea. Acta Chiropterologica, 16 (1): 139–147.

III **J. Šuba**, Vintulis V., Pētersons G. 2011. Body weight provides insight into the feeding strategy of swarming bats. Hystrix – The Italian Journal of Mammalogy, 22 (1): 179–187.

IV **J. Šuba**, Petersons G., Rydell J. 2012. Fly-and-forage strategy in the bat *Pipistrellus nathusii* during autumn migration. Acta Chiropterologica, 14 (2): 379–385.

V **J. Šuba.** 2014. Migrating Nathusius's pipistrelles *Pipistrellus nathusii* (Chiroptera: Vespertilionidae) optimise flight speed and maintain acoustic contact with the ground. Environmental and Experimental Biology, 12: 7–14.

VI J. Eklöf, **Šuba J.,** Petersons G., Rydell J. 2014. Visual acuity and eye size in five European bat species in relation to foraging and migration strategies. Environmental and Experimental Biology, 12: 1–6.

Contribution

	I	II	III	IV	V	VI
Original idea	JŠ, VV	AH	JŠ	JŠ, GP	JŠ, JR	JR, JŠ
Logic of Reasoning	JŠ, GP, VV	JR, JŠ, GP, LB	JŠ	JŠ, GP	JŠ	JR, JE JŠ
Data collection and preparation	JŠ, VV, GP	AH, LB, GP, JŠ, VV, others	JŠ, VV, GP	JŠ	JŠ	JE, JŠ, GP
Analyses	JŠ	JŠ	JŠ	JŠ	JŠ	JŠ
Manuscript	JŠ	JR, JŠ, LB	JŠ	JŠ	JŠ	JE, JR, JŠ

JŠ – Jurģis Šuba, GP – Gunārs Pētersons, JR – Jens Rydell, AH – Anders Hedenström, VV – Viesturs Vintulis, LB – Lothar Bach, JE – Johan Eklöf, others – Petra Bach, Laura Guia Diaz, Nina Hagner-Wahlsten, Ineta Kalniņa, Eeva-Maria Kyheröinen, Thomas Lilley, Marian Max Meyer, Alda Stepanova and Ville Vasko.

Annotation

From the end of breeding season until the onset of hibernation, several bat species migrate long distances from summer roosts to winter roosts. At the same time other species that hibernate underground perform a particular "swarming" behaviour at the hibernacula. Autumn swarming at underground sites in Latvia of locally hibernating bats as well as behaviour related to migration flight and feeding strategy of migratory bats was studied within the framework of this dissertation.

Anotācija

No vairošanās sezonas beigām līdz pārziemošanas sākumam dažas sikspārņu sugas veic tālus pārlidojumus no vasaras mītnēm uz ziemošanas vietām. Turpretī citas sugas, kuras pārziemo pazemes mītnēs, ziemošanas vietās veic īpatnēju lidināšanos jeb „spietošanu". Šai darbā aplūkota Latvijā ziemojošo sikspārņu rudens spietošana pie pazemes mītnēm, migrējošo sikspārņu migrācijas lidojuma īpatnības, kā arī barošanās stratēģija.

Contents

Abbreviations and terms

BCI	Body condition index, calculated by dividing the body mass with forearm length
Optomotor response	response to movement of a visible pattern
P_{fuel}	Fuel accumulation rate during migration
V_{migr}	Migration speed; the total migration distance divided by the total time of migration
V_{mp}	Minimum power speed; flight speed with minimum total energy expenditure per unit of time
V_{mr}	Maximum range speed; flight speed with minimum total energy expenditure per unit of distance
V_{mt}	Minimum time speed; flight speed with minimum achieved migration time

Saīsinājumi un termini

ĶSI	Ķermeņa stāvokļa indeks, aplēsts, izdalot ķermeņa masu ar apakšdelma garumu
Optomotora reakcija	Atbildes reakcija uz redzamas ainas kustību
P_{fuel}	Enerģijas uzkrāšanas intensitāte migrācijas laikā
V_{migr}	Migrācijas ātrums; kopējais migrācijā veiktais attālums pret kopējo migrācijas ilgumu
V_{mp}	Mazākās jaudas ātrums; lidojuma ātrums ar minimālu enerģijas patēriņu laika vienībā
V_{mr}	Tālākā pārvietojuma ātrums; lidojuma ātrums ar minimālu enerģijas patēriņu attāluma vienībā
V_{mt}	Īsākā ilguma ātrums; lidojuma ātrums ar minimālu lidojuma kopējo ilgumu

Introduction

Importance of the research

The autumn season is of particular interest in the life history of bats for at least three reasons. First, the peak of mating activity is believed to occur during autumn prior to the winter hibernation period (e.g. Thomas et al. 1979; Lundberg 1989; Rivers et al. 2006; Sachteleben, von Helversen 2006).

Second, in late summer and autumn, thousands of locally hibernating bats visit underground sites to perform a peculiar swarming behaviour, generally of unknown function (Fenton 1969). The behaviour is apparently associated with mating, information transfer regarding suitable hibernacula, resting during movements between summer roosts and winter hibernacula (e.g. Parsons et al. 2003a) and probably also thermoregulation and fat deposition (Piksa et al. 2011).

Third, the autumn season also brings challenging tasks and risks to migratory bats as they move from summer roosts to winter hibernacula sometimes over long distances across different environments (Fleming, Eby 2003). Extensive studies on avian migration have provided a good theoretical background and testable hypotheses for the investigation of seasonal long-distance migrations in bats (Hedenström 2009; McGuire, Guglielmo 2009). From a conservation point of view, understanding the biology of bat migration seems to be of particular importance with respect to increasing numbers of wind-power facilities, since wind turbines kill many bats, particularly during their spring and autumn migration flights (Rydell et al. 2010).

While the phenology of autumn migration of bats has been studied intensively and over a long time at the Baltic coast of Latvia (Pētersons 1990; 2004), several other aspects of the activity and behaviour during this particular season have received much less attention. For this thesis, behaviour and energetics of autumn swarming and migration behaviour were investigated, based on field work conducted in 2005–2012. It was hypothesised that both locally hibernating and migrating bats would feed intensively throughout the night to meet increased energy requirements for consecutive flight activities (i.e. swarming and migration) and migration flight would employ relatively fast speeds to minimise energy consumption. Data on active use of sonar and visual acuity of migrating bats were collected and analysed in the context of orientation and navigation.

Main novelties

- For the first time autumn swarming of bats at underground hibernacula has been investigated in Latvia, providing also evidence for local movements between different underground sites.

- For the first time patterns of nocturnal feeding have been investigated for migrating bats.

- For the first time flight speed of migrating bats has been measured in the field, comparing the data to theoretical predictions.

Aim and objectives

The aim of this thesis was to describe the autumn activities of migrating and locally hibernating bats in Latvia by investigating autumn swarming at underground sites as well as behaviour related to migration flight and feeding strategy. The following objectives were set:

1. To investigate a) which species and cohorts of locally hibernating bats swarm at underground sites and b) are such sites used as diurnal roosts in late summer and autumn, which is important information for local bat conservation (Papers I, III).

2. To describe the phenology of bat migration in northern Europe, comparing available data from several sites around the Baltic Sea and in the south of North Sea (Paper II).

3. To investigate nocturnal feeding patterns for swarming and migrating bats, testing hypotheses on utilisation of time resources (Papers III, IV).

4. To test hypotheses on optimal speed for Nathusius's pipistrelles *Pipipistrellus nathusii*, chosen as representatives for migratory species (Paper V).

5. To estimate the visual acuity and measure the length of sonar pulse intervals in Nathusius's pipistrelles in order to test the hypothesis that migrating individuals of this species a) may use stars as visual navigation cues (Paper VI) and b) keep acoustic contact with the ground by using the sonar (Paper V).

Theses

- In late summer and autumn, underground sites in Latvia, such as caves, abandoned cellars and fortifications, are visited by all sex and age groups of bats for swarming activities and sometimes used as diurnal roosts prior to the extended winter hibernation period.

- Migrating bats apply fly-and-forage strategy.

- Migrating bats apply relatively fast flight to optimise energy consumption according to theoretical predictions.

Brief description of applied methods

The species, sex and age composition of swarming bats was studied by mist-netting at three underground sites in Gauja National Park in Latvia in 2005–2007. Captured bats were banded prior their release to facilitate the study of their movements between swarming sites and other underground hibernacula. These sites were then surveyed during the subsequent winters.

In order to compile an overall picture of the occurrence and timing of bat migration in the Baltic region, data collected in 2007–2009 at 19 localities along the Baltic Sea coast and south-eastern North Sea were analysed. The data base consisted mostly of bat detector surveys conducted by several researchers.

Data on foraging performance, flight speed and migration intensity of Nathusius's pipistrelles were collected at Pape Ornithological Research Station (SW Latvia) in August and September 2010–2011. Presence or absence of so called 'feeding buzzes' in audio-recordings of bats' echolocation pulses allowed indirect estimation of foraging intensity. The speed and altitude of migration flights were measured on a known migration flyway using a stopwatch and two reference poles erected 20 metres apart. Collection of morphometric data and visual acuity tests were performed on individual bats captured in a Helgoland type funnel trap at Pape Ornithological Research Station.

Approbation of the results

International conferences and symposia

- Pētersons G., **Šuba J.,** Vintulis V. Importance of coastal area on bat migration at the western coast of Latvia – implication for localization of wind farms. Conference on Wind Power and Environmental Impacts, Stockholm, Sweden, 2013. Theses published in: Book of Abstracts. Conference on Wind Power and Environmental Impacts. Stockholm 5–7 February. Naturvårdsverket, Stockholm, report 6546, p. 82.

- **Šuba J.** Feeding in Nathusius's pipistrelle during autumn migration. XII European Bat Research Symposium, Vilnius, Lithuania, 2011. Theses published in: XII European Bat Research Symposium. August 22–26, 2011. Vilnius, Lithuania, pp. 44–45.

- **Šuba J.,** Pētersons G. Research possibilities on autumn migration of bats using Helgoland-type funnel trap in Pape (SW Latvia). A Hans Kristiansson and CAnMove Symposium. Bat Migration in the Baltic Area. Lund University, Sweden, 12–14 November 2009.

- **Šuba J.** Movements of sedentary and semi-migratory bat species in Latvia. 1st International Symposium on Bat Migration. Berlin, Germany, 16–18 January 2009.

- **Šuba J.** Swarming of northern bats *Eptesicus nilssonii* at underground hibernacula in Latvia. XI European Bat Research Symposium, Cluj-Napoca, Romania, 17–22 August 2008. Theses published in: Abstracts of the XIth European Bat Research Symposium, Cluj-Napoca, Romania, p. 144.

- **Šuba J.** Ziemeļu sikspārņa *Eptesicus nilssonii* spietošana pie pazemes ziemošanas mītnēm Latvijā (Swarming of northern bats *Eptesicus nilssonii* at underground hibernacula in Latvia). 50th International Scientific Conference of the University of Daugavpils, Daugavpils, 15 May 2008. Theses published in: Daugavpils Universitātes 50. starptautiskās zinātniskās konferences tēzes, Daugavpils, Latvija, p. 22.

Local conferences

- **Šuba J.,** Pētersons G. Natūza sikspārņu rudens migrācijas lidojuma raksturojums (Characteristics of migration flight in Nathusius's bats). 71st Scientific Conference of the University of Latvia. Oral presentation at zoology and animal ecology section, Rīga, 1 February 2013. Theses published in proceedings of the conference.

- **Šuba J.,** Dinsbergs I., Tšernova J. Redzes un sonara nozīme Natūza sikspārņu rudens migrācijā (The Role of vision and sonar in autumn migration of Nathusius's bats). 70th

Scientific Conference of the University of Latvia, oral presentation at zoology and animal ecology section, Rīga, 10 February 2012. Theses published in proceedings of the conference.

- **Šuba J.,** Vintulis V., Pētersons G. Sikspārņu vēlās vasaras un rudens spietošana Kazugravas Sikspārņu alās (Late summer and autumn swarming of bats at Sikspārņu caves in Kazugrava). 66th Scientific Conference of the University of Latvia, oral presentation at zoology and animal ecology section, Rīgā, 8 February 2008.

- **Šuba J.** Sikspārņu rudens spietošanas fainoloģija Latvijā (On phenology of autumn swarming of bats in Latvia). 65th Scientific Conference of the University of Latvia, oral presentation at animal ecology section, Rīga, 9 February 2007.

- **Šuba J.,** Vintulis V., Pētersons G., Čakare I. Sikspārņu rudens aktīvitātes pētījumi pie pazemes ziemošanas vietām: pirmie rezultāti (Investigations on autumn activity of bats at underground hibernacula: preliminary results). 64th Scientific Conference of the University of Latvia, oral presentation at zoology and animal ecology section, Rīga, 9 February 2006.

Other publications

- Voigt C.C., Sörgel K., **Šuba J.,** Keišs O., Pētersons G. 2012. The insectivorous bat *Pipistrellus nathusii* uses a mixed-fuel strategy to power autumn migration. Proceedings of the Royal Society of London B, 279: 3772–3778.

- **Šuba J.,** Vietniece D., Pētersons G. 2010. The parti-coloured bat *Vespertilio murinus* (L.) in Rīga (Latvia) during autumn and winter. Environmental and Experimental Biology, 8: 93–96.

- Pētersons G., Vintulis V., **Šuba J.** 2010. New data on the distribution of the barbastelle bat *Barbastella barbastellus* in Latvia. Estonian Journal of Ecology, 59 (1): 62–69.

- Vintulis V., **Šuba J.** 2010. Autumn swarming of the pond bat *Myotis dasycneme* at hibernation sites in Latvia. Estonian Journal of Ecology, 59 (1): 70–80.

1. Theoretical basis of the thesis

1.1. Life history of temperate bats in autumn

All the European bats (order Chiroptera) are small-sized insectivorous mammals that inhabit all major natural and anthropogenic habitat types, reproduce once a year and usually have one or two offspring per litter (Altringham 2001; Hutson et al. 2001). Due to slow reproduction rate, specific habitat and food requirements and essential ecological value as top predators, the need for bat conservation has been recognised (Hutson et al. 2001) and is maintained by international (EC 1992) and local legislation (LR MK 2000; LR Saeima 2000).

Bats in temperate environments respond to seasonally low ambient temperatures and decline in insect availability by entering a state of hibernation (Speakman, Thomas 2003), either after moving to more or less local underground hibernacula (Ransome 1990; Speakman, Rowland 1999) or after migrating to warmer wintering climate, where hibernation may occur above the ground in trees and buildings (Fleming, Eby 2003; Hutterer et al. 2005).

Late summer and autumn is believed to be the peak time of mating for most bat species. Particularly in long-distance migrants, such as Nathusius's pipistrelles, pygmy pipistrelles *P. pygmaeus* and common noctules *Nyctalus noctula*, territorial males monopolise certain roosts before their departure from the summer range, where they mate with females passing on migration (Lundberg 1989). Other bats, mostly of the genus *Myotis,* have been observed mating in underground sites, employing a promiscuous strategy (Thomas et al. 1979; Harrje 1994; Trappmann 2005), although there are many exceptions to this (Dwyer 1970; Horáček, Gaisler 1986).

In late summer, bats rapidly accumulate substantial fat reserves for the following winter (Kunz et al. 1988; McGuire et al. 2009) and migration (McGuire et al. 2011; Voigt et al. 2012). The nocturnal foraging pattern of bats is often bimodal, because it follows the peaks in insect activity that occurs at dusk and dawn (e.g. Racey, Swift 1985; Rydell et al. 1996). However, in the autumn it may be expected that bats feed throughout the night in order to meet increased energy demands at the time of reduced insect availability.

1.2. Previous bat research in Latvia

Sixteen bat species have been found in Latvia so far (Pētersons, Vintulis 1998; Pētersons 2003), all of which belong to the family Vespertilionidae. In the Baltic countries and Latvia in particular, studies on ecology of bats have focussed on the autumn migration (see also Chapter 1.4.). Seven of Latvian bat species perform seasonal long-distance

migrations to central and southern Europe (Pētersons 2004; Pētersons, Vintulis 1998), but eight locally hibernating species exploit underground sites throughout the year (Vintulis 2013) and one species (the parti-coloured bat *Vespertilio murinus*), which also performs long-distance migrations (Masing 1989), can be observed in cities as they perform mating song-flights near tall buildings during late September, October and November (Šuba et al. 2010). Occasional observations that indicate mating activity, such as presence of 'harems' of Nathusus's pipistrelles and pond bats *Myotis dasycneme* in various roosts (Pētersons 1990; Pētersons and Vintulis, unpubl. data), capture of aroused male pond bat in a cave (Vintulis, Šuba 2010) and Daubenton's bats *M. daubentonii* observed mating during autumn swarming (Šuba, unpubl. data), tend to support observations made by others (e.g. Thomas et al. 1979; Gerell, Lundberg 1985).

1.3. Autumn swarming

Underground sites are visited by bats also outside the winter hibernation period, but most of the activity, which may involve thousands of individuals, is observed during late summer and early autumn (e.g. Harrje 1994; Degn et al. 1995; Furmankiewicz, Górniak 2002; Parsons et al. 2003b). In late summer, bats usually fly around, enter the hibernaculum, apparently engage in social activities and examine the site (Fenton 1969; Thomas et al. 1979; Kretzschmar, Heniz 1995; Simon et al. 2004). The swarming populations are usually dominated by males and non-reproducing females (Furmankiewicz, Górniak 2002; Parsons et al. 2003a; Rivers et al. 2006; Piksa 2008). Later in the season some individuals enter torpor inside the hibernaculum and mating may also occur (e.g. Thomas et al. 1979; Harrje 1994; Trappmann 2005). Cool underground sites provide suitable conditions for torpor and fat accumulation, which is essential prior to the winter hibernation period (Krzanowski 1961; Speakman, Rowland 1999; McGuire et al. 2009).

For bats of genus *Myotis,* autumn swarming is believed to be primarily related to intra- and even inter-specific mating, which has been observed (e.g. Thomas et al. 1979) and suggested after investigation of population structure by molecular methods (Kerth et al. 2003; Rivers et al. 2005; Bogdanowicz et al. 2012). For bat species where males defend mating territories and attract females, e.g. common pipistrelles *P. pipistrellus* (Kretzschmar, Heinz 1995; Simon et al. 2004), this may not be the case because the mating strategy is different. In this case mating occurs in the summer range or along the migration routes rather than in the hibernacula (Gerell, Lundberg 1985).

Other hypothesis suggests that bats inform their conspecifics about the location of suitable hibernacula by flying around the site (Fenton 1969; Baurerová, Zima 1988). Adult

males tend to arrive first, and they are later followed by adult females and young individuals of both sexes (Simon et al. 2004; Piksa 2008). Popular hypothesis suggests that females arrive later than males after weaning, while males, having already located the sites, perform swarming to attract attention of other individuals (Parsons et al. 2003a).

Banding studies have indicated that swarming bats arrive from a large catchment area (Parsons, Jones 2003; Rivers et al. 2006), but perhaps tend to visit the same site year after year, because individuals have rarely been caught while also swarming at other sites (Parsons et al. 2003a; Rivers et al. 2006). However, Natterer's bats *M. nattereri* have been found hibernating as far as 20.8 and 36.2 km from the original swarming site (Parsons, Jones 2003), and the situation may be similar for other swarming species (cf. Hutterer et al. 2005).

1.4. Autumn migration

Long-distance migrations of bats in Europe are seasonal and reflect common directional patterns (Hutterer et al. 2005). Among typical long distance migrants, the Nathusius's pipistrelles are the most abundant in Latvia (Pētersons, Vintulis 1998). The peak in the migration of this species along the coastline of the Baltic Sea occurs from the middle of August until the beginning of September, and the males of this species tend to migrate later than females (Pētersons 2004).

It has been suggested that the extensive base of knowledge on bird migration may be used to understand the biology behind migration of bats. However, comparisons between birds and bats are not always straightforward, because there are considerable differences in the physiology between the two groups of animals (Hedenström 2009; McGuire, Guglielmo 2009). For instance, birds are more efficient in storing and using fat as energy source than mammals (Guglielmo 2010). On the other hand, bats may achieve a high fuelling rate by aerial feeding (Voigt et al. 2010; 2012) and using torpor to reduce energy expenditure during the day (McGure et al. 2011). Indeed such differences in the basic physiology are likely to result in different migration strategies.

Continuous flapping flight, as applied by bats, requires an energy consumption of 10–20 times, sometimes even 30 times, the basal metabolic rate (Thomas, Suthers 1972; Rayner 1999). Aerodynamic predictions (Pennycuick 1975; Norberg 1990) as well as empirical studies (e.g. Thomas 1975; Rayner 1994; Ward et al. 2001; Tobalske et al. 2003) suggest a U-shaped relationship between the power required to fly and the flight speed (Fig. 1). This relationship leads to prediction of two characteristic flight speeds that a bat may apply to minimise the energy consumption in flight (e.g. Hedenström 2009). The minimum power speed (V_{mp}) would be applicable to situations when the total energy expenditure is to be

minimised in order to maximise the duration of the flight (e.g. to maximise foraging time). But flying at the maximum range speed (V_{mr}) would minimise the energy consumption per distance travelled (i.e. cost of transport per distance). Insectivorous bats adjust the flight speed according to the ecological context (e.g. Grodzinski et al. 2009). The migration speed (V_{migr}) is defined as the total migration distance divided by the total migration time and depends on the rate of energy accumulation (Alerstam 1991; Hedenström 2009). Estimate of the mean migration speed of Nathusius's pipistrelles (47 km d^{-1}; Pētersons 2004) agrees well with the prediction based on fat accumulation rates in other bat species (46 km d^{-1}; Hedenström 2009). The minimum time speed (V_{mt}) exceeds the maximum range speed to some extent and depends on the fuelling rate of the animal (Hedenström, Alerstam 1995; Hedenström 2009).
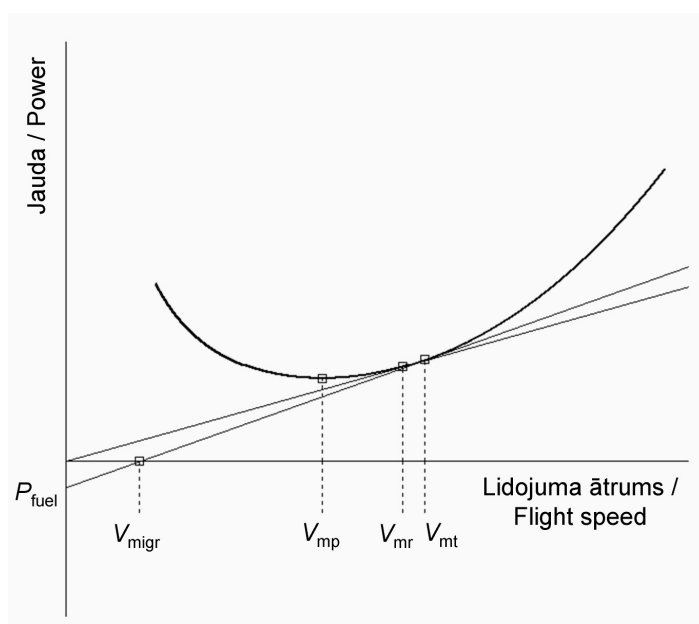

Fig. 1. Relationship between the power required for horizontal flapping flight and the flight speed through the air. V_{migr}, V_{mp}, V_{mr} and V_{mt} refer to overall migration speed, minimum power speed, maximum range speed and minimum time speed, according to the net fuelling rate P_{fuel}.

1. att. Sakarība starp horizontālam vēzienveida lidojumam nepieciešamo jaudu un lidojuma ātrumu attiecībā pret gaisu. V_{migr}, V_{mp}, V_{mr} un V_{mt} apzīmē vidējo migrācijas, mazākās jaudas, tālākā pārvietojuma un īsākā migrācijas ilguma ātrumu, kas atkarīgs no enerģijas uzkrāšanas intensitātes P_{fuel}.

In many cases migrating bats fly ca. 10 m above the water surface (Ahlén et al. 2009) or the ground (Pētersons 2004). Such a low altitude would fall within the range of the bat's sonar perception (Lawrence, Simmons 1982) and may indicate that migrating bats routinely keep acoustic contact with the ground by their ultrasonic sonar.

Homing experiments on displaced untreated vs. blind-folded bats suggest that vision is essential for successful homing (Smith, Goodpaster 1958; Williams et al. 1966; Layne 1967; Williams, Williams 1967; 1970). It has been demonstrated experimentally that some bats are able to perceive the light of the stars (Childs, Buchler 1981). Hence bats apparently use vision for landmark recognition and may apply stellar navigation in long-distance migration.

2. Methods

2.1. Bat captures at swarming sites and on migration (Papers I, III, V)

To determine species, sex and age of swarming bats that visited underground sites in late summer and autumn, mist-netting was employed at three underground sites (one dolostone and two sandstone caves) in Gauja National Park from the end of June until the beginning of November 2005–2007 (Papers I, III). Bat nettings were restricted to one night per fortnight to minimise disturbance. The bats were classified as either adults or young individuals (i.e. born in the same year). Most captured individuals were also measured and banded with numbered aluminium wing bands, placed on the bats' forearm. The bats were released at the site of capture immediately after measuring and marking. All the important hibernacula in Gauja National Park as well as many sites in other parts of Latvia had been surveyed every winter since 1992 (Vintulis 2013). Within the framework of this survey program bats with wing bands were searched for to check for possible movements among the swarming sites and hibernacula. Permit to conduct the research was granted by Administration of Gauja National Park.

To obtain morphometric data and conduct visual acuity tests on migrating Nathusius's pipistrelles, bats were captured in August and September 2011–2012 using a semi-permanent Helgoland type funnel trap at Pape Ornithological Research Station (56°09'57"N 21°01'02"E). Measurements included body mass (to 0.1 g), wing span (0.1 cm) and wing area (0.25 cm²). The body mass was measured using an electronic balance. The wing span and wing area were obtained from outlines drawn along the bat's body and spread wings, gently pressed and held on a sheet of millimetre paper (Pennycuick 2008). All the bats were released at the site of capture immediately after the data collection was made. Permit to capture bats at Pape Ornithological Research Station was granted by the Nature Conservation Agency.

2.2. Autumn migration pattern (Papers II, IV)

To investigate the phenology of bat migration along the Baltic Sea and south-eastern North Sea coasts and islands, available information on the occurrence and timing of migratory bat activity, based on ultrasonic monitoring projects at 19 localities in 2007–2009, was collected and analysed (Paper II). Slightly different methods were used to estimate bat activity at the various localities, but it could be assumed that the recorded data, regardless of sampling methods, were correlated with the actual bat activity. For each data set (bat species, locality, season and year) the median date of activity and the total number of days the activity

continued were calculated. The analysis was restricted to the years 2007–2009, for which data from most sites were collected more or less simultaneously. Data from some localities were truncated, because the sampling started too late or ended too early and therefore did not include the first and/or the last presumed migration events. Truncated datasets were used with caution and omitted in the statistical analyses.

The local field study on autumn migration of Nathusius's pipistrelle was made between 5 August and 13 September 2010 within a 4.5 km² area near Pape Ornithological Research Station at the Baltic coast of Latvia (Paper IV). In this site, autumn migration patterns of bats have been documented over the preceding two decades (Pētersons 1990; 2004; Vintulis 2013). Seven selected sites represented the principal habitats of the study area (Fig. 2). As shown earlier, flights of Nathusius's pipistrelles along the coastal dunes were generally fast, straight and nearly always directed towards the south. Hence this site was used for observations of the bats' migratory behaviour.
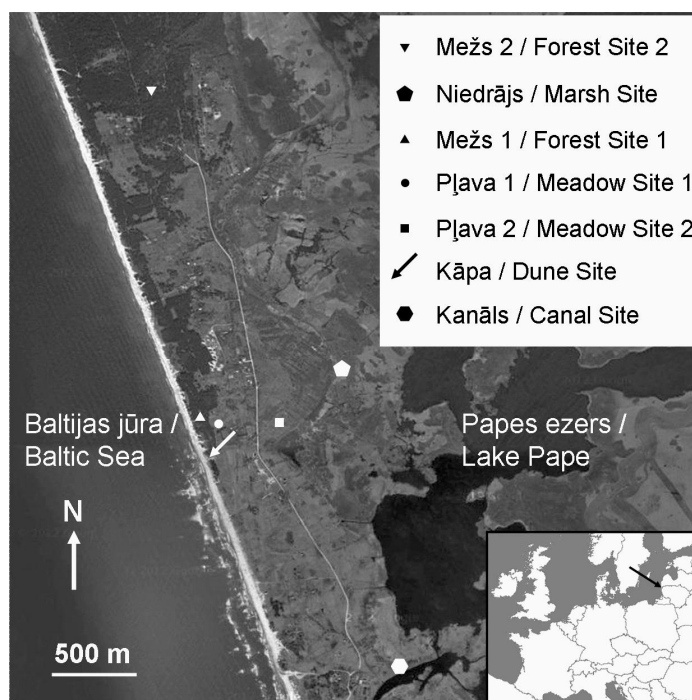

Fig. 2. The study area near Pape Ornithological Research Station and location of study sites (the background satellite image obtained from Cnes/Spot Image, DigitalGlobe, GeoEye 2012).

2. att. Pētījuma vietas un to apkaime netālu no Papes Ornitoloģisko pētījumu stacijas (satelītattēls iegūts no Cnes/Spot Image, DigitalGlobe, GeoEye 2012).

2.3. Foraging patterns (Papers III, IV)

To investigate whether bats arrive at swarming sites after intensive nocturnal feeding, changes in body mass-to-forearm ratio – the body condition index (BCI) – of captured bats were analysed (Paper III). Assuming that insectivorous bats ingest up to 3 g of insect prey per hour (Gould 1955), which comprises for ca. 30% of their body mass, a significant increase in

mean BCI of captured bats was expected throughout the night. Dividing the body mass by forearm length minimises the impact of body size, since bigger individuals are supposed to be heavier than smaller individuals.

Field observations of the foraging behaviour of migrating Nathusius's pipistrelles were conducted in the vicinity of Pape Ornithological Research Station (Paper IV). Presence of so called 'feeding buzzes' in recordings of bats' sonar unambiguously indicates attempted feeding (Surlykke et al. 2003). Acoustic recordings of echolocation pulses were made, using four digital sound recorders VN-550PC (Olympus Imaging America Inc., Pennsylvania, USA) connected to heterodyne ultrasound detectors D-200 (Pettersson Elektronik AB, Uppsala, Sweden). The detectors were set to 40 kHz, which is appropriate to recognise sonar calls of the Nathusius's pipistrelles (clear smacking sounds) and easily distinguish them from those of other species (obscure non-smacking sounds at this frequency). Connected devices were kept in plastic 13 x 13 x 6 cm boxes to protect the equipment from moisture, and a 0.5 cm diameter hole was made for the microphone of the detector (Ahlén et al. 2007). Altogether 88 recordings, each representing one night of observation, were used in the analysis. Recordings that lasted for less than six hours due to discharge of the batteries or that were heavily disturbed by noise such as bush-cricket chirring, strong wind or heavy rain were omitted ($n = 68$).

2.4. Measurements of flight speed and altitude (Paper V)

Actual flight speeds of Nathusius's pipistrelles were measured at the Dune Site at Pape Ornithological Research Station (see Fig. 2) 13–18 August and 5 September 2011 (Paper V). For distance and altitude references, two poles ($h = 10$ and 7 m, respectively) were erected along a frequently used migration flyway 20 meters apart, with the longest pole at the northernmost end of the flight path. The long pole was fitted with light reflectors 1 m apart, to facilitate estimates of the flight height of the bats. The duration of the 20 m flight between the two poles was measured using a stopwatch. All the bats were clearly seen as they passed the reference poles. At several occasions ($n = 7$), it was possible to see the bats in the moonlight, but in most cases ($n = 90$), a 100 W light source was used to facilitate observations of the bats. Only measurements of straight and uninterrupted flights were registered and analysed ($n = 97$). Theoretical estimates of characteristic flight speeds from morphometric data were made according to Grodzinski et al. (2009).

Sonar sequences of passing bats were recorded as they flew at various altitudes ($n = 20$). The durations of pulses and inter-pulse intervals were measured and the correlations between these parameters and the flight altitude were tested.

2.5. Visual acuity tests and migration intensity (Paper VI)

To test the visual acuity of migrating Nathusius' pipistrelles, a rotating drum was constructed and applied, similar to that used by others (e.g. Suthers 1966; Bell, Fenton 1986; Eklöf 2003), in which the bats were tested for optomotor responses. The bats were captured in the Helgoland type funnel trap and immediately placed in the drum where they were tested as soon as they had come to rest (Paper VI). The visual acuity tests were conducted indoors, keeping the light intensity to 3–7 lux (Lutron YK-2001 TM with aYK-200PLX light meter probe, Lutron Electronics Enterprise Co. Ltd.). The testing device consisted of a 30 cm high and 60 cm diameter revolving drum with a 20 cm high and 10 cm diameter plexiglass cylinder in the centre, where the experimental bats were put inside. The drum could be rotated freely and independently of the cylinder by hand in both directions. Inside the drum, a paper was attached with a sinusoidal grating pattern from white to black of varying fineness. Six gratings were used with different width, equivalent to subtending angles of 5, 2.5, 1, 0.75, 0.5 and 0.25 degrees of arc, as seen from the bat's point of view (i.e. from the centre of the plexiglass cylinder). The drum was rotated around the bat by hand at ca. 5 rpm randomly in both directions. When a response from the bat – movement of the head following the movement of the drum – was recorded, the grating was switched to a finer pattern until no response was recorded, indicating that the bat could no longer resolve the pattern. At this point a wider pattern was reintroduced, to make sure that the bat still responded to the moving stripes.

Assuming that a clear sky provides the best conditions for stellar navigation, preference for migration at clear nights of Nathusius's pipistrelles was tested by using data from a long term survey of migrating bats at Pape Ornithological Research Station between 10 August and 10 September 2003–2012 (Pētersons, unpubl. data). The dataset included number of passes of migrating bats recorded during 15-min periods at the second hour after sunset. An ultrasound detector (D 200 or D 240x, Pettersson Elektronik AB, Uppsala, Sweden) was used to detect an approaching bat. Cloudiness was assessed on a four-grade scale: 0 – clear sky, 1 – 20–50% cloud cover, 2 – 50–80% cloud cover and 3 – more than 80% cloud cover. Other factors such as ambient temperature, wind speed and wind direction were also recorded and included in the analysis. Records that contained fog, rain or strong wind (> 6 m s^{-1}) were not included in the analysis, because much fewer bats migrate under such conditions (Pētersons, unpubl. data).

2.6. Statistical analyses

All statistical analyses were performed by SPSS for Windows 16.0 (SPSS Inc., Chicago, Illinois) or R version 2.13.0 (The R Foundation for Statistical Computing, Wienna, Austria). Non-parametrical methods were preferred in cases when deviations from normal distribution where found. Detailed information on the applied methods is given in the papers.

3. Results

3.1. Use of underground sites (Papers I, III)

For most species the peak swarming activity was observed at the end of August and in September. Most swarming bats captured in late July and early August, were adult males. However, in late August and September, the percentage of adult females and young individuals increased (Paper I). In July and August, most bats captured at the dolostone cave were leaving the cave after having spent the day there (Paper III). Most of them (60–90%) were caught during the first two hours after sunset. The proportion of bats that arrived to the cave from other places gradually increased from early August (33%) until late September (92 %). At the two sandstone caves only a few bats rested during the day.

Most of the banded bats were recaptured or found hibernating at the same sites where they were banded. Altogether 9–11% [variation among years] of the bats banded at the dolostone cave ($n = 3,285$) were later recaptured at the same site in the same year, but this increased to 25–32% in the following season (Paper I). Only three bats were recaptured > 1 km from the sites where they were banded (range 5–21 km).

3.2. Timing of migration (Papers II, IV)

In autumn, the migratory activity of Nathusius's pipistrelles along the coast around the Baltic Sea and in the south of North Sea generally extended from early August to early October, with the mean time elapsing from the first to the last recorded bat of 41.5 days (range 30–76 days, N = 19 localities). Unlike in spring, there was no significant relationship between the median date of activity and latitude (Spearman's rank correlation, $r_S = 0.16$, $d.f. = 14$, $p = 0.74$). Hence the peak activity occurred at more or less the same time regardless of latitude (from Finland to northern Germany; Fig. 3). Likewise, there was no difference in duration of the autumn activity periods between the northern (Finland, seven localities) and the southern sites of the investigated region (Denmark and Germany, six localities; Wilcoxon signed rank test, $W = 18.5$, $p = 0.78$).

At Pape Ornithological Research Station, the first sonar calls of Nathusius's pipistrelles were recorded 40–100 minutes after sunset (Paper IV), a little earlier at wooded (shaded) sites compared to open sites. In August and September 2010, the nocturnal activity of Nathusius's pipistrelles lasted for 7.3 h on average (SD = 0.8, $n = 13$) and did not increase significantly during the season (Pearson's product-moment correlation, $r = 0.379$, $t = 1.36$, $df = 11$, $p = 0.20$). The migration activity, recorded at the dune site, varied considerably from night to

night, but within each night the activity typically increased before midnight and then decreased again until sunrise (Paper IV).
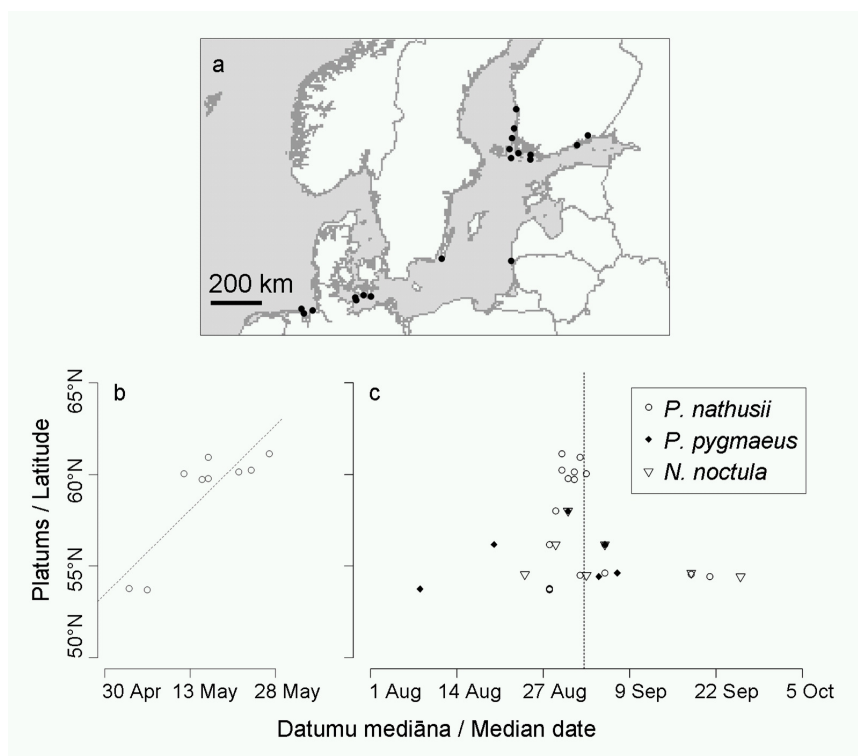

Fig. 3. Location of 19 sites were bat activity was monitored (a – simplified, see Paper II) and found relationships between median dates of bat occurrence and latitude for the spring (b) and autumn migration (c) periods.

3. att. 19 vietas, kur veikti sikspārņu aktīvitātes novērojumi (a – vienkāršots, skat. II rakstu), kā arī konstatētās sakarības starp sikspārņu novērojumu datumu mediānām un ģeogrāfiskā platuma gradiem pavasara (b) un rudens migrācijas (b) laikā.

3.3. Foraging and fat accumulation (Papers III, IV)

In late July and early August, the Body Condition Index (BCI) of captured swarming bats increased significantly during the course of night for most age groups of most species (Paper III). In September, adult bats had increased their body mass by 18–21%. However, there was no significant increase in BCI throughout the night for most cohorts and species except for young Daubenton's bats (Fig. 4).

In migrating Nathusius's pipistrelles at the Dune site at Pape Ornithological Research Station, 51% of the recorded five-minute sections ($n = 860$) contained feeding buzzes (Fig. 5). The fraction of sections that contained feeding buzzes was uniformly distributed throughout the night (Pearson's chi-squared test, $\chi^2 = 4.2$, $df = 6$, $p = 0.65$). There were slightly different foraging patterns observed in the other habitats. For example, in two forest sites most capture attempts were recorded during the first hour after sunset.
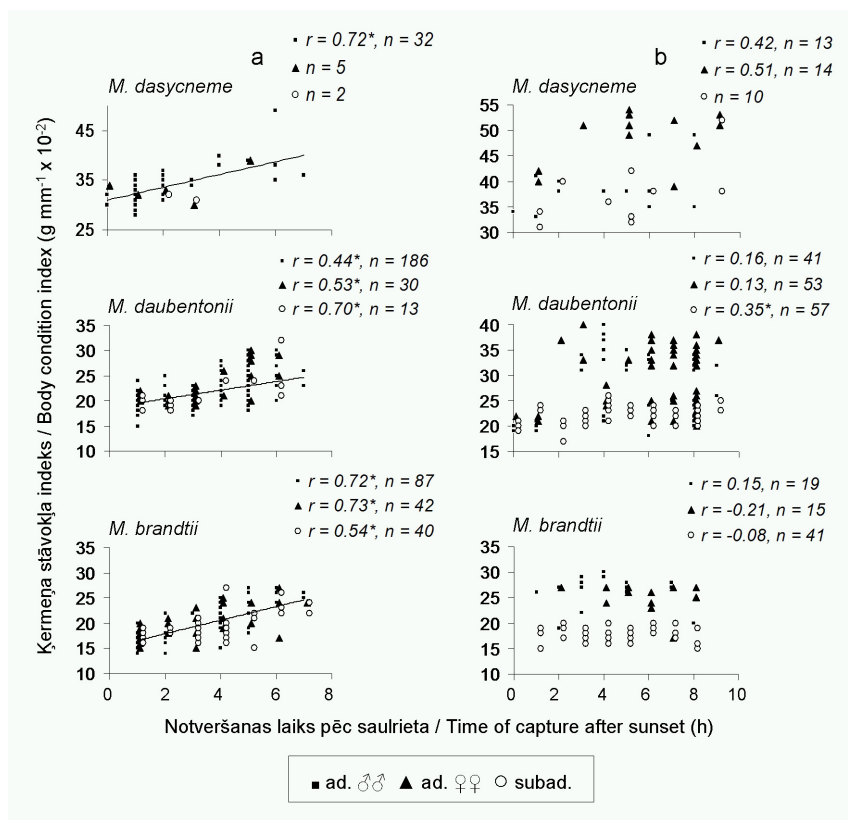
Fig. 4. Relationship between body condition indices of captured swarming bats and time of their capture in early August (a) and early September (b) 2010. Time of capture was noted as hour after sunset (0 – the sunset hour). Asterisk indicates a significant correlation ($p < 0.01$, Spearman's rank correlation analysis). Lines indicate the trends for all captured individuals.

4. att. Sakarība starp notverto spietojošo sikspārņu ķermeņa stāvokļa indeku un notveršanas laiku 2010. gada augusta sākumā (a) un septembra sākumā (b). Notveršanas laiks izteikts kā notveršanas stunda pēc saulrieta (0 – saulrieta stunda). Zvaigznīte apzīmē būtisku korelāciju ($p < 0{,}01$; Spīrmana rangu korelācija). Līnijas rāda kopējo pieauguma tendenci visiem notvertiem īpatņiem.
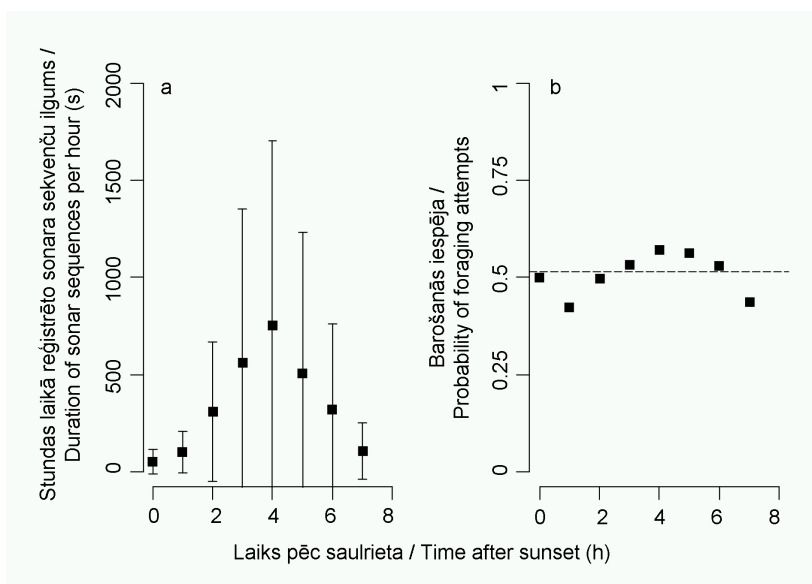

Fig. 5. Mean durations (± SD) of recorded sonar sequences of Nathusius's pipistrelles per hour (a) and the probability of foraging attempts (b) on the migration flyway (the dashed line indicates the mean probability). 0 on the abscissa accounts for the sunset hour.

5. att. Vidējais (± SD) stundas laikā reģistrēto Natūza sikspārņu sonara sekvenču ilgums (a) un barošanās iespēja (b) migrācijas koridorā (pārtrauktā līnija apzīmē vidējo varbūtību, ka nejaušs sikspārnis barosies). 0 uz abscisu ass atbilst saulrieta stundai.

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3.4. Characteristics of migration flight (Paper V)

The mean duration of a 20 m migration flight for Nathusius's pipistrelles was 1.5 s (SD = 0.4, $n = 97$), corresponding to mean flight speeds of 11.2 m s^{-1} (SD = 2.2, $n = 7$), recorded using moonlight, and 13.2 m s^{-1} (SD = 3.8, $n = 90$), recorded using a lamp (Paper V). The wind speed was slow to moderate and had a negligible effect on the measurements. Estimated minimum power and maximum range speeds were 5.8 m s^{-1} and 11.0 m s^{-1}, respectively (Fig. 6). Assuming the mean observed flight speed to be equal to the minimum time speed, the predicted migration speed was ca. 4–16 km h^{-1} or 30–120 km per night.

The mean altitude of the observed flights was 11.5 m (SD = 2.4, $n = 26$).
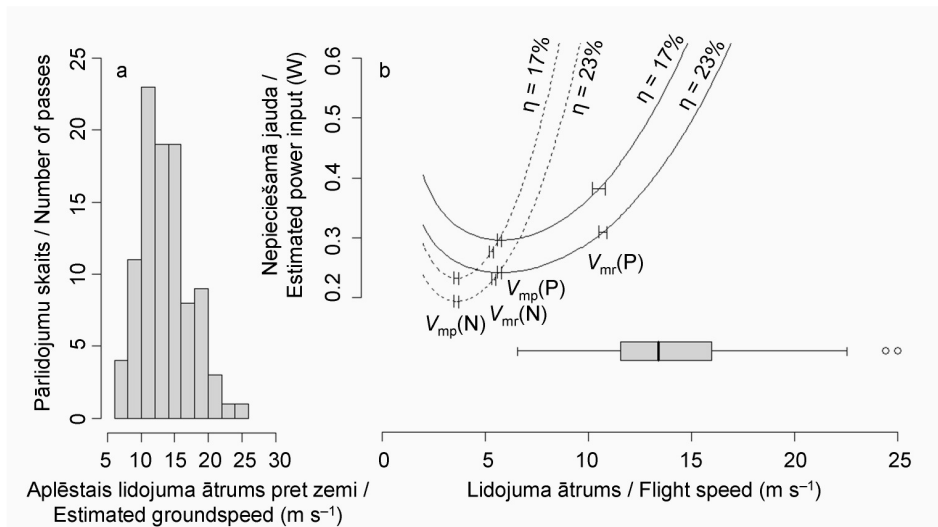

Fig. 6. Estimated flight speed for migrating Nathusius's pipistrelles (a) and comparison with predictions (b) based on two aerodynamic models (dashed lines – Norberg 1990, solid lines – Pennycuick 1975, 2008) and different flight muscle efficiency values (η). Whiskers indicate one standard deviation of estimated minimum power (V_{mp}) and maximum range speeds (V_{mr}). The box plot indicates the 10th, 25th, 75th and 90th percentiles as well as the median flight speed as measured.

6. att. Migrējošo Natūza sikspārņu lidojuma ātruma vērtējums (a) un tā salīdzinājums ar teōrētiskām prognōzēm (b), pamatojoties uz diviem iepriekš publicētiem lidojuma aerodinamikas modeļiem (pārtrauktas līnijas – Norberg 1990, nepārtrauktas līnijas – Pennycuick 1975, 2008) un divējādām lidošanā izmantojamo muskuļu efektīvitātes (η) vērtībām. Ūsiņas apzīmē mazākās jaudas (V_{mp}) un tālākā pārvietojuma ātruma (V_{mr}) vienas standartnovirzes intervālu. Kastīšu un ūsiņu diagramma parāda vērtētā lidojuma ātruma 10-to, 25-to, 75-to un 90-to procentili, kā arī mediānu.

3.5. Sonar and visual acuity (Papers V, VI)

The mean duration of sonar pulses and inter-pulse intervals of Nathusius's pipistrelles flying over the dunes at Pape Ornithological Research Station was 6.6 (SD = 1.50, $n = 116$) and 103.7 ms (SD = 25.6, $n = 116$), respectively. The duration of the inter-pulse intervals was positively correlated with the flight altitude (Pearson's product-moment correlation, $r = 0.66$, $t = 2.5$, $d.f. = 8$, $p = 0.04$). Also, there was an almost significant relationship between the pulse duration and the flight altitude ($r = 0.60$, $t = 2.1$, df = 8, $p = 0.07$).

In the visual acuity tests most individuals of Nathusius's pipistrelles responded down to 1° of arc ($n = 7$ or 54% of all tested individuals). The observed migration intensity varied considerably in relation to the cloud cover (Fig. 7). On average, more passes were registered under clear sky, as expected, and the effect was statistically significant (ANCOVA, $F_{3, 168} = 3.4$, $p = 0.019$).
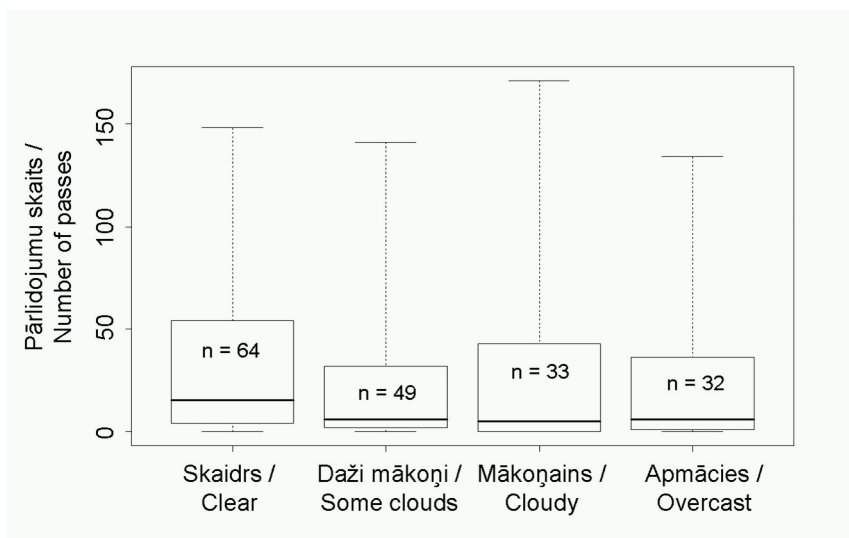

Fig. 7. Number of passes of migrating Nathurisus's pipistrelles in relation to cloud cover. Passes were registered during 15-minute intervals at Pape Ornithological Research Station during autumn migration (from 10 August until 10 September). Stripes indicate the medians, whiskers of box-whisker plots indicate the maximum and minimum numbers and the boxes show the inter quartiles (n refers to number of observations per class).

7. att. Migrējošo Natūza sikspārņu pārlidojumu skaita saistība ar mākoņu daudzumu. Pārlidojumi reģistrēti 15 minūšu uzskaitēs Papes Ornitoloģisko pētījumu stacijā rudens migrācijas laikā (no 10. augusta līdz 10. septembrim). Svītras apzīmē mediānas, ūsiņas rāda mazākās un lielākās skaita vērtības, bet kastītes apzīmē kvartiles (n atbilst klases novērojumu skaitam).

4. Discussion

4.1. Use of underground sites (Papers I, III)

The peak swarming activity occurred in late August and in September. Data from the Czech Republic (Berková, Zukal 2006), Denmark (Degn et al. 1995), Germany (Harrje 1994), Great Britain (Parsons et al. 2003b; Rivers et al. 2006) and Poland (Furmankiewicz, Górniak 2002) suggest that the time of autumn swarming in Latvia does not differ much from that of central Europe and the British Isles. However, it is slightly later than in Sweden, where swarming occurs in August (Karlsson et al. 2002). In the beginning of the swarming season, mostly adult males were captured, but later proportion of females and young individuals gradually increased, which is also consistent with other observations (e.g. Simon et al. 2004). Hence autumn swarming is an important part of the life history of bats in Latvia (see also Vintulis, Šuba 2010), which needs to be acknowledged in management of underground sites (e.g. in case of tourism) to ensure effective bat conservation.

Swarming bats used one of the caves also during the day, and most of the bats leaving the cave were captured during a two-hour period after sunset. Such individuals probably settle down in the cave at dawn and leave the next evening (similar pattern was observed by Degn et al. 1995). In late summer, swarming sites may function as special day-roosts that provide suitable environment for short-term torpor, which probably facilitates the conversion of ingested energy into fat (Krzanowski 1961; Speakman, Rowland 1999).

All bat species that were captured at the caves, except brown long-eared bats *Plecotus auritus,* are known to perform long-distance flights of more than 100 km (Hutterer et al. 2005). Tracking studies have demonstrated that the maximum distance from the diurnal roosts or hibernacula to the swarming sites can be from 20 up to 60 km (Parsons, Jones 2003; Rivers et al. 2006). Capture-mark-recapture and radio-tracking studies have indicated that bats from different summer roosts visit a common swarming site, which may also function as a hibernaculum for these bats (Fenton 1969; Parsons, Jones 2003; Parsons et al. 2003a; Rivers et al. 2006). The movements among sites found in this study indicate that two distant caves may serve as swarming sites for the same individuals, which supports the hypothesis that underground sites may be used as stopover sites during autumn movements of locally hibernating bats.

4.2. Timing of migration (Papers II, IV)

There was no obvious relationship between the latitude and the timing of autumn activity, which means that migration occurs more or less at the same time everywhere in

northern Europe. Such a relationship may not necessarily be expected because the migration activity coincides with the mating season and perhaps also with other social activities (e.g. Sluiter, van Heerdt 1966). The observed variance in the duration of the activity period in some of the southern localities may suggest that the recorded bat activity did not always represent migration alone, but may have been dominated by mating (Pētersons 1990) or foraging activities.

Each evening during the migration period, the earliest observations of Nathusius's pipistrelles were typically in woodland habitats, where bats started to feed some 40–50 minutes after sunset. These woodlands were probably used as roosting habitats. At open tree-less areas the bats were recorded considerably later, which has been observed in other studies as well (Rydell et al. 1996). The presence of trees probably facilitates the exploitation of flies and other insects that swarm at dusk in such places. The trees also provide bats with protection from raptorial birds that may still be active at that time.

4.3. Foraging and fat accumulation (Papers III, IV)

The present study indicates that bats in Latvia arrive at swarming sites after feeding. This has been observed in other species, including the little brown bat *M. lucifugus* (Fenton 1969), where 80% of the individuals returned to the cave with extended stomachs. Similarly in the present study, individuals captured later during the night in August had higher BCIs than individuals captured earlier. The increasing trend probably indicates that swarming bats feed throughout the night. It should be mentioned, however, that body mass (or BCI) is not a fully reliable indicator for feeding performance, since bats are likely to loose ingested mass by faeces after a relatively short time.

In September, the body mass of adult bats was increased by 18–21% than in late August. Other studies have also demonstrated a rapid increase in body mass among adult bats at this time of the year (Kunz et al. 1998; Encarnação et al. 2004), corresponding to the accumulation of fat reserves. No correlation between the BCI and the time of capture during the night was found at this time. Fenton (1969) found that only 20% of swarming bats captured in September had distended stomachs. However, in present study, some adult male and female Daubenton's bats, which left the cave after sunset, had lower BCIs than those that arrived to the cave later. These individuals may not yet have stored fat or may have expended the stored energy reserves on mating activities. The BCI of young Daubenton's bats were positively correlated to the time of capture, indicating that young individuals continue to feed intensively in early autumn despite the supposedly low insect abundance (see Speakman, Rowland 1999). A study by McGuire et al. (2009) suggests that young bats gradually lose

their body mass from late summer until early autumn probably due to lower foraging efficiency and higher foraging effort comparing to adults.

This study demonstrates that migrating Nathusius's pipistrelles use a fly-and-forage migration strategy when migrating south along the Baltic coastline. This also suggests that the abundance of insects was sufficient to permit energetically profitable foraging. Generally, insectivorous bats are able to fuel their flight by ingested nutrients from consumed insect prey (Voigt et al. 2010), but fat reserves may be used when insect prey is not available (Voigt et al. 2012). Energy accumulation is accelerated by reduced energy expenditure through the use of torpor (Carpenter, Hixon 1988; Speakman, Rowland 1999; McGuire et al. 2009), which may be an advantage during migration (McGuire et al. 2011).

4.4. Migration flight (Paper V)

Commuting and migration flights are predicted to be faster than foraging flights (Norberg 1981; Houston 2006), and this has been demonstrated for common pipistrelles (Jones, Rayner 1989) and Kuhl's pipistrelles *P. kuhlii* (Grodzinski et al. 2009). On average, foraging Nathusius's pipistrelles fly at 5–6 m s^{-1} (Baagøe 1987), so the present estimate of 11–13 m s^{-1} for migration flight agrees with this prediction. More precise three-dimensional methods exist for measuring flight speed of the bats (e.g. Grodzinski et al. 2009), which have already been applied (Holderied, Šuba, unpubl. data). However, the estimates made in the present study are attributable to slow wind conditions (0–2 m s^{-1}), which probably have little effect on the flight speed. However, wind speed and direction are important factors that most certainly influence the migration flight of bats (Pennycuick 1978; Alerstam 1979; Liechti et al. 1994; Weber et al. 1998; Hedenström 2002; 2009). Also migrating bats may presumably fly higher than recorded in this study, because ultrasound detectors are able to record the sonar calls only over relatively short distances (20–50 m in Nathusius's pipistrelles).

The recorded speed of migration flight slightly exceeded the predicted maximum range speed (Figs. 1, 6) and would result in a migration speed of 4–16 km h^{-1}. In a previous capture-recapture study by Pētersons (2004), it was documented that two individual Nathusius's pipistrelles, for which the time of capture and recapture were known exactly, migrated at 5.1 and 10.2 km h^{-1}, which is in good agreement with the present estimate. Assuming that the bats are active for 7.3 hours each night, the predicted average migration speed from the data of this study would be ca. 30 to 120 km per night. The analysis of capture-recapture data by Pētersons (2004) suggests that Nathusius's pipistrelles migrate on average 47 km per night (range 32 to 77 km per night), which again is in agreement with the estimates of this study.

4.5. Sonar and visual acuity (Papers V, VI)

The results of this study support the hypothesis that Nathusius's pipistrelles adjust sonar parameters according to flight height in a low-altitude migration flight. The duration of the intervals between consecutive sonar pulses was correlated with the flight height, which would be expected if bats aim the sonar towards the ground. There are published examples of bats showing this behaviour and it is likely a common phenomenon (e.g. Rydell 1990). The reason why the bats maintain contact with the surface while flying low over water during migration over the sea (Ahlén et al. 2009) may seem quite obvious, but why they do so also when flying at several metres over land is not clear at all. It may be hypothesised that bats routinely check the substrate of the ground by maintaining contact.

The visual acuity of Nathusius's pipistrelles was $1°$ of arc, which is similar to that of some other aerial-hawking bats, such as big brown bats *Eptesicus fuscus* (Bell, Fenton 1986), a species that seems to use visual cues for orientation and navigation purposes (Buchler, Childs 1982). A visual acuity greater than $6°$ of arc is sufficient to distinguish the unique position of the brightest stars and there is experimental evidence that the big brown bats can see single bright stars against the night sky (Childs, Buchler 1981). The present study demonstrates that the migration activity of Nathusius's pipistrelles increased considerably on clear nights, but relatively high activity at overcast nights suggests that the bats do not exclusively use stars for navigation purposes. Another possible visual cue that migrating bats may use at overcast nights might be the post-sunset glow in the west (Holland et al. 2006; Holland 2007).

Conclusions

1. Underground hibernacula in Latvia, such as caves, abandoned cellars and fortifications, are used from mid-summer until early autumn as swarming sites and diurnal roosts by bat species that hibernate in such sites during winter.

2. Swarming bats in Latvia may swarm and hibernate at the same or nearby underground sites, but individual bats during seasonal movements use several remote underground sites.

3. In Latvia, as in other parts of Europe, adult males tend to visit underground sites earlier than adult females and young individuals.

4. In August, bats that participate in swarming activities feed intensively throughout the night. Body fat accumulation in *Myotis* spp. occurs in late August and September, when the body mass of adults increases by 18–21%. Young bats accumulate fat reserves at slower rates and over a longer period.

5. Around the Baltic Sea, autumn migration in Nathusius's pipistrelles occurs from August to October and currently available data indicate no phenological trends.

6. Migrating Nathusius's pipistrelles feed throughout the night during their migration flight.

7. At slow wind, the mean flight speed of migrating Nathusius's pipistrelles is 11–13 m s^{-1}, which implies a migration speed of 30–120 km per night.

8. In a low-altitude migration flight, Nathusius's pipistrelles adjust their sonar according to the flight height, presumably to keep acoustical contact with the ground.

9. Visual acuity of Nathusius's pipistrelles is similar to other vespertilionid bats and would allow the bats to use the position of the brightest stars and stellar constellations for directional and positional cues during migration.

Acknowledgements

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Paper I

J. Šuba, Vintulis V., Pētersons G. 2008. Late summer and autumn swarming of bats at Sikspārņu caves in Gauja National Park. *Acta Universitatis Latviensis,* **745(Biology): 43–52.**

Late summer and autumn swarming of bats at Sikspārņu caves in Gauja National Park

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Abstract

Late summer and autumn swarming of bats at underground hibernacula has so far been poorly investigated in the north-eastern part of Europe. This study was conducted at Sikspārņu caves in Gauja National Park in 2005 to 2007 with the main aim to determine the species composition of swarming bats and the swarming phenology for different species. Mist-nettings of swarming bats were performed once per fortnight from the end of June until the beginning of November. Altogether 3,448 bats of seven species were caught of which *Myotis daubentonii* and *M. brandtii* were the most numerous. For all species adult males predominated initially, but numbers of adult females and subadult individuals increased as the season progressed. The capture-mark-recapture method revealed an individual-specific trend of visitations by adult males of *M. daubentonii* in subsequent swarming seasons. Migration between different swarming and hibernation sites located at 5- to 21-km distances were also recorded.

Key words: autumn swarming, bats, Gauja National Park, *Myotis brandtii*, *Myotis daubentonii*.

Introduction

At the end of summer and in autumn bats gather at underground sites in great numbers and perform a peculiar flying behaviour, which involves circling inside or outside the hibernaculum, chasing each other and emitting various social calls (Fenton 1969; Thomas et al. 1979; Kretzschmar, Heinz 1995). This behaviour was first reported from North America in the 1960s and was termed autumn 'swarming' (Davis 1964). The most popular hypotheses regarding this behaviour are: (i) assessing hibernacula, (ii) show the location of hibernacula to offspring (Fenton 1969) and (iii) mating activities, hence facilitating the gene flow and preventing inbreeding (Kerth et al. 2003; Veith et al. 2004; Rivers et al. 2005). In the Baltics this phenomenon has been reported previously (Liiva, Masing 1987; V. Vintulis, unpublished data), but so far it has remained without further examination.

Sikspārņu (Bat) caves were discovered in the 1980s and a colony of about 150 hibernating *Myotis dasycneme* was found at this site (Busha 1986). Since then census of hibernating bats at these caves has been conducted every year.

The main aim of this study was to describe changes in the species composition, sex

and age structure of the bats during the autumn swarming period (further referred to as swarming season) to obtain basic knowledge about this phenomenon. Capture-mark-recapture method was used to check for possible migration between swarming sites and hibernacula and to analyze visitation tendencies for recaptured individuals within the same season and in consecutive seasons.

Materials and methods

The Sikspārņu caves are located in Gauja National Park near the town of Cēsis (57° 19', 25° 21'). Altogether six dolomite caves and holes have been discovered in this area. The largest of them – Lielā Sikspārņu cave (ca. 60 m in length) – was chosen as a study site for this research (Fig. 1). Seven bat species are known to hibernate in these caves regularly: *Myotis daubentonii* (Kuhl), *M. dasycneme* (Boie), *M. brandtii* (Eversmann, 1845), *M. mystacinus* (Kuhl), *M. nattereri* (Kuhl), *Eptesicus nilssonii* (Keyserling & Blasius) and *Plecotus auritus* (Linnaeus).

The study was conducted in 2005 to 2007. Swarming bats were mist-netted from the end of June until the beginning of November. During this period bat nettings ($n =$ 6 in 2005, $n = 7$ in 2006, $n = 8$ in 2007) were performed only once per fortnight (usually twice per month) to minimize disturbance. Weather conditions varied during the netting events. We avoided only nights with strong wind and heavy rain, when nettings were not performed. The main entrance of the cave was covered by a mist-net for the entire night (Kunz, Kurta 1988), and two nearby entrances were closed by polythene, branches, and leaves. Captured bats were identified to species, sexed, aged and banded with numbered wing bands. We used aluminum bird rings, which were specially adapted for the bats (for *M. dasycneme* the ring diameter was 4.5 mm, but for other species – 3.0 mm). There were two classes of age (adults and subadults) used for age estimation according to degree of ossification and form of the metacarpal-phalageal joints (Anthony 1988). The bats were released after banding at the site of capture. Bat nettings using the same approach were additionally performed at two sandstone caves in the Gauja National Park at 8- and 21-km
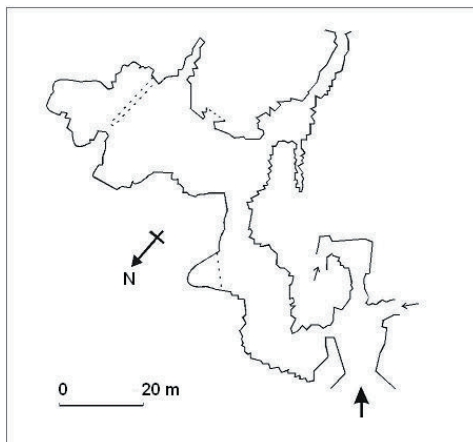
Fig. 1. Schematic plan of the Lielā Sikspārņu cave adapted from Eniņš (2004) (the main entrance and two other entrances covered in netting events are shown by arrows).

distances from the study site.

To compare species composition of bats in swarming and hibernation seasons at the Sikspārņu caves data from the annual hibernating bat census were used. In 2005 to 2007 census was conducted once every year in December or January. Hibernating bats were identified to species, except *M. brandtii* and *M. mystacinus*, which were pooled in one group '*M. brandtii/mystacinus*] (the accurate determination of these sibling species is impossible without disturbing their torpor). There are many deep and immense crevices in these caves, hence the actual number of hibernating bats might be considerably larger than recorded. Since 1992 all the important hibernacula in Gauja National Park as well as in other parts of Latvia have been surveyed every winter (V. Vintulis, unpublished data), and in the framework of this survey, search was made for bats with wing bands to check for possible migration between sites.

During most of the study period the presence of a roaming cat was noticed at the study site. This cat had adapted itself to catch and kill bats in the narrowest paths of the cave. The corpses and remains of the bats as well as the wing bands found were collected in every netting event. Dead recoveries were taken into account only in tests where the exact time of recapture was not required.

To compare the species composition between swarming and hibernation seasons Pearson's chi-squared goodness-of-fit test was used. This test was also performed in sex and age structure analysis and to compare the number of recoveries within one swarming season and consecutive swarming seasons, respectively. Spearman's rank correlation analysis was used to test the relationship of visitation timing in consecutive swarming seasons for individual bats if the sample size was greater than 15.

Results

During the swarming seasons altogether 3,448 individual bats of seven species were caught. The same species were found both in swarming and hibernation seasons, but their proportions differed between seasons (Table 1). In comparison with the swarming

Table 1. Number of bats found during hibernation seasons and caught during swarming seasons at the Lielā Sikspārņu cave in 2005 to 2007 (recaptures are not included)

Species	Hibernation seasons	Swarming seasons
M. daubentonii	23 (12.4 %)	1601 (46.4 %)
M. dasycneme	43 (23.1 %)	387 (11.2 %)
M. brandtii	–	973 (28.2 %)
M. mystacinus	–	141 (4.1 %)
M. brandtii/mystacinus	76 (40.9 %)	–
M. nattereri	5 (2.7 %)	289 (8.4 %)
Myotis sp.	12 (6.5 %)	–
E. nilssonii	3 (1.6 %)	36 (1.0 %)
P. auritus	15 (8.1 %)	21 (0.6 %)
Not identified	9 (4.8 %)	–
Total	186 (100 %)	3448 (100 %)
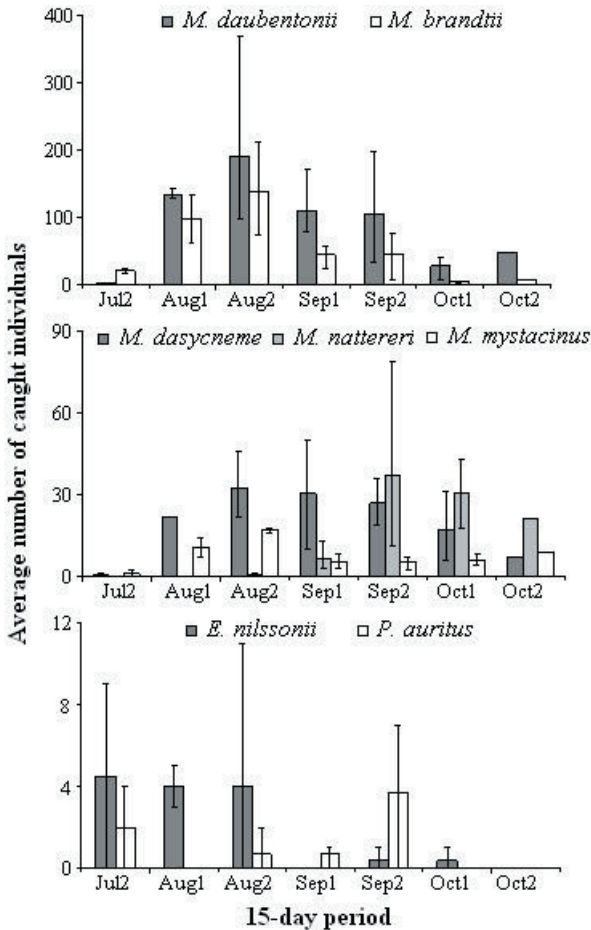
Fig. 2. Seasonal changes in mean, minimum and maximum number of caught bats during swarming seasons at the Lielā Sikspārņu cave in 2005 to 2007.

seasons, in the hibernation seasons *M. dasycneme* (χ^2 = 25.77, d.f. = 2, p < 0.001) and *M. brandtii/mystacinus* (χ^2 = 6.15, d.f. = 2, p < 0.05) were observed significantly more than expected, while *M. daubentonii* were found significantly less often than expected (χ^2 = 48.91, d.f. = 2, p < 0.001).

For most species the greatest swarming activity was observed at the end of August and in September. Temporal distribution of swarming activity differed among species (Fig. 2). For *M. brandtii* and *M. mystacinus* the greatest swarming activity was observed at the end of August. *M. daubentonii* reached its peak activity at the end of August and in September. For *M. dasycneme* a clear maximum was not observed; the swarming activity for this species was high at the end of August and in September. *M. nattereri* was the last species to begin swarming with peak activity at the end of September and beginning of October. The greatest activity of *E. nilssonii* was observed at the end of July and in August, reaching its peak at the end of August. Later this species rarely visited the study site. The majority of *P.*

Table 2. Number of all autumn swarming captures at the Lielā Sikspārņu cave in 2005 to 2007 (recaptures are not included). The male dominance between adults and subadults tested by Pearson's chi-squared goodness-of-fit test (* – $p < 0.05$, ** – $p < 0.01$, *** – $p < 0.001$)

Sex and age group	M. daubentonii	M. dasycneme	M. brandtii	M. mystacinus	M. nattereri	E. nilssonii	P. auritus
Ad. males	654 (40.8 %)***	152 (39.3 %)***	357 (36.7 %)***	62 (44.0 %)*	142 (49.1%)**	14 (38.9 %)	12 (57.1%)
Ad. females	379 (23.7 %)	86 (22.2 %)	202 (20.8 %)	37 (26.2 %)	93 (32.2%)	7 (19.4 %)	6 (28.6 %)
Total ad.	1027 (64.5 %)	238 (61.5 %)	559 (57.5 %)	99 (70.2 %)	235 81.3%)	21 (58.3 %)	18 (85.7 %)
Subad. males	330 (20.6 %)***	94 (24.3 %)***	216 (22.2 %)	21 (14.9 %)	23 (8.0%)	6 (16.7%)	2 (9.5 %)
Subad. females	229 (14.3 %)	49 (12.7 %)	183 (18.8 %)	21 (14.9 %)	25 (8.7%)	7 (19.4 %)	1 (4.8 %)
Total subad.	559 (34.9 %)	143 (37.0 %)	399 (41.0 %)	42 (29.8 %)	48 (16.6%)	13 (36.1 %)	3 (14.3 %)
Indet. males	4 (0.2 %)	4 (1.0 %)	7 (0.7 %)	0	3 (1.0%)	0	0
Indet. females	3 (0.2 %)	2 (0.5 %)	8 (0.8 %)	0	1 (0.3%)	0	0
Indet. sex	2 (0.1 %)	0	0	0	2 (0.7%)	2 (5.6 %)	0
Total indet.	9 (0.6 %)	6 (1.6 %)	15 (1.5 %)	0	6 (2.1%)	2 (5.6 %)	0

Table 3. Number of recaptures in different years during swarming seasons at the Lieā Sikspārņu cave in 2005 to 2007 (dead recoveries included)

| Year of banding	Year(s) of recapture	M. daubentonii	M. dasycneme	M. brandtii	M. mystacinus	M. nattereri	Total
2005	2005	8 (8.3 %)	4 (10.5 %)	4 (12.9 %)	0	2 (16.7 %)	18 (10.1 %)
2005	2006	26 (27.1 %)	15 (39.5 %)	14 (45.2 %)	1 (50 %)	2 (16.7 %)	58 (32.4 %)
2005	2006, 2007	1 (1.0 %)	1 (2.6 %)	0	0	1 (8.3 %)	3 (1.7 %)
2005	2007	7 (7.3 %)	4 (10.5 %)	2 (6.5 %)	0	7 (58.3 %)	20 (11.2 %)
2006	2006	13 (13.5 %)	2 (5.3 %)	3 (9.7 %)	1 (50 %)	0	19 (10.6 %)
2006	2007	31 (32.3 %)	8 (21.1 %)	6 (19.4 %)	0	0	45 (25.1 %)
2007	2007	10 (10.4 %)	4 (10.5 %)	2 (6.5 %)	0	0	16 (8.9 %)
Total		96 (100 %)	38 (100 %)	31 (100 %)	2 (100 %)	12 (100 %)	179 (100 %)
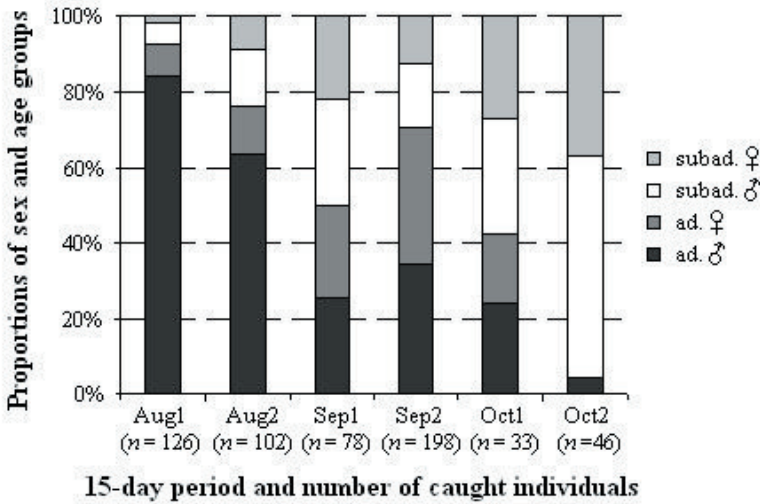
Fig. 3. Dynamics of particular sex and age groups of *M. daubentonii* netted at the Lielā Sikspārņu Cave in 2007 (recaptures are included).

auritus individuals were caught at the end of July and at the end of September.

The sex and age structure of caught individuals is shown on Table 2. Among adults significantly more males than females were observed for all *Myotis* species, but this difference was not significant for *E. nilssonii* (χ^2 = 2.38, d.f. = 1, p = 0.12) and *P. auritus* (χ^2 = 2.06, d.f. = 1, p = 0.15). The difference in numbers of subadult males and subadult females was not significant except for *M. daubentonii* (χ^2 = 18.25, d.f. = 1, p < 0.001) and *M. dasycneme* (χ^2 = 14.17, d.f. = 1, p < 0.001) – in these cases subadult males predominated. Temporal changes in sex and age structure during the swarming season, however, were common for all species. At the beginning of swarming the dominant group was formed by adult males, but the proportion of the adult females and subadult individuals increased as the season progressed (Fig. 3).

In this study 3,285 individual bats were banded. Only *Myotis* species were recaptured (Table 3). The total number of recaptured individuals, including dead recoveries, was 177 (5.4 %). There were significantly more cases where bats were recaptured in consecutive swarming seasons rather than in the same season (χ^2 = 31.35, d.f. = 3, p < 0.001, the sample size for *M. mystacinus* was too small to include in this test). Spearman's rank correlation analysis revealed a significant relationship of visitation timing in consecutive swarming seasons for *M. daubentonii* adult males (r = 0.97, d.f. = 27, p < 0.001). For other species and sex-age groups this test was not performed due to small sample sizes.

Three bats were recaptured outside the banding sites (Fig. 4). One swarming *M. nattereri* subadult male was first caught and banded at an artificial sandstone cave ca. 21 km southwest of the study site, but later in the same year recaptured at the study site. At the same sandstone cave a lactating *M. mystacinus* female was recaptured, which was banded at the Lielā Sikspārņu cave in the previous year. Another *M. nattereri* adult male banded at the study site was found hibernating in a sandstone cave ca. 5 km northeast of the study site.
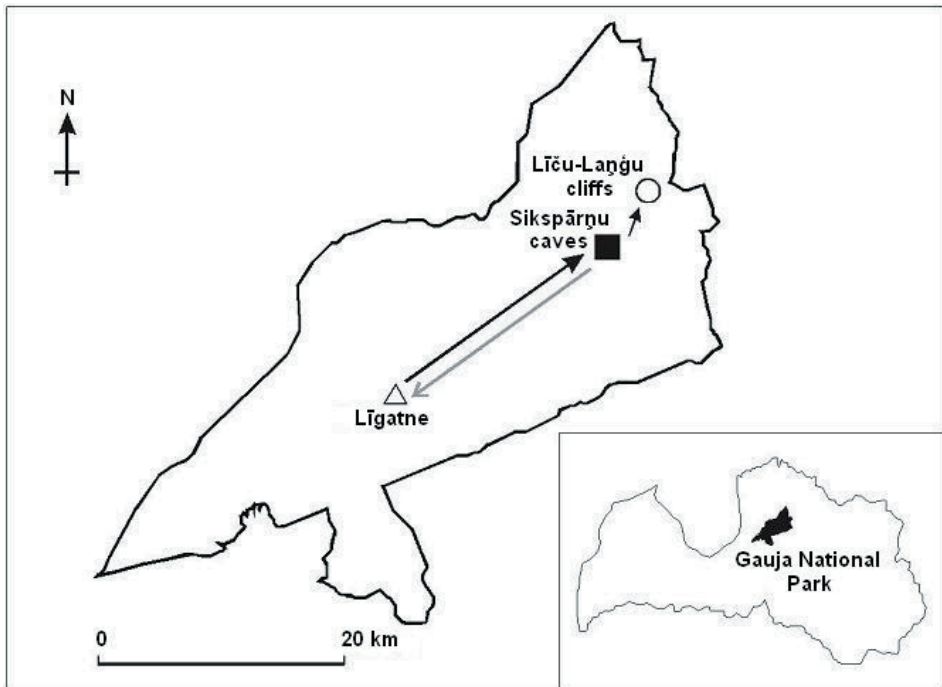
Fig. 4. Discovered bat movements among the Lielā Sikspārņu cave and other swarming (△) and hibernation (○) sites. Movements of *M. nattereri* are showed by black arrows, but the gray arrow represents *M. mystacinus* (see details in the text).

Discussion

In this study swarming behaviour was recorded for seven bat species, which all usually hibernate in underground sites. This supports the general opinion that autumn swarming behaviour is characteristic to those bat species using underground sites for hibernation (Fenton 1969; Kretzschmar, Heinz 1995; Parsons et al. 2003a). Therefore, swarming can be distinguished from another behaviour of bats at the end of summer called 'invasions' (Sachteleben 1991), which usually involves subadult and inexperienced individuals of *Pipistrellus* species, which accidentally enter buildings.

The differences in the species composition of the bats during the swarming and hibernation seasons can be explained by different habitat selection of species regarding hibernation in deep and large crevices (Furmankiewicz, Górniak 2002). For example, *M. dasycneme* are more likely to hibernate in bigger crevices than smaller species. Hence the proportions of this species observed in hibernation seasons may appear greater than they really are.

In this study the greatest swarming activity for most species was observed at the end of August and in September. Other studies performed in Czech Republic (Berková, Zukal 2006), Denmark (Degn et al. 1995), Germany (Harrje 1994), Great Britain (Parsons et al. 2003b; Rivers et al. 2006) and Poland (Furmankiewicz, Górniak 2002) suggest that the autumn swarming phenology in Latvia does not differ much from other parts of Europe.

The temporal distribution of swarming activity was species-specific. For example, *M. brandtii* and *M. mystacinus* had their activity peak in August, *M. daubentonii* – at the end of August and in September, and *M. nattereri* at the end of September and in October. It is known that these species leave their hibernacula in spring in the opposite order (Degn 1987; Parsons et al. 2003a). Parsons et al. (2003a) associate these observations with the foraging strategies of these species. *M. nattereri* is a gleaning species, which is able to capture prey from surfaces. Therefore, this species might be active for a longer period in the year than *M. daubentonii* and *M. brandtii*, which are specialized in catching flying insects. Moreover, *M. brandtii* and *M. mystacinus* are considerably smaller in size than other *Myotis* species. Hence their early swarming and start of hibernation could be related to thermoregulation as they have a large body surface-to-volume ratio (Ransome 1990).

In previous studies the visits of *E. nilssonii* at underground sites during the swarming seasons were considered occasional (Furmankiewicz, Górniak 2002; Karlsson et al. 2002). This study and other research in Latvia (J. Šuba, unpublished data) confirm that the swarming behaviour is characteristic of this species. For *Myotis* species it is known that their swarming activity overlaps with the start of hibernation (Fenton 1969; Harrje 1994; Trappmann 2005). In contrast, *E. nilssonii* actively swarm in August and up to the beginning of November they visit underground sites rarely.

Overall the proportions of different sex and age groups among the caught individuals tended to be species-specific, yet the temporal changes of the sex and age structure were common for all species. At the beginning of the swarming season the study site was mostly visited by adult males, but at the end of the season subadult individuals of both sexes predominated. Fenton (1969) suggests that swarming behavior could be related to the information transfer from adults to subadults, indicating the location of the hibernacula. Adult males may emerge earlier than females due to their idleness during the summer while females are rearing their offspring (Parsons et al. 2003a).

There were significantly more cases when bats were recaptured in consecutive swarming seasons than in the same season. An exhausting behaviour like swarming would considerably inhibit the fat deposition for the winter if performed continuously. Therefore, bats are expected to visit the swarming sites only once or a few times per season. The analysis of recaptured *M. daubentonii* adult males in consecutive swarming seasons shows that these bats tended to visit the swarming site at the same time every year. Similar results have been obtained in other studies (e.g. Fenton 1969; Parsons et al. 2003a).

The maximum distance of the diurnal roosts or hibernacula to swarming sites can be from 20 up to 60 km (Parsons, Jones 2003, Rivers et al. 2006). Capture-mark-recapture and radio-tracking studies indicate that bats from different summer roosts visit a common swarming site, which may also function as a hibernaculum, though migrations to other hibernacula have also been recorded (Fenton 1969; Parsons et al. 2003a; Parsons, Jones 2003; Rivers et al. 2006). There are two opinions about the swarming sites per se. There is evidence that bats show a great fidelity to a particular swarming site and do not visit other swarming sites (Parsons et al. 2003a; Parsons, Jones 2003), however, migration between different swarming sites have been recorded (Rivers et al. 2006). Bat migration found in this study indicate that two distant caves may serve as swarming sites for the same individuals.

Acknowledgements

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Sikspārņu vēlās vasaras un rudens spietošana Gaujas nacionālā parka Sikspārņu alās

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Kopsavilkums

Rakstā aplūkota Eiropas ziemeļaustrumu daļā maz pētīta tēma – sikspārņu „spietošana" pie ziemošanas mītnēm vasaras beigās un rudenī. Pētījums veikts Sikspārņu alās (Gaujas nacionālajā parkā) no 2005. līdz 2007. gadam, un tā galvenais mērķis bija noskaidrot spietojošo sikspārņu sugu sastāvu un to spietošanas fenoloģiju. No jūnija beigām līdz novembra sākumam reizi divās nedēļās veikta spietojošo sikspārņu ķeršana un gredzenošana. Pavisam pētījuma periodā noķerti 3448 sikspārņi no septiņām sugām. Visām sugām spietošanas sezonas sākumā dominēja pieaugušie tēviņi, bet sezonas laikā ievērojami palielinājās pieaugušo mātīšu un nepieaugušo īpatņu īpatsvars. Pieaugušajiem ūdeņu naktssikspārņa tēviņiem konstatēta individuāla spietošanas laika izvēles tendence dažādās spietošanas sezonās. Konstatētas arī atsevišķu īpatņu pārvietošanās starp dažādām spietošanas un ziemošanas mītnēm piecu līdz divdesmit viena kilometra attālumā.

Paper II

Phenology of migratory bat activity across the Baltic Sea and the south-eastern North Sea

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We compiled the available information on the occurrence and timing of migratory bat activity across the Baltic Sea and south-eastern North Sea coasts and islands, based on ultrasonic monitoring projects at 19 localities in 2007–2009. The data refer to three species; Nathusius' pipistrelle *Pipistrellus nathusii*, soprano pipistrelle *P. pygmaeus* and common noctule *Nyctalus noctula*. *Pipistrellus nathusii* occurred at all sites (north to 61°N in Finland), while the other species were scarcer, particularly at the northernmost sites. The status of the recorded individuals is unknown. However, the activity most likely was of migrating individuals or individuals on migration stopover, because very few observations were made during the maternity period. Spring activity occurred predominantly in May, with the median observation date of *P. nathusii* 20 days earlier in the south (Germany) than in the north (Finland). Autumn migration was observed throughout August and September and activity that may or may not indicate migration was also observed in October and November. The median date of such activity in autumn usually occurred in September and without any significant difference in timing in relation to latitude. Migratory bats in the Baltic area apparently move on a broad front in most cases. The estimated speed of migration for *P. nathusii* in spring was 55 km/day. The entire coastline and islands around the Baltic Sea are of potential importance for migrating bats in spring (April–May) and autumn (August–September) and should achieve relevant protection according to EU legislation and its implementations.

Key words: Europe, life history, migration, wind turbines, *Pipistrellus*, *Nyctalus*

Introduction

Long-distance migration in bats is a world-wide phenomenon. It may have evolved in response to seasonal variations in food availability at least in some cases, such as in nectar feeding tropical bats, while in hibernating bats at high latitudes, the reason behind the migration pattern is less clear. Nevertheless, it is usually assumed that long-distance migration in bats has to do with the avoidance of seasonally inclement weather and/or low food availability (Fleming and Eby, 2003).

There is an explicit need for a better understanding of bat migration in general and for the identification of important migration routes used by bats in particular. This is partly because there is a potential conflict with humans in areas frequented by migrating bats, arising from demands for exploitation of such areas, e.g., coastlines frequently used for the construction of wind farms. It has become

increasingly obvious that wind turbines kill many migratory bats and that protective measures are becoming urgent (Kunz *et al.*, 2007; Rydell *et al.*, 2010; Voigt *et al.*, 2012).

At the same time the European legislation asks for protection of migration routes of importance to bats, but this requires that the routes are identified spatially and temporally. In northern Europe this is generally not the case, except for some specific sites where bats concentrate (e.g. Ahlén, 1997; Pētersons, 2004; Furmankiewicz and Kucharska, 2009). Understanding the basic biology of bat migration is also important for the same reason.

Five bat species are considered as long-distance migrants in the Baltic area (Hutterer *et al.*, 2005), namely the common noctule *Nyctalus noctula* (Schreber, 1774), Leisler's bat *Nyctalus leisleri* (Kuhl, 1817), Nathusius' pipistrelle *Pipistrellus nathusii* (Keyserling and Blasius, 1839), the soprano pipistrelle *Pipistrellus pygmaeus* (Leach, 1825) and the parti-coloured bat *Vespertilio murinus* Linnaeus, 1758. In parts of north-eastern Europe, bat migration was traditionally studied by banding of large numbers of bats caught in their summer- or winter quarters (Eisentraut, 1935, 1943; Strelkov, 1969; Markovets *et al.*, 2004; Hutterer *et al.*, 2005), or, in some cases, particularly in Estonia, Lithuania and Latvia, in Helgoland-type traps on the migration routes (Pētersons, 1990; Masing *et al.*, 1999; Hutterer *et al.*, 2005). The results of these activities have been summarized by Steffens *et al.* (2004), Hutterer *et al.* (2005) and Popa-Lisseanu and Voigt (2009).

Migratory activity of bats in northern Europe has also been studied by acoustic observations (i.e., using bat detectors) at off-shore (Ahlén *et al.*, 2007, 2009; Poerink *et al.*, 2013) and coastal sites, where bats congregate before they fly out over the sea, e.g. in southern Sweden (Ahlén, 1997; Ahlén *et al.*, 2009), near Saint Petersburg in Russia (Chistiakov, 2011), on the coast of Poland (Ciechanowski *et al.*, 2010) and further south along the river Oder (Furmankiewicz and Kucharska, 2009). Many migrating bats occur along the Baltic coast of Estonia, Latvia and Lithuania on their southern or south western migration towards central Europe (Masing, 2011; Pētersons, 2004; Šuba *et al.*, 2012), but others appear to take shorter routes either across the eastern part of the Baltic Sea between Sweden and Poland (a non-stop flight of ca. 200 km) or by using the Danish Islands as stepping stones (Ahlén *et al.*, 2009; Seebens *et al.*, 2013). From an energy point of view it may be advantageous to cross the Baltic Sea

from Estonia or Latvia to northern Germany rather than follow the Baltic coast (Hedenström, 2009). An estimated 35,000 bats cross the Fehmarn Belt between Denmark and Germany (12 km) in late summer and autumn each year (Meyer, 2011). To the west of Denmark, bats regularly cross the southeastern part of the North Sea at Helgoland (Vauk, 1974; Skiba, 2007; Walter *et al.*, 2007; O. Hüppop, in litt.) and the East-Friesian islands (Bach *et al.*, 2009; Frey *et al.*, 2011; L. Bach and P. Bach, unpublished data). In this case the distance across the sea is ca. 120 km, but with the possibility of a stop-over at Helgoland about half way. Further north along the Baltic coasts of Sweden and Finland, migrating bats have been recorded as far north as the Bothnian Bay at 62–64°N, depending on species (Wermundsen and Siivonen, 2004; Ahlén, 2011; Hagner-Wahlsten, 2011; Blank and Gylje Blank, 2013).

We have summarised the results of several relatively recent (2007–2009) bat detector surveys that were carried out around the Baltic Sea and adjacent parts of the North Sea. The goal of this compilation was to provide an overall picture of the occurrence and timing of bat migratory movements in this northern region. We hypothesize that there would be phenological trends in bat activity across the range of latitudes covered, principally because insect availability may be a limiting factor, at least early in the spring and late in the autumn. Specifically, we predict later arrival of bats to northern localities in spring and perhaps also later departure from these areas in the autumn. We also attempt to provide a gross estimate of the speed of migration, to be compared with a previous estimate based on ringing recoveries (Pētersons, 2004).

MATERIALS AND METHODS

The original data for this study were collected for various purposes such as surveys for Environmental Impact Assessments (e.g., Meyer, 2011; L. Bach and P. Bach, unpublished data) or as part of long-term monitoring (e.g., the data from Pape Ornithological station in Latvia; Pētersons *et al.*, 2013). The data from Finland are in part the result of a specific bat migration project coordinated by an NGO the Finnish Chiropterological Society (E.-M. Kyheröinen, V. Vasko, N. Hagner-Wahlsten, E. Inberg, E. Kosonen, M. Lappalainen, T. Lilley, R. Lindstedt, U.-M. Liukko, and K. Norrdal, unpublished data). We included published and unpublished data sets. The locations of the 19 sites covered in this summary are shown in Fig. 1.

The data were collected by automatic continuous and remote field recordings of echolocation calls (indicating bat activity) of the species of bats mentioned above or by counting passes of bats manually, using a heterodyne ultrasound detector. The species included in this study use high-intensity echolocation and their calls are picked up easily by all modern ultrasound
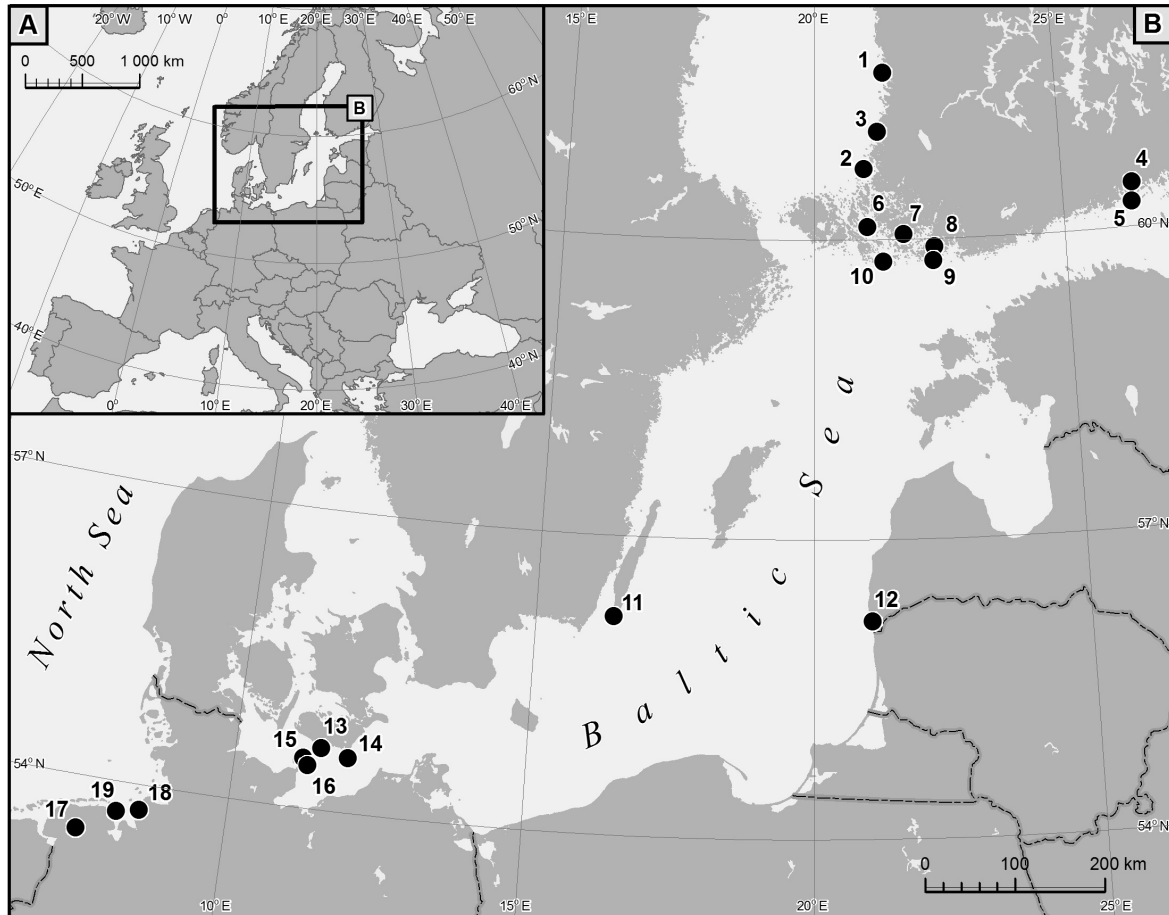
FIG. 1. Map showing the 19 localities included in this survey. Finland: 1 — Anttoora (61.67°N, 21.43°E); 2 — Isokari (60.71°N, 21.01°E); 3 — Rihtniemi (61.08°N, 21.30°E); 4 — Ruotsinpyhtää (60.44°N, 26.43°E); 5 — Aspskär (60.25°N, 26.40°E); 6 — Jungfruskär (60.13°N, 21.07°E); 7 — Berghamn (60.05°N, 21.79°E); 8 — Kasnäs (59.92°N, 22.40°E); 9 — Kuggskär (59.78°N, 22.37°E); 10 — Utö (59.78°N, 21.37°E); Sweden: 11 — Ottenby (56.19°N, 16.40°E); Latvia: 12 — Pape (56.18°N, 21.05°E); Denmark: 13 — Hyllekrog (54.62°N, 11.47°E); 14 — Gedser (54.55°N, 11.95°E); Germany: 15 — Fehmarn N (54.50°N, 11.18°E); 16 — Fehmarn E (54.43°N, 11.27°E); 17 — Wangerooge (53.47°N, 07.53°E); 18 — Cappel (53.75°N, 08.53°E); 19 — Mellum (53.70°N, 08.15°E)

detectors and microphones. The equipment differed between the projects. The exact methods employed, such as the positioning of the microphones and settings of the detectors, were usually not specified and certainly varied somewhat among the sites as well. In Finland, Denmark and Germany, automatic surveys with Ana-Bat SD1™ frequency division detectors (Titley Scientific, Brisbane, Australia) were used, while in Ottenby in Sweden (locality 11) an automatic real time full spectrum detector (Pettersson D-500X; Pettersson Elektronik AB, Uppsala, Sweden) was employed. At Pape in Latvia (locality 12) a hand held detector (Pettersson D-200 or D-240X) was used in the heterodyne mode. In this case the detector was tuned to 40 kHz, i.e. to the frequency used by *P. nathusii*. Hence other species were not counted at this particular site. At Pape the detector was operated manually from one point near the sea shore during three 15 min periods each night between 10 August and 10 September, starting 2, 4 and 6 hours after sunset, respectively. The equipment and monitoring method used at each site is summarized in Table 1. The analysis of all automatically recorded echolocation calls, including species recognition, was made using software such as BatSound (Pettersson Elektronik,

Uppsala, Sweden) and AnalookW (Titley Scientific, Brisbane, Australia).

We did not attempt to control for differences in the equipment and methods. Such an exercise would have been extremely complicated or impossible to do afterwards and probably of limited use anyway (Adams *et al.*, 2012). Most likely differences in the systems themselves, including the microphones, or variations in the settings of the recording equipment influenced the detection rates. However, this is likely of minor importance in our case, since we are only interested in the phenology and not in the absolute or relative levels of activity at each site. We assumed that the recorded data, regardless of the methods used, were correlated with the actual bat activity. For each data set (species, locality, season and year) a median date of activity and the total number of days that the activity continued were calculated (see below). The relative frequency of recordings for each day at some of the localities is shown for illustration purposes in Fig. 2.

We restricted the analysis to the years 2007–2009, for which we had access to data from several sites that were monitored more or less simultaneously. For some localities (5, 10, 13, 18

TABLE 1. Summary of the acoustic monitoring systems and sampling methods used in each study and sources of the data. Localities as in Fig. 1

Locality no.	Monitoring system	Sampling method	Sources
1–10 & 13–19	Ana-Bat SD1 Frequency-division	Continuous Automatic	Bach *et al.* (2009), Frey *et al.* (2011), L. Bach and P. Bach (unpublished data), E.-M. Kyheröinen, V. Vasko, N. Hagner-Wahlsten, E. Inberg, E. Kosonen, M. Lappalainen, T. Lilley, R. Lindstedt, U.-M. Liukko, and K. Norrdal (unpublished data), M. M. Meyer (unpublished data)
11	Pettersson D-500X Full spectrum real-time	Continuous Automatic	A. Hedenström and L. Guia Diaz (unpublished data)
12	Pettersson D-240 Heterodyne	Continuous Manual	G. Pētersons, V. Vintulis, and J. Šuba (unpublished data)

and 19), data from more than one year were available, but for most of them we had data from only one year (usually 2009). Data from some localities (11, 12 and 18) were truncated, because the sampling started too late and/or ended too early and therefore did not include the first and/or the last presumed migration events. Data sets were considered truncated unless they started and ended with nights without any bat activity being recorded. Truncation presumably influenced the duration of the migration period to some extent, and perhaps also the median date of the presumed migration period. Bat migration data are often multi-modal with peaks in recorded activity during nights with particular weather conditions, and the effect of the truncation is very difficult to evaluate. We therefore used truncated and non-truncated data without any adjustments and concentrated on patterns rather than details throughout.

We restricted this study to three of the five presumed migratory species in the region, namely *N. noctula*, *P. nathusii* and *P. pygmaeus*. The other two (*N. leisleri* and *V. murinus*) were excluded, because recordings that potentially refer to any of them were few (three sites) and could not be identified with confidence and distinguished from similar calls of the serotine *Eptesicus serotinus* (Schreber, 1774), given the monitoring methods used. The remaining three species are easy to distinguish, because they use search pulses with narrow-band components of species-specific and well separated frequency bands (ca. 20, 40 and 55 kHz, respectively; Ahlén, 1981).

For the statistical analyses we used Microsoft Excel 2003 (Microsoft Corporation, USA) and R version 2.13 (The R Foundation for Statistical Computing, Vienna, Austria). The main analysis was conducted on the 2009 data sets, which were the most complete. We used non-parametric tests throughout due to non-normal distribution of much of the data. Latitudinal trends in timing of the median activity at different localities were investigated using Spearman's Rank Correlation. The difference between the durations of the activity periods at the northernmost and the southernmost localities was examined using Wilcoxon's signed rank test with continuity correction. For this analysis, we used only the non-truncated data sets from seven localities in Finland and six localities from Denmark and Germany, respectively. Latitudinal differences in the duration of the activity periods were examined only for autumn, because we had no representative spring data from the German and Danish localities. Wilcoxon's test was also used to compare the duration of the spring and autumn activity periods at each locality. For this analysis we used the non-truncated spring and autumn data from seven Finnish localities and one German locality and employed a pair-wise test to minimize the effect of large variation in the sample size across the different localities. The

difference in the median date of activity among the three bat species was examined using Kruskal-Wallis Rank Sum Test.

We assumed that the bat activity as recorded represented migration activity or at least that it was closely correlated with such activities. This was probably true for localities consisting of small islands largely surrounded by open water. However, the situation may have been slightly different on peninsulas such as e.g. Ottenby (locality 11) and Gedser (locality 14; Fig. 1), where bats accumulate in large numbers, and where the maximum activity may occur as the bats congregate at the site, and not when they actually migrate out over the sea (Ahlén, 1997). The potential magnitude of this bias in the estimated median date of activity is hard to evaluate, because the behaviour of the bats (such as feeding and local flight activity versus migration flight) is strongly dependent on the prevailing weather (Ahlén, 1997). We did not account for this.

RESULTS

Species Occurrence

Pipistrellus nathusii was found at all sites (Fig. 1); it was also the most frequently recorded species at most localities. *Pipistrellus pygmaeus* was more restricted particularly in the north. Only occasional observations (1–3 recordings per site) of this species were made at 59–61°N in Finland (e.g. at localities 3, 9 and 10). A similar situation applied to *N. noctula*, which was occasionally observed north to 61°N (at localities 3, 5 and 10). Further south, all three species were recorded more or less regularly at each locality with the exception of the German North Sea localities (16 and 17), where *P. nathusii* and *N. noctula* were recorded regularly but *P. pygmaeus* only occasionally.

Observations in Summer

In the 2009 season, the Finnish sites (localities 2, 3, 5, 6, 7, 9 and 10) and two of the German North Sea sites (17 and 19) were monitored continuously throughout the summer, and this was also the case at two Finnish sites (5 and 10) and one German site
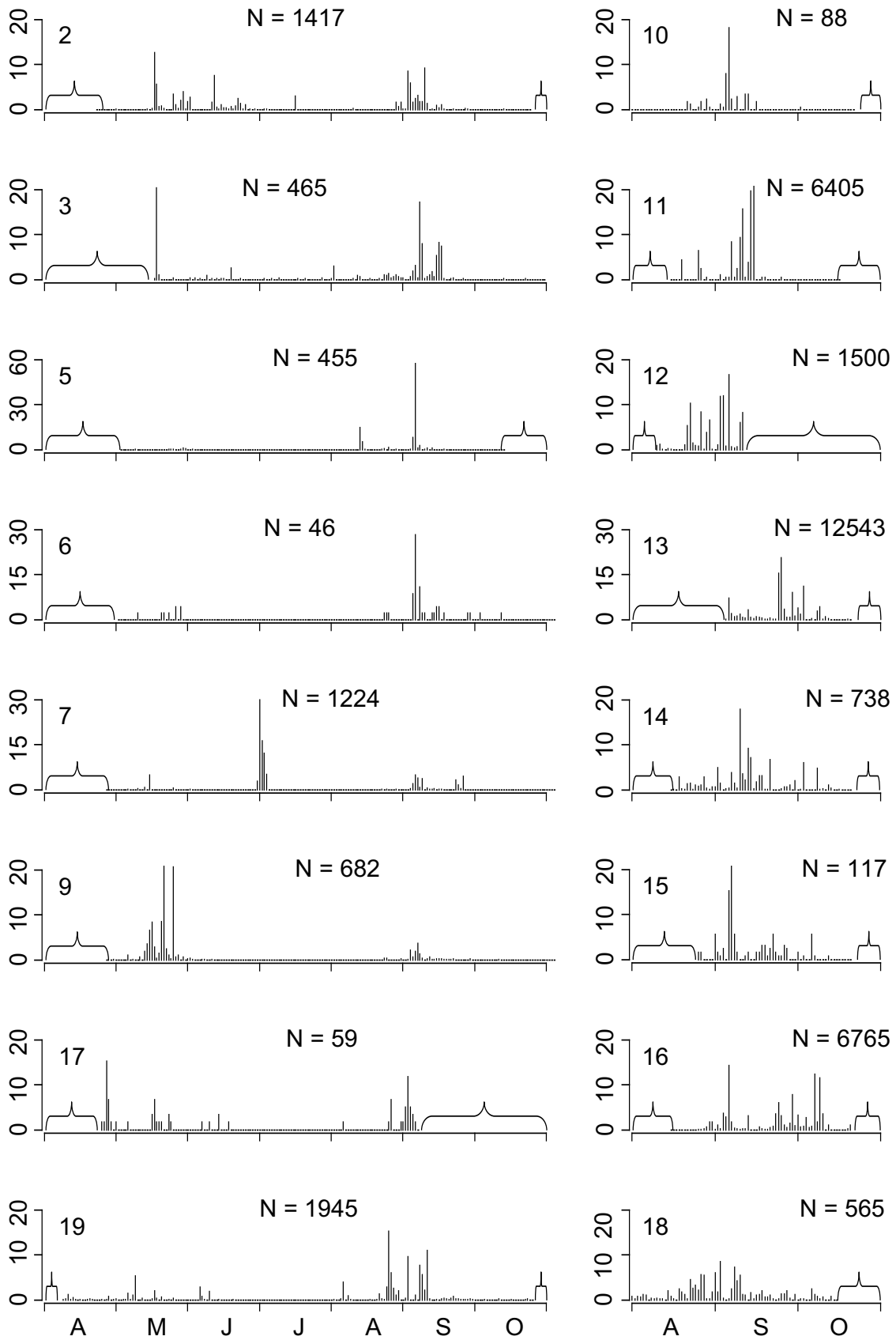
FIG. 2. Changes in occurrence (%) of *P. nathusii* throughout the season in 2009 at some of the localities monitored. The left column covers 1 April to 31 October, the right column covers 1 August to 31 October. Crochets denote periods without observations. The numbers refer to locality as in Fig. 1

(17) in 2008. Bats belonging to any of the three species included in this study were absent from these sites throughout July and in most cases also in late June, i.e. during the period of late pregnancy and lactation (Fig. 2).

Timing of Spring and Autumn Activity

In spring, *P. nathusii* was the only species observed regularly at the sites monitored (i.e. in Finland and at the German North Sea coast; Table 1). Generally, the median date of activity occurred in early May in the south (54°N in Germany; $N = 2$ localities) and in late May in the north (60–61°N in Finland; $N = 7$ localities), with a difference of 20 days between the two regions (Fig. 3a). Hence, there was a significant latitudinal trend in the median date of activity (Spearman's rank correlation, $r_s = 0.85$, $d.f. = 7$, $P < 0.01$). The distance between the German and the Finnish localities is about 1100 km, so the average distance covered by *P. nathusii* in spring was about 55 km/day (1100 km/20 days).

At three localities, for which we had data from both 2008 and 2009, the median date of spring activity differed by 10 days between the years on average (Table 2). The difference was smaller at the southernmost site (six days) than at the two northernmost sites (11 and 12 days, respectively).

The presumed southward migration generally extended from early August to early October. In this case, there was no significant relationship between the median date of activity and latitude for *P. nathusii* ($r_s = 0.16$, $d.f. = 14$, $P = 0.74$; Fig. 3b). Hence, the peak activity occurred at more or less the same

time regardless of latitude. For *N. noctula* and *P. pygmaeus*, the sample sizes were smaller and there were no significant latitudinal trends in the median autumn activity dates for either of them (Fig. 3b; *P. pygmaeus*, $r_s = -0.38$, $d.f. = 5$, $P = 0.40$; *N. noctula*, $r_s = 0.17$, $d.f. = 4$, $P = 0.74$). Likewise, there was no consistent difference in the median activity date among the three species (Kruskal-Wallis test, $\chi^2 = 14.9$, $d.f. = 16$, $P = 0.53$).

In localities for which we had data from more than one year, the median autumn activity date of *P. nathusii* differed among years by no more than 1–3 days (Table 2). However, at Cappel in Germany (locality 19), the difference between 2007 and 2008 was as much as 14 days for this species. At this site, the median activity dates for *N. noctula* differed by 3 and 15 days between 2007 and 2008 and 2008 and 2009, respectively.

Duration of Spring and Autumn Activity

The mean time elapsing from the first to the last recorded *P. nathusii* at each site was 40 days in spring and 41.5 days in autumn (range 19–68 and 30–76 days, respectively). Hence, there was no significant difference in the duration of autumn and spring activity periods for this species (Wilcoxon matched-pairs signed ranks test, $V = 11$, $P = 0.38$), although the variance was higher in the autumn samples. Comparing the duration of the autumn activity periods of *P. nathusii* between the northern (Finland, seven localities) and the southern (Denmark and Germany, six localities) sites, using the non-truncated data from 2009, we found no significant
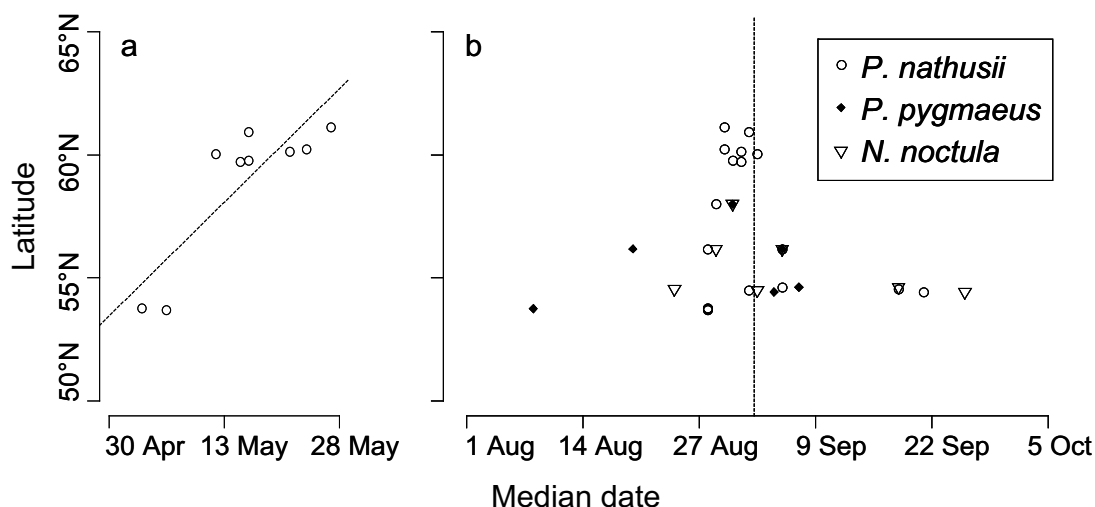

FIG. 3. Relationships between median dates of bat occurrence and latitude for the spring migration (a) and autumn migration (b) periods

TABLE 2. Comparison of median dates of recorded bat activity at sites studied for more than one year (number of observations in parentheses)

Species	Season	Site	Latitude	Locality	2007	2008	2009
P. nathusii	Spring	Aspskär	60.25	5	–	7 Jun (21)	26 May (12)
		Utö	59.73	10	–	29 May (31)	18 May (73)
		Wangerooge	53.78	17	–	30 Apr (245)	6 May (35)
P. nathusii	Autumn	Aspskär	60.25	5	–	5 Sep (9)	3 Sept (102)
		Pape	56.18	12	29 Aug (310)	1 Sep (670)	31 Aug (1500)
		Cappel	53.75	18	16 Sep (1115)	2 Sep (644)	31 Aug (565)
N. noctula	Autumn	Cappel	53.75	18	22 Aug (219)	25 Aug (222)	10 Aug (229)

difference between the two regions (Wilcoxon signed rank test, $W = 18.5$, $P = 0.78$). At some of the southern localities, the autumn activity period most likely did not correspond to migration alone, as assumed, particularly for *P. pygmaeus.* At the Fehmarn E (locality 16), for example, the peak activity of this species occurred in late September and early October, almost a month later than at the adjacent locality at Fehmarn N (locality 15, Fig. 3b).

DISCUSSION

Timing of Migration

Previous studies have revealed that bat migration occurs in the Baltic region and along the German North Sea coast (e.g., Ahlén, 1997; Pētersons, 2004; Ahlén *et al*., 2009; Bach *et al*., 2009; Kurvits *et al*., 2011; Šuba *et al*., 2012; O. Hüppop, in litt.), but this study provides the first overview of bat migration activity in the region. The bats arrived later at higher latitudes in spring, according to our hypothesis, since they moved in a north-eastern direction (Petersons, 2004; Hutterer *et al*., 2005). The distance that can be covered in a day in spring is probably constrained by the availability of food (aerial insects), which in turn depends on the weather, particularly the air temperature (Avery, 1985; Racey and Swift, 1985; Rydell, 1989) and, in the north, also on the clearing of the ice cover, which prevents the emergence of water insects such as chironomids and plecopterans. While warm weather in spring could be used as external cue for migration timing, there is still a risk of encountering low temperatures at night and little or no activity of flying insects. Hence, assuming that bats on migration use a fly-and-forage strategy (McGuire *et al*., 2012; Šuba *et al*., 2012), presumably after fat reserves have been depleted during hibernation, they may continue their northern migration only on nights that are warm enough for insects to be active. Periods of cold weather also

result in longer gestation and later parturition, because the females enter torpor during such conditions (Racey and Swift, 1981).

Contrary to the spring data and to our hypothesis, the autumn data did not indicate any relationship between latitude and timing of activity. This could be because the migration activity coincides with the mating season and perhaps also with other social activities (e.g., Sluiter and van Heerdt, 1966; Gerell and Lundberg, 1985), which we did not account for. The observed increase in the variance in the duration of the activity period in some of the southern localities in autumn may suggest that the data (flight activity) did not always represent migration activity alone, but may have been dominated by mating (Pētersons, 1990) or feeding activities (Šuba *et al*., 2012). This was particularly obvious at the Fehmarn E locality, where bat activity was high as late as October. It seems likely that the migrating bats may have met with local populations at this site. Indeed, *N. noctula*, *P. nathusii* and *P. pygmaeus*, which regularly migrate along the river Oder in south-western Poland, are abundant throughout the summer in this area, where maternity colonies are also known (Furmankiewicz and Kucharska, 2009). However, at most localities monitored in this study, breeding populations of the migratory bat species were not recorded. The bats monitored must therefore have reproduced elsewhere in most cases.

The energetic constraint, which seems so obvious for the spring migration, does not seem to apply to the autumn migration, presumably because nights are on average warmer and insects more abundant. Indeed, bats migrating over large expanses of open sea may even feed extensively on rich patches of migrating or drifting insects in certain areas particularly in late summer and autumn (Ahlén *et al*., 2009). Nevertheless, cool nights may still be encountered in late autumn. Our data suggest that the duration of the migration periods was almost the same in spring and autumn. While the autumn migration may

compete with other time-consuming activities, such as mating, migration in spring is probably slowed down by limitations in the availability of food, as discussed above.

Speed of Migration

We assume that the two activity peaks of *P. nathusii* (in Germany and Finland, respectively) represent a northward migration wave, which is supported by some ringing recovery data (Pētersons, 2004), and we estimated the average migration speed in spring to 55 km/day. This compares well with the previous estimate of 48 km/day for the same species during the autumn migration, based on ringing recoveries (Pētersons, 2004).

Implication for Bat Conservation

This and previous studies indicate that bats migrate more or less regularly all along the Baltic and south-eastern North Sea coasts and also cross the open sea and island far off-shore like Helgoland and Bornholm (Baagøe and Jensen, 2007; O. Hüppop, in litt.). Migrating bats sometimes accumulate in large numbers at stop over sites before they embark on open sea crossings, such as at Ottenby and Falsterbo in southern Sweden (Ahlén, 1997; Ahlén *et al*., 2009), or where they pass through a narrow corridor along the coast of the Baltic Sea at Pape in Latvia (Pētersons *et al*., 2013) and presumably elsewhere as well (Masing *et al*., 1987; Pauza and Pauziene, 1998). The conservation implication of this is that not only sites where bats are known to congregate, but indeed any coastal or island locality in the Baltic region, is likely to be used by migrating bats during spring and autumn. This should be adequately assessed as part of planning processes to avoid careless exploitation, e.g. for wind farming, according to the EU legislation and the EUROBATS agreement.

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Paper III

J. Šuba, Vintulis V., Pētersons G. 2011. Body weight provides insight into the feeding strategy of swarming bats. *Hystrix – the Italian Journal of Mammalogy,* **22(1): 179–187.**

BODY WEIGHT PROVIDES INSIGHT INTO THE FEEDING STRATEGY OF SWARMING BATS

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ABSTRACT **-** Temperate bat species that hibernate in underground sites are known to visit hibernacula in late summer where they perform an activity known as 'swarming'. We analysed trends in body mass-to-forearm ratio – the body condition index (BCI) - to investigate whether bats arrive at swarming sites following intensive nocturnal feeding. In a two-year study, *Myotis daubentonii, M. brandtii* and *M. dasycneme* were captured by mist-net at one swarming site from late July until early October. In late summer, the BCIs of captured males, females and subadult bats were positively correlated to the time of their capture during the night. In September, adult bats had higher BCIs than in late summer and the BCI did not increase during the night. For subadult *M. daubentonii,* the BCI was positively correlated to the time of capture in early autumn. Our results indicate that in late summer bats feed intensively during the first hours of the night before visiting swarming sites. In early autumn, subadult bats may go on feeding to complete fat accumulation.

Key words: Chiroptera, body condition index, feeding strategy*, Myotis*

RIASSUNTO - ***Deduzioni sul comportamento alimentare dei pipistrelli durante lo "swarming" a partire dall'analisi del peso corporeo***. I pipistrelli delle aree temperate che utilizzano rifugi sotterranei sono soliti visitarli a partire dalla fine dell'estate, un attività definita come "swarming". Abbiamo analizzato la variazione nel rapporto peso corporeo – lunghezza dell'avambraccio – l'Indice di Condizione Corporea (ICC) – per verificare se i pipistrelli arrivano ai siti di swarming dopo essersi alimentati a sufficienza. Nel corso di due anni, dalla fine di luglio a inizio ottobre *Myotis daubentonii, M. brandtii* e *M. dasycneme* sono stati catturati tramite mist-net presso una cavità. Alla fine dell'estate, l'ICC di maschi, femmine e subadulti è risultato correlato positivamente all'ora di cattura. In settembre, l'ICC degli adulti è risultato maggiore e stabile nel corso della notte. All'inizio dell'autunno, l'ICC dei *M. daubentonii* subadulti è risultato correlato positivamente all'ora di cattura. I risultati ottenuti suggeriscono che in tarda estate i pipistrelli si nutrono in modo intensivo prima di raggiungere i siti di swarming, mentre, all'inizio dell'autunno, i subadulti devono ancora completare le riserve lipidiche.

Key words: Chiroptera, indice di condizione corporea, strategie alimentari*, Myotis*

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INTRODUCTION

In late summer and autumn, temperate bat species gather at underground hibernacula in large numbers to perform an activity known as 'swarming' (Fenton 1969; Kretzschmar and Heinz 1995; Parsons et al. 2003a; Piksa 2008). This behaviour has been associated with either the assessment of hibernacula prior to hibernation or information transfer from adults to subadults to familiarise them with suitable hibernation sites (Fenton 1969; Bauerová and Zima 1988; Veith et al. 2004). Swarming may also facilitate gene flow among summer colonies through mating (Kerth et al. 2003; Rivers et al. 2005).

The peak in swarming activity is observed around or after midnight (Degn et al. 1995; Parsons et al. 2003b; Berková and Zukal 2006; Rivers et al. 2006). This suggests that bats arrive at swarming sites from distant locations or after foraging. Feeding seems to be a reasonable explanation, since bats enter a state of hyperphagia before hibernation (McGuire et al. 2009a): the more the time bats spend on feeding, the more the fat they can accumulate for hibernation (Kunz et al. 1998). There may, however, be some trade-offs between longer feeding and early arriving at the swarming site, e.g. adult males may lose an opportunity to select and occupy strategic mating spots (Piksa 2008).

Gould (1955) observed that insectivorous bats are able to capture 1–3 g of insects per hour, which represents 9–51% of their pre-feeding body mass. Hence, feeding performance can be estimated by measuring individual body weights. The condition of a bat's digestive tract (full or empty) can also be evaluated by touch (Fenton 1969). To our knowledge, no study has analysed the feeding performance of swarming bats by monitoring the variation in their body mass during the night. In some studies on body mass variation (e.g. Encarnação et al. 2004), weighing wild bats after feeding was avoided, since stomach content could impair the correct assessment of body condition.

We conducted a field study to investigate whether bats arrive at swarming sites following intensive feeding. Most feeding activity may occur in the first hours of the night, since aerial insect density is the highest around sunset (Racey and Swift 1985). We hypothesized that in late summer the body weight of captured bats would be positively correlated to the time of their capture, assuming that those individuals which spent more time on feeding would have increased body weight. In early autumn, when adult bats have accumulated enough fat for hibernation, subadult bats (young of the year) may be supposed to still feed intensively to complete fat accumulation (Kunz et al. 1998; McGuire et al. 2009a).

MATERIALS AND METHODS

1. Study site

Bats were captured at a semi-natural cave in the Devon dolomite (ca. 60 m in length), situated in Gauja National Park (central Latvia), ca. 5 km NE of Cēsis (57°19', 25°21'). The cave is located in woodland

next to a ravine, a narrow gorge and agricultural land. Seven bat species are known to hibernate and swarm there, of which *Myotis daubentonii, M. dasycneme,* and *M. brandtii* are the most abundant (Šuba et al. 2008).

2. Trapping methods

From late July until early October 2006–2007, bats were captured by a polyester mist-net (2.5 x 3.0 m, Ecotone, Gdańsk, Poland) placed in front of the cave entrance (Kunz and Kurta 1988). We started netting just after sunset and removed the net after sunrise (netting duration varied between 5 and 12 hours across the season). Other minor entrances were covered by polythene, branches and leaves. The individuals caught flying from the inside of the cave (i.e. departing individuals) were separated from the individuals captured while trying to enter into the cave (i.e. arriving individuals). Netting ($n = 7$ in 2006, $n = 8$ in 2007) was performed fortnightly (approximately on the same dates in both years) to minimize disturbance on bats. Nights with strong wind and heavy rain were avoided.

Time of capture, flight direction, species, sex, age, forearm length and body mass of captured individuals were recorded. Age (adult or subadult) was assessed according to the degree of ossification and shape of the metacarpal-phalangeal joints (Anthony 1988). The individuals were weighed and measured within the hour of capture. We weighed bats using a 50 g Pesola balance (± 0.25 g) and measured forearm length using callipers (± 0.1 mm). Captured bats were handled with care and released at the site of capture.

3. Data analysis

Since large bats are expected to weigh more than small ones, for any captured individual we calculated the body condition index (BCI), defined as the ratio between body mass and forearm length, which allows for the effect of size on body mass (Speakman and Racey 1986; Pearce et al. 2008). The analyses covered adult males, adult females and subadults (both sexes pooled) of *M. daubentonii, M. dasycneme* and *M. brandtii.* To increase sample size, data from both years were pooled for five periods (late July, early August, late August, early September and late September). Sample size for early October was insufficient and therefore we did not include those data in the analysis.

The relationship between the BCI of captured bats and time of their capture (expressed in hours after sunset, with sunset hour = 0) was analysed by Spearman's rank correlation. We assumed that departing and arriving bats captured during the first hour after sunset had their stomachs still empty. Statistical analyses were performed by SPSS for Windows 16.0 (SPSS Inc., Chicago, Illinois).

RESULTS

In the study period, we captured and measured 746 *M. daubentonii* (380 males, 149 females, 217 subadults), 489 *M. brandtii* (200 males, 106 females, 183 subadults) and 241 *M. dasycneme* (98 males, 54 females, 89 subadults). Most bats were captured in August ($N = 835$) and September ($N = 440$). In late July and early August, most bats captured were adult males of all the studied species (71.1 %). In late August and September, captured bats were mostly subadults (41.8 %). In August, most bats captured were departing individuals (65.7%). From late July until early September 60.1– 91.7 % of departing individuals were caught during the first two hours after sunset. Individuals of all studied species (*M. daubentonii*, 56.5%; *M. brandtii*, 30.8%;

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Table 1 - Mean body mass (m) and body condition index (BCI) (± SE) of arriving swarming bats captured in summer and early autumn.

	Cohort	Late July and August			September		
		m (g)	BCI (g mm^{-1})	N	m (g)	BCI (g mm^{-1})	N
M. daubentonii	Ad M.	8.46 (±0.15)	0.227 (± 0.004)	72	11.17 (± 0.28)	0.299 (± 0.007)	52
	Ad F.	9.15 (± 0.27)	0.237 (± 0.007)	15	11.74 (± 0.23)	0.307 (± 0.006)	69
	Subad.	8.31 (± 0.15)	0.218 (± 0.004)	40	9.00 (± 0.16)	0.239 (± 0.004)	80
M. brandtii	Ad M.	7.10 (± 0.15)	0.203 (± 0.004)	68	9.08 (± 0.16)	0.258 (± 0.004)	38
	Ad F.	7.39 (± 0.27)	0.208 (± 0.007)	26	9.07 (± 0.11)	0.257 (± 0.003)	30
	Subad.	6.41 (± 0.10)	0.184 (± 0.003)	65	6.47 (± 0.13)	0.185 (± 0.004)	38
M. dasycneme	Ad. M.	16.55 (±0.38)	0.362 (± 0.010)	19	20.19 (± 0.80)	0.435 (± 0.017)	20
	Ad. F.	18.96 (±1.69)	0.402 (± 0.039)	6	23.17 (± 0.44)	0.499 (± 0.009)	24
	Subad.	15.75	0.335	2	19.32 (± 0.52)	0.416 (± 0.010)	29

M. dasycneme, 12.7%) were caught leaving the cave in the evening. The proportion of arriving individuals gradually increased from early August (32.6%) until late September (92.1%).

In late July, most of the bats captured were adult males of *M. brandtii* (88.9 % of all captured *M. brandtii*), for which the BCI was correlated with the time of their capture (r_S = 0.51, p < 0.01, n = 34). In early August, the BCI of captured individuals increased significantly during the course of night for most cohorts of analysed species (Fig. 1). The increase occurred also in late August, but the BCI was not significantly correlated to the time of capture for *M. brandtii* adult males (r_S = 0.11, p = 0.46, n = 28), *M. daubentonii* adult females (r_S = 0.28, p = 0.14, n = 30) and *M. dasycneme* adult females (r_S = 0.26, p = 0.40, n = 13) and subadults (r_S

= 0.05, p = 0.86, n = 17). It must be mentioned, however, that in these cases most individuals were captured during the first hours of night, hence data on later hours were insufficient or lacking. In September, captured individuals had higher mean BCI than in late summer, except *M. brandtii* subadult individuals (Tab. 1). However, BCIs for departing *M. daubentonii* adult males and females captured during the two-hour period after sunset was low (0.198 g mm^{-1}, SD = 0.008, n = 6 and 0.218 g mm^{-1}, SD = 0.005, n = 4, respectively). In early September, no relationship was found between the BCI and time of capture for most cohorts, except for *M. daubentonii* subadult individuals (Fig. 2). In late September, the BCI was also correlated to the time of capture for *M. daubentonii* subadults (r_S = 0.61, p < 0.01, n = 45).

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Figure 1 - Relationship between body condition indexes of captured swarming bats and time of their capture in early August. Time of capture was noted as hour after sunset (0 = sunset hour). Asterisk indicates significant correlation ($p < 0.01$, Spearman's rank correlation analysis). The line indicates the trend for all captured individuals.
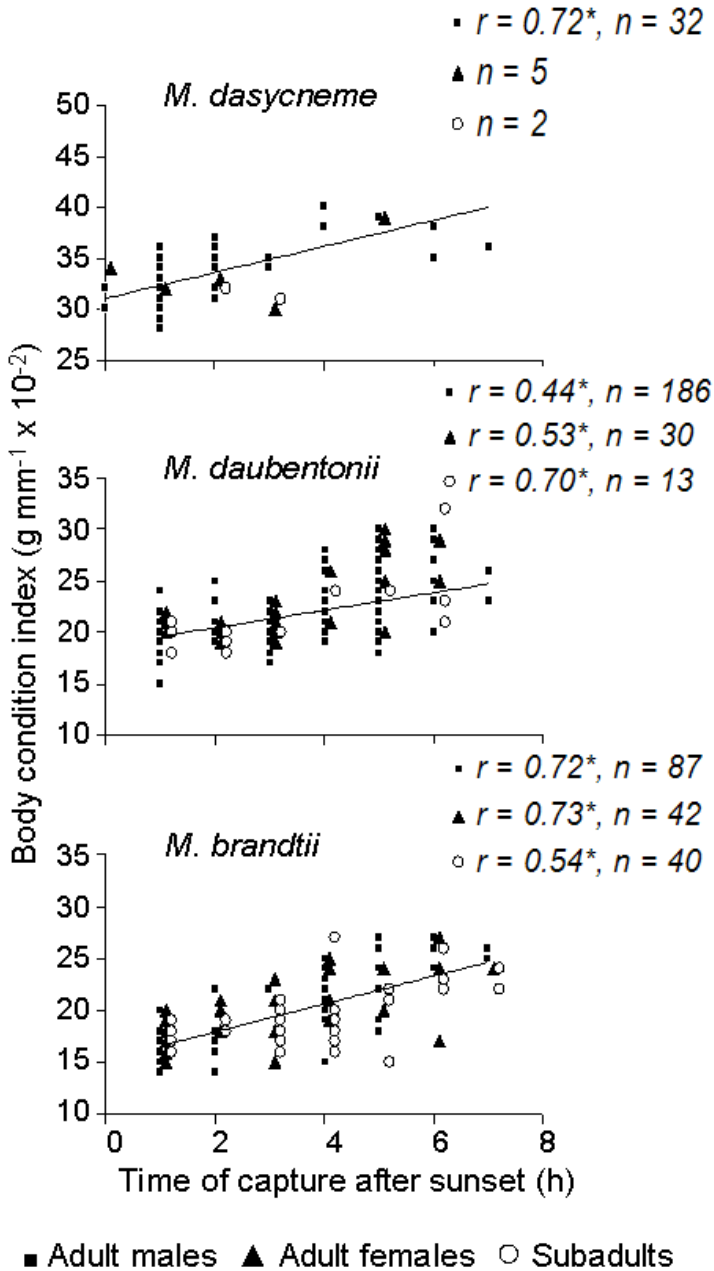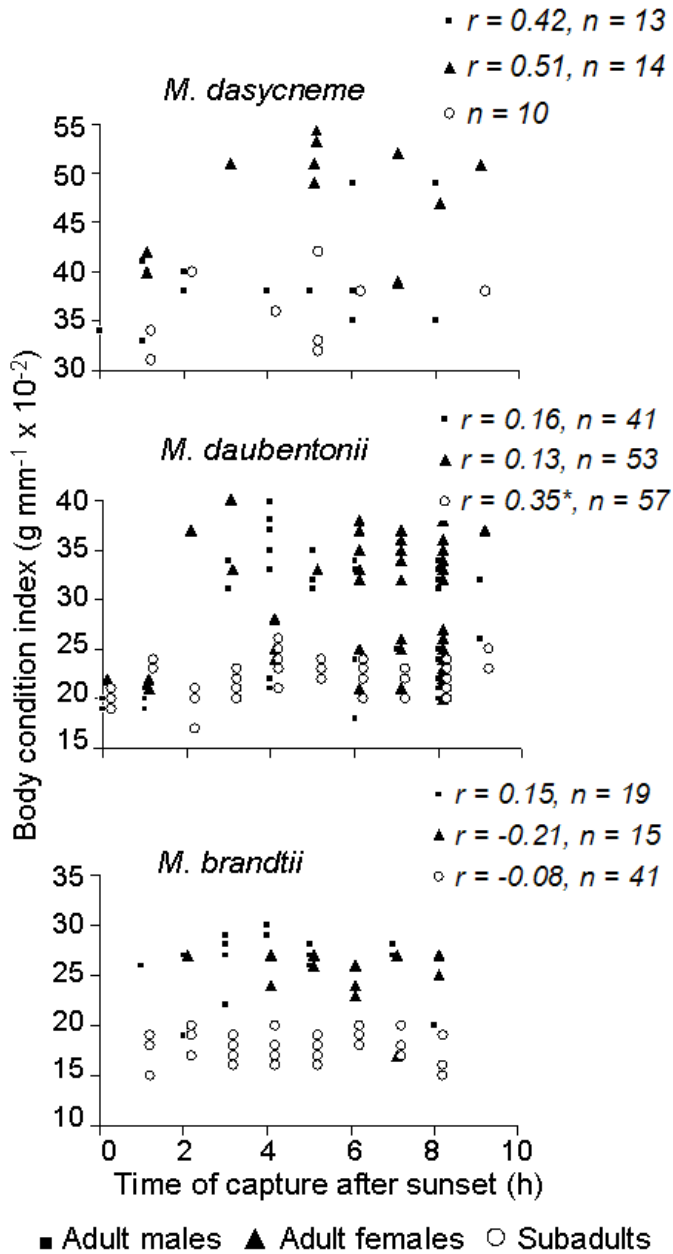
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Figure 2 - Relationship between body condition indexes of captured swarming bats and time of their capture in early September. Time of capture was noted as hour after sunset (0 = sunset hour). Asterisk indicates significant correlation (p < 0.01, Spearman's rank correlation analysis).

DISCUSSION

In late summer, individuals captured later during the night had on average higher BCIs than individuals captured after sunset, confirming the hypothesis that bats arrive at swarming sites after feeding. Accordingly, Fenton (1969) reported that, in August, 90% of swarming bats had distended stomachs. The increasing trend suggests that bats may feed even at midnight, when insect availability is low (Racey and Swift 1985). Since flying is an energy-consuming activity that requires intensive feeding, the duration of swarming activity is likely to be restricted to a relatively short period of time, after which the bat should go on feeding. Accordingly, Sendor and Simon (2000, cited in Simon et al. 2004) found that *Pipistrellus pipistrellus* spends 3.2-13.8 minutes swarming at underground hibernacula and afterwards leaves the site. We hypothesise that in late summer individual bats spend a relatively short time on swarming and go on feeding for the rest of the night. This hypothesis is supported by recent evidence that bats become hyperphagic at the end of summer to accumulate fat for hibernation (McGuire et al. 2009a).

The high proportion of departing bats captured within two hours after sunset in late summer suggests that swarming sites may coincide with day-roosts for some bats. Such individuals probably settle down after feeding and leave the next evening, which corresponds to activity pattern observed by Degn et al. (1995). In late summer, swarming sites may function as special day-roosts that provide a suitable environment for tor-

por, allowing bats to convert ingested energy into fat (Krzanowski 1961; Speakman and Rowland 1999).

In September, no correlation between the BCI and time of capture was found. Fenton (1969) found that only 20% of swarming bats captured in September had distended stomachs. At this time of the year, most adults have already accumulated fat stores (Kunz et al. 1998; Encarnação et al. 2004) and arrive at underground sites to hibernate or mate (Fenton 1969; Thomas et al. 1979; Šuba, unpublished data) and insect availability is lower than in the previous month (Speakman and Rowland 1999). However, the BCIs of some *M. daubentonii* adults suggested that they had not yet completed fat accumulation or had expended stored energy reserves for mating.

In early autumn, subadult individuals of *M. daubentonii* and *M. dasycneme* also had slightly increased BCIs, compared to late summer, but this was not the case for *M. brandtii.* In September, the BCI of *M. daubentonii* subadult individuals was positively correlated to the time of capture, suggesting that subadult *M. daubentonii* may continue to feed intensively in early autumn. McGuire et al. (2009a) found that subadult *Myotis lucifugus* gradually lose mass from late summer until early autumn, probably as a consequence of their lower foraging efficiency compared to adults. Further studies on the feeding strategies of bats are needed to highlight the causes of intra- and interspecific variation in their feeding behaviour in autumn.

Our study provided new data about the feeding strategy of swarming bats. As both body mass and BCIs are not fully

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reliable indicators for feeding performances since bats may quickly lose ingested mass as faeces, further studies are needed, using more accurate techniques (e.g. plasma metabolite analysis; McGuire et al. 2009b).

ACKNOWLEDGMENTS

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Paper IV

J. Šuba, Pētersons G. Rydell J. 2012. Fly-and-forage strategy in the bat *Pipistrellus nathusii* **during autumn migration.** *Acta Chiropterologica,* **14(2): 379–385.**

Fly-and-forage strategy in the bat *Pipistrellus nathusii* during autumn migration

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Populations of *Pipistrellus nathusii* (Nathusius's bat), an insectivorous aerial-hawking species that breeds in north-eastern Europe, perform long-distance migrations between breeding sites and hibernation areas in central and southern Europe. The feeding strategy of migrating *P. nathusii* was investigated in Latvia on the east coast of the Baltic Sea, exploring evidence for and against two non-mutually exclusive predictions that i) the bats feed shortly after dusk at highest aerial insect activity and continue to migrate thereafter or ii) apply a 'fly-and-forage' strategy and frequently interrupt their migration flight to feed. Echolocation calls and feeding buzzes of *P. nathusii* were recorded throughout the night from August until September on a known migration flyway over coastal dunes and at potential foraging sites in adjacent woodlands, over meadows and wetlands. The results indicate that *P. nathusii* applies a fly-and-forage strategy along the Baltic coast. However, a threshold in aerial insect availability may exist, below which no foraging occurs and migration continues.

Key words: Baltic Sea, feeding strategy, Latvia, Pape Ornithological Research Station

Introduction

In autumn, some bat species from Fennoscandia and north-eastern Europe, such as *Pipistrellus nathusii* (Nathusius's bat)*,* migrate south along the Baltic coast towards central and southern Europe to overwinter (Popa-Lisseanu and Voigt, 2009). Recoveries of wing-banded individuals (Strelkov, 1969; Pētersons, 2004; Hutterer *et al.*, 2005) and stable hydrogen isotope composition analysis (Voigt *et al.*, 2012*a*) suggest that this migration can be as long as 2000 km between summer breeding and winter hibernation areas (maximum distance documented from recapture data is 1905 km — see Pētersons, 2004). Meeting energy demands of migration is presumably of primary importance for survival and reproductive success of the bats. Bats are able to forage and feed during flight, thus replenishing energy loss due to flight by rapid mobilisation and oxidation of ingested nutrients (Welch *et al.*, 2008; Voigt *et al.*, 2010; Suarez *et al.*, 2011). Direct and indirect observations suggest that migrating bats may feed while migrating (Ahlén *et al.*, 2009; Valdez and Cryan, 2009). Prior to hibernation and migration bats feed intensively to store fat (Kunz *et al.*, 1998; McGuire *et al.*, 2009; Šuba *et al.*, 2011). Stored fat is also utilised for energy during migration flights, complementing or substituting the exogenous fuel source obtained directly from consumed prey (Voigt *et al.*, 2012*b*).

By acoustically monitoring migrating *P. nathusii* in the field at the Baltic coast of Latvia, we investigated how bats allocate their time between migration flights and foraging efforts. At high latitudes, nocturnal insect abundances typically peak shortly after dusk and then decline until a second peak occurs just before sunrise (Taylor, 1963). This bimodal pattern is usually reflected in the foraging activity of aerial-hawking bats (Racey and Swift, 1985; Rydell *et al.*, 1996). We may therefore expect that bats on migration would allocate most feeding efforts to the period after dusk and before dawn, and show a reduced feeding rate in between. However, if insect abundance remains high throughout the night, they may apply a 'fly-and-forage strategy' en-route (Strandberg and Alerstam, 2007), perhaps interrupting the migration flight to feed whenever rich food patches are encountered.

MATERIALS AND METHODS

The study was undertaken at Pape Ornithological Research Station at the Baltic coast of Latvia (56°09'57"N, 21°01'02"E), where autumn migration patterns of bats have been documented over the preceding two decades (Pētersons, 2004). The study area consists of low sand dunes covered by unmanaged *Pinus sylvestris* (scots pine) woodlands and grasslands crossed by dirt roads, occasional buildings and Lake Pape with adjacent marshlands. The lake is connected to the sea at its southern part through a canal with natural vegetation such as *Salix* spp. (willows) and *Phragmites australis* (syn. *P. communis*; reeds).

Observations were made between the 5th of August and the 13th of September 2010 within a 4.5 km² area (Fig. 1). The selected study sites represented the principal habitats of the study area: 1) 'the dune site', located on sand dunes ca. 100 m from the coastline, 2) 'the canal site', located at the bank of the canal, 3) 'the marsh site', located in marshland at the western shore of the lake, 4) and 5) 'meadow sites 1 and 2', located on open grasslands, 6) and 7) 'forest sites 1 and 2', located in *P. sylvestris* woodlands. The sites were separated by at least 200 m. At the dune site, surveys of autumn bat migration have been conducted annually during 1993–2012. Previously observed flights of *P. nathusii* at this site are generally fast, straight and nearly always directed towards the south over the dunes along the coast, hence the dune site was identified as a candidate for the bats' migration flyway. *P. nathusii* is by far the most abundant

bat species at this site in August and September (89% of all captured individuals — see Hutterer *et al.*, 2005).

Acoustic recordings of echolocation calls were made at each of the seven study sites, using four digital sound recorders VN-550PC (Olympus Imaging America Inc., Pennsylvania, USA) connected to heterodyne ultrasound detectors D-200 (Pettersson Elektronik AB, Uppsala, Sweden). The detectors were assumed to have equal sensitivity and set to 40 kHz, which in most cases is appropriate to recognise sonar calls of *P. nathusii* (clear and 'wet' sounds) and easily distinguish them from those of other species (obscure or 'dry' sounds at this frequency). Connected devices were kept in a plastic 13 × 13 × 6 cm box to protect the equipment from moisture and a 0.5 cm diameter hole was made for the microphone of the detector (Ahlén *et al.*, 2007). The microphone was directed with an angel (30–45º) upwards and exposed to the north (at the dune site, meadow sites and the marsh site), randomly (at forest sites) or towards the water (at the canal site). The four boxes were either placed on the ground (Meadow Sites) or on a pole 2 m above the water level (Marsh Site) or in trees 2, 2, 5 and 7 m above the ground (the Dune, Canal and two Forest Sites, respectively). At the Dune Site recordings were made every night, but the other sites were surveyed on alternative nights — Forest Site 1, Meadow Site 1 and Canal Site were surveyed on the same night followed by Forest Site 2, Meadow Site 2 and Marsh Site on the following night. Normally recordings were conducted from sunset until sunrise. Altogether 88 recordings were used in the analysis. Recordings that lasted for less than six hours due to
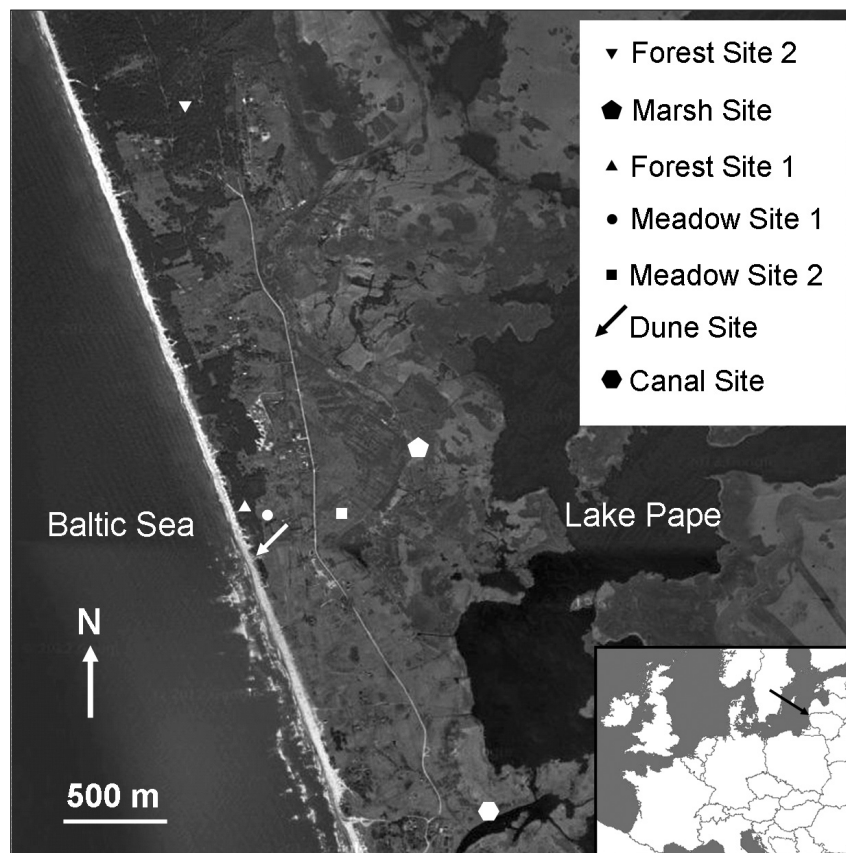

FIG. 1. The study area and location of study sites (the background satellite image obtained from Cnes/Spot Image, DigitalGlobe, GeoEye 2012)

discharge of the batteries or were heavily disturbed by noise such as katydid/bush-crickets chirring, strong wind or heavy rain were omitted ($n = 68$).

The audio recordings were analysed with the sound editing software Sound Forge 9.0 (Sony Creative Software Inc., Middleton, UK). They were divided into five-minute sections (further referred as 'sections'), for which the following were registered: a) duration of continuous echolocation call sequences (further referred as 'sonar sequences'), b) time of occurrence (in minutes after sunset) and c) presence or absence of so called 'feeding buzzes', which unambiguously indicate attempted feeding (Surlykke *et al.*, 2003). Sonar sequences were easily distinguishable by silent intervals between them (> 4 s). No attempts were made to distinguish passes of individual bats, since there were no visual information and two or more bats occasionally passed by simultaneously. Occasional sonar sequences and associated feeding buzzes of species other than *P. nathusii* were not considered in the analysis.

Statistical analyses were carried out using the program R (version 2.13.0; The R Foundation for Statistical Computing, 2011). The cumulative duration of all sonar sequences per hour and the number of sections containing feeding buzzes per hour were used as indices of activity and feeding intensity, respectively. Feeding rate was expressed as number of sections containing feeding buzzes divided by the number of all sections that contained echolocation calls, which also equals to probability that passing bats would interrupt their flight and feed. For the null hypothesis, a constant feeding rate each hour throughout the night was assumed and fit to a uniform distribution was tested using Pearson's chi-squared test. Kruskal-Wallis (K-W) rank sum tests were used to compare different parameter values among the study sites. Pair-wise comparisons were made by Wilcoxon rank sum test with continuity correction. Significance of relationships was tested by Pearson's product moment correlation, for which data normality was tested by Shapiro-Wilk normality test.

Results

In total, 88 recordings (740h) were analysed. Every evening the first sonar calls of *P. nathusii* were recorded 40–100 minutes after sunset (Table 1), with significant differences among the sites (Kruskal-Wallis test, $\chi^2 = 36.5$, *d.f.* = 6, $P < 0.001$). Generally at the two forest sites, the first sonar calls were recorded earlier than at the open sites. During the study period from the 5th of August until the

13th of September, night length (sunset to sunrise) increased from 8.1 to 10.9h, but there was no significant increase in the length of the nocturnal activity period of *P. nathusii* (Pearson's product-moment correlation, $r = 0.379$, $t = 1.36$, *d.f.* = 11, $P = 0.20$). At the migration flyway (the dune site) and at one of the feeding sites (the canal site), sonar calls were recorded for 7.3 h on average (SD = 0.8, $n = 13$) throughout the night, and there were no significant differences between these two sites (Wilcoxon test, $W = 11.5$, $P = 0.24$). For other study sites, sample sizes were too low to be considered representative and due to low activity of bats the sonar calls were usually not recorded in late hours of night. At the forest site 2, the meadow site 2 and the marsh site, the bats were recorded for 6.9 (SD = 1.0, $n = 4$), 6.5 (SD = 0.2, $n = 2$) and 6.2 (SD = 1.2, $n = 4$) h on average, respectively.

The activity of *P. nathusii* was significantly higher at the dune site and the canal site than at the other sites (K-W test, $\chi^2 = 163.3$, *d.f.* = 6, $P < 0.001$). The frequency of feeding attempts also differed significantly among the sites (K-W test, $\chi^2 = 65.6$, *d.f.* = 6, $P < 0.001$), being highest at the dune site and the canal site (Table 1).

At the dune site, the recorded activity varied considerably from night to night, but within each night, the activity typically increased before midnight and then decreased again until sunrise (Fig. 2a). Of all the five-minute sections that contained echolocation calls ($n = 860$) from the site, 51.4% included feeding buzzes (the mean probability that feeding attempts were recorded from a passing bat was 0.514). The fraction of sections containing feeding buzzes was uniformly distributed over the course of the night ($\chi^2 = 4.2$, *d.f.* = 6, $P = 0.65$). Hence, bats migrating over the dunes made feeding attempts with the same frequency throughout the night (Fig. 2b).

At forest sites 1 and 2, the maximum activity was registered during the first hour of the night and for forest site 1 changes in the feeding rate reflected this

TABLE 1. The time of the earliest recorded sonar calls of *P. nathusii* in the evening, the duration of sonar sequences and the number of five-minute sections containing feeding buzzes per hour at the study sites ($\bar{x} \pm$ SE, sample sizes in parentheses)

| Site	Time of the earliest sonar calls (min after sunset)	Duration of sonar sequences per hour (s)	Number of 5-min sections containing feeding buzzes per hour
Dune	54 ± 9 (19)	307.8 ± 52.4 (119)	3.7 ± 0.4 (119)
Forest 1	43 ± 14 (13)	49.4 ± 10.2 (94)	1.2 ± 0.2 (94)
Forest 2	49 ± 10 (13)	5.5 ± 1.0 (99)	0.3 ± 0.1 (99)
Meadow 1	82 ± 10 (11)	37.6 ± 6.8 (84)	1.2 ± 0.2 (84)
Meadow 2	86 ± 20 (12)	36.0 ± 7.0 (78)	1.0 ± 0.2 (78)
Canal	59 ± 6 (8)	128.3 ± 24.4 (63)	2.6 ± 0.3 (63)
Marsh 1	06 ± 18 (12)	36.5 ± 8.0 (90)	1.0 ± 0.2 (90)
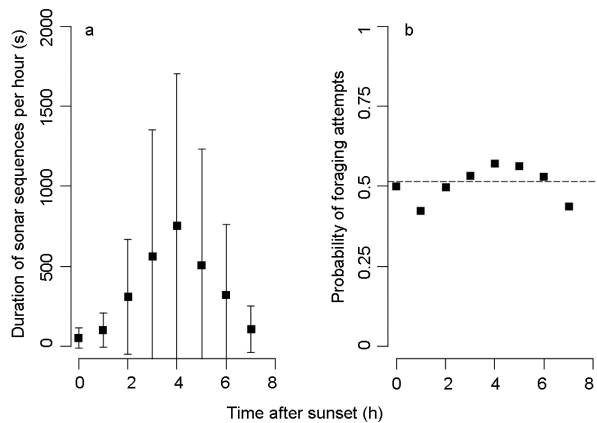
FIG. 2. Mean durations (± SD) of recorded sonar sequences of *P. nathusii* per hour (a) and the probability of feeding attempts (b) at the dune site — the migration flyway (the dashed line indicates the mean probability). 0 on the abscissa accounts for the sunset hour

pattern (Fig. 3a–b). At the forest site 1, 27.9% of the sections ($n = 409$) contained feeding buzzes. The highest proportion of sections containing feeding buzzes was recorded during the first hour of night and later on the probability for a passing bat to feed was significantly lower than expected according to a uniform distribution ($\chi^2 = 52.3$, $d.f. = 6$, $P < 0.001$). However, no significant deviation from a uniform distribution was found for the forest site 2 ($\chi^2 = 7.5$, $d.f. = 6$, $P = 0.28$), where 18.7% of all sections ($n = 134$) contained feeding buzzes.

At meadow sites 1 and 2, maximum activity was usually recorded around midnight (Fig. 3c). For the meadow site 1, 28.2% of all sections ($n = 362$) contained feeding buzzes. No significant deviation from a uniform distribution was found ($\chi^2 = 6.0$, $d.f. = 6$, $P = 0.42$ — Fig. 3d). For the meadow site 2, 28.7% of all sections ($n = 279$) contained feeding buzzes. Deviation from a uniform distribution was almost significant ($\chi^2 = 12.4$, $d.f. = 6$, $P = 0.055$). In this case, the fraction of sections containing feeding buzzes was highest during the second hour after sunset while the lowest feeding intensity occurred during the sixth hour after sunset.

At the canal site and the marsh site, activity peaks were observed at mid- and late night (Fig. 3e). For the canal site, 44.6% of all sections ($n = 368$) contained feeding buzzes compared to 34.9% ($n = 261$) for the marsh site. At both sites, the number of sections containing feeding buzzes were uniformly distributed throughout the night (the canal site: $\chi^2 = 10.1$, $d.f. = 6$, $P = 0.12$; the marsh site: $\chi^2 = 6.6$, $d.f. = 6$, $P = 0.36$).

DISCUSSION

The results agree with the hypothesis that *P. nathusii* uses a fly-and-forage migration strategy when migrating south along the Baltic coastline. On the migration flyway at the dune site, the mean probability of a passing bat to interrupt its flight and feed on available insects was 0.514 and did not change significantly over the course of the night. This also suggests that the flying insect abundance was always sufficient to permit energetically profitable foraging by the migrating bats. This situation may be different from that prevailing during spring migration, when the nights often are colder and insects are generally less active (Taylor, 1963; Avery, 1985; Rydell, 1989).

Generally, insectivorous bats are able to fuel their flight by ingested nutrients from consumed insect prey (Voigt *et al*., 2010), but fat reserves may be used when insect prey is not available (Voigt *et al*., 2012*b*). Energy accumulation is accelerated by reduced energy expenditure through the use of torpor (Carpenter and Hixon, 1988; Speakman and Rowland, 1999; McGuire *et al*., 2009), which may be an advantage during migration — 'torpor assisted migration' (McGuire *et al*., 2011). In contrast, most migratory birds spend a greater part of the journey on fuelling before non-stop flights or refuelling during stopovers (Schaub *et al*., 2001; Lindström, 2003). Similarly bats have been suspected to consume body fat stores during migration (Thomas and Suthers, 1970; O'Shea, 1976) and refuel during stopovers (Fleming and Eby, 2003; Hedenström, 2009; McGuire and Guglielmo, 2009). However, the capability to use body fat stores at a high rate is limited in mammals, and, therefore, carbohydrates and proteins are consumed instead (Roberts *et al*., 1996; McGuire and Guglielmo, 2009; Guglielmo, 2010). Migrating *Lasionycteris noctivagans* (silver-haired bats) have been observed to use short stopovers, lasting for one or two days, before crossing lake Ontario in Canada on their way south (McGuire *et al*., 2011). A similar behaviour of migrating bats of several species has been observed at peninsulas and islands in southern Scandinavia (Ahlén *et al*., 2009). The fly-and-forage strategy observed in *P. nathusii* and the stopover strategy observed in some other species do not necessarily indicate that the species have different strategies. Due to mammalian physiology and the ability to use daily torpor for energy accumulation, migrating bats probably apply a stopover strategy only in extreme cases, such as in front of major barriers, but otherwise feed on the
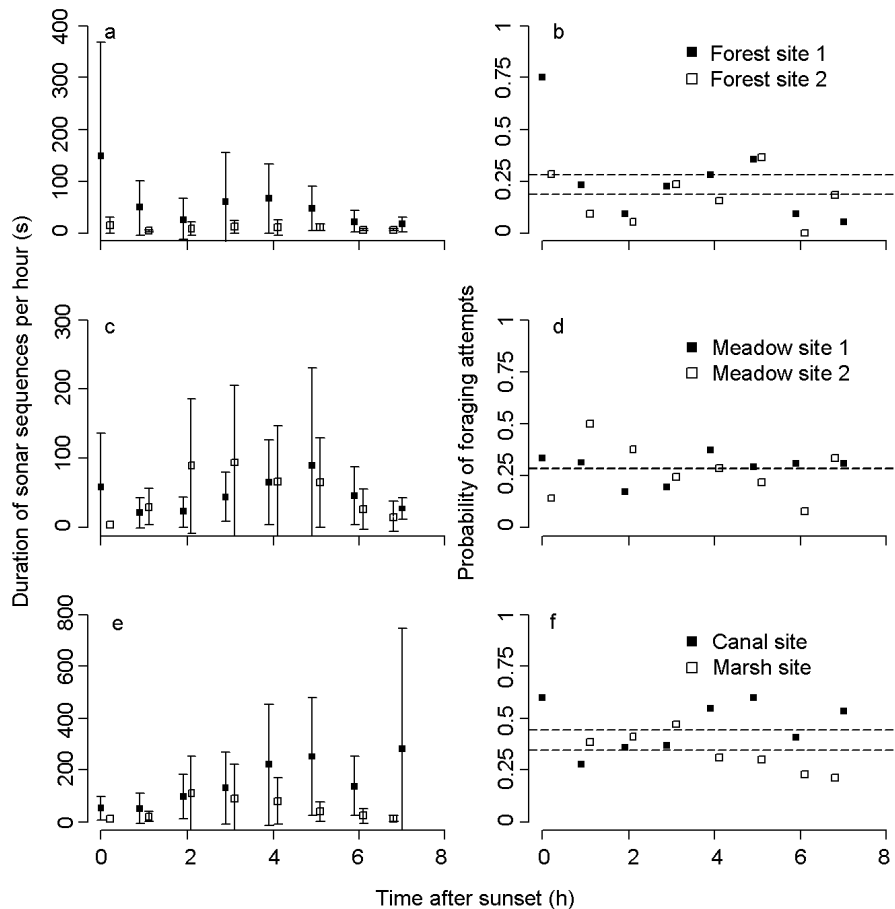
FIG. 3. Mean durations (± SD) of recorded sonar sequences of *P. nathusii* per hour (a, c, e) and the probability of feeding attempts (b, d, f) at studied forest sites (a, b), meadow sites (c, d) and wetland sites (e, f). The dashed line indicates the mean probability. 0 on the abscissa account for the sunset hour

wing, at least as long as the weather and insect availability permit.

The knowledge of habitat use during migration is of particular importance in environmental impact assessments of wind turbine power plants (e.g., Kunz *et al*., 2007), motorways (Gaisler *et al*., 2009) and other major exploitation projects (Rydell *et al*. 2010). In our study, feeding buzzes of *P. nathusii* were more frequently recorded in wetland habitats than in the meadow and forest habitats. This probably relates to the frequent emergence of non-biting midges (Diptera: Chironomidae) and other small insects associated with shallow water. Wetlands are frequently preferred as feeding habitats by *P. nathusii* (Ciechanowski *et al*., 2009; Flaquer *et al*., 2009) and other *Pipistrellus* species (Racey and Swift, 1985) and this also applies to our case.

Each night the first sonar calls of *P. nathusii* were typically recorded in *P. sylvestris* woodland habitats some 40–50 minutes after sunset; these woodlands were probably used as roosting habitats. The presence of trees facilitates the exploitation of flies and other insects that swarm at dusk, because they provide the bats with protection from raptorial birds that may still be active at that time. Open tree-less areas are typically avoided by aerial-hawking bats early in the evening (Rydell *et al*., 1996). At the two forest sites, the feeding rate was lower than at the other study sites and the maximum feeding rate was recorded during the first hour after sunset, which most likely corresponded to the peak activity in small flies (Rydell *et al*., 1996). During the later hours, the feeding rate decreased and remained relatively low, suggesting a decline in aerial insect availability (Lundy *et al*., 2012). Therefore the importance of pine forests as feeding habitats for *P. nathusii* during the migration flights may be relatively low, compared to wetland habitats, for example, but woodland habitats still need to be considered as potential roosting habitats.

Woodland edge habitats are normally used more intensively by bats than core-habitats (Hein *et al.*, 2009), which was supported by our observations at forest sites 1 and 2. Edges of continuous woodlands may be used as migration corridors in the same way as rivers (Furmankiewicz and Kucharska, 2009) and other linear landscape elements (Verboom and Huitema, 1997). This problem needs to be addressed in future research, so that essential migration corridors for bats can be identified and protected.

The results of this study can be referred mainly to low-altitude migration flight, because ultrasound detectors used in this study are able to record the sonar calls over relatively short distances (20–50 m in *P. nathusii*). However, migrating bats may presumably fly higher as well.

We conclude that during autumn migration individual *P. nathusii* apply a fly-and-forage strategy throughout the night as long as the aerial insect availability is high enough to provide profitable feeding. A stopover strategy may be used in other cases such as, for example, when autumn migration coincides with mating (Lundberg, 1989). In future research, nocturnal time budgets of individual bats during migration should be investigated using satellite tracking (e.g., Trierweiler *et al.*, 2007; Holland and Wikelski, 2009; Strandberg *et al.*, 2009) or small radio transmitters tracked from the ground or from aircraft (Parsons and Jones, 2003; Holland *et al.*, 2006).

Acknowledgements

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Paper V

J. Šuba. 2014. Migrating Nathusius's pipistrelles *Pipistrellus nathusii* (Chiroptera: Vespertilionidae) optimise flight speed and maintain acoustic contact with the ground. *Environmental and Experimental Biology,* **12: 7–14.**

Migrating Nathusius's pipistrelles *Pipistrellus nathusii* (Chiroptera: Vespertilionidae) optimise flight speed and maintain acoustic contact with the ground

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Abstract

Populations of Nathusius's bats *Pipistrellus nathusii* breeding in north-eastern Europe migrate seasonally to and from hibernation sites in central Europe. Characteristic flight speeds of *P. nathusii* were calculated based on aerodynamic theory (C.J. Pennycuick and U.M. Norberg) and morphometric data of captured individuals. Actual flight speeds and altitudes of migrating individuals were measured in the field at the Baltic coast of Latvia. The bats flew on average 11.5 m above the ground. The average flight speed ranged from 11.2 up to 13.1 m s^{-1} (40.3 and 47.2 km h^{-1}) and exceeded the predicted minimum power and maximum range speeds, indicating that *P. nathusii* minimise the cost of transport or perhaps the duration of the autumn migration flight. The length of the inter-pulse intervals was correlated with the flight height, indicating that *P. nathusii* adjust the sonar according to the flight altitude to maintain acoustic contact with the ground.

Key words: aerodynamics; Chiroptera; migration; *Pipistrellus nathusii;* sonar.
Abbreviations: ORS, Ornithological Research Station.

Introduction

Seasonal migration is an essential part of the life history of many bats (Griffin 1970; Fleming, Eby 2003; Popa-Lisseanu, Voigt 2009). Bat migration has been studied to a lesser extent than avian migration, but research on avian migration has provided a foundation from which testable predictions about migration strategies of bats have been formulated (e.g. Hedenström 2009; McGuire, Guglielmo 2009). For example, to make optimal use of time and energy during migration flights is believed to be very important for birds (Hedenström, Alerstam 1995) and presumably for bats as well.

Continuous flapping flight, as applied by bats, requires an energy consumption of 10 to 20 times, sometimes even 30 times, the basal metabolic rate (Thomas, Suthers 1972; Rayner 1999). Aerodynamic models (Pennycuick 1975; Norberg 1990) as well as empirical studies (e.g. Thomas 1975; Rayner 1994, Ward et al. 2001; Tobalske et al. 2003) suggest a U-shaped relationship, referred to as 'the power curve', between the power required to fly (*P*) and the flight speed (*V*; Fig. 1). This relationship has become an icon in studies of animal flight (Norberg, Rayner 1987; Hedenström 2002) and many studies on bats have been made to test various predictions arising from it (e.g. Jones, Rayner 1989; Norberg et al. 1993; Sahley et al. 1993; Jones 1995; Grodzinski et al. 2009).

The power curve leads to the prediction of two characteristic flight speeds that a bat may apply to minimize the energy consumption in flight (e.g. Hedenström 2009). First, the minimum power speed (V_{mp}) would be applicable to situations when the total energy expenditure is to be minimised in order to maximise the duration of the flight (e.g. to maximise foraging time). Second, applying the maximum range speed (V_{mr}) would minimise the energy consumption per distance travelled (i.e. cost of transport per unit distance). For example, skylarks *Alauda arvensis* fly close to the minimum power speed during their hovering song-flight, while they migrate nearly at the maximum range speed (Hedenström, Alerstam 1996). Insectivorous bats may also adjust the flight speed according to the ecological context (Grodzinski et al. 2009). For instance, they fly slower (at V_{mp}) while foraging and faster (near or above V_{mr}) when commuting between the roost and foraging sites (Jones, Rayner 1989; Britton et al. 1997; Grodzinski et al. 2009).

Seasonal migration seems to involve additional ingredients, necessary to maximise the overall speed of migration (e.g. Hedenström 2009). The migration speed (V_{migr}) is defined as the total migration distance divided by the total time of migration (Alerstam 1991; Hedenström, Alerstam 1995; Hedenström, Alerstam 1998; Hedenström 2008; Hedenström 2009). In migratory bats, fast migration would presumably be important for early arrival at
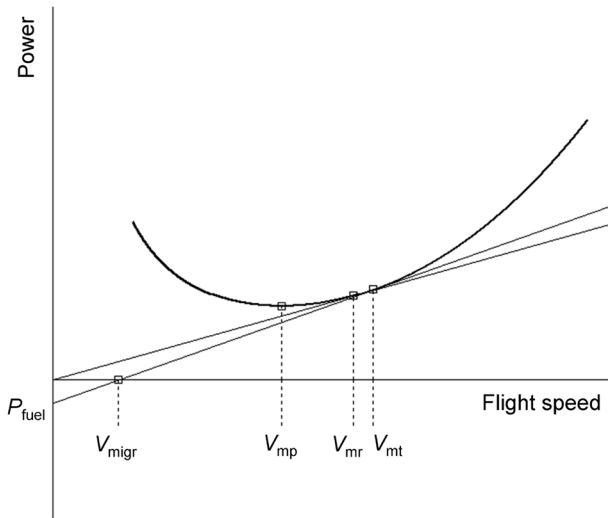
Fig. 1. Relationship between power required for horizontal flapping flight P and flight speed through the air V ($P = \alpha V^{-1} + \beta V^3$, where α and β are constants that include physical and morphological properties of the animal and the air and acceleration due to gravity). V_{migr}, V_{mp}, V_{mr} and V_{mt} refer to overall migration speed, minimum power speed, maximum range speed and minimum time speed according to the net fuelling rate P_{fuel}.

hibernation sites from breeding areas and *vice versa*. The total time spent on migration consists of travelling time (T_{flight}), used to cover the distance between consecutive fuelling or stopover sites, and fuelling time (T_{fuel}), when the energy deposits are restored. The overall migration speed can be calculated as

$$V_{migr} = VT_{flight} / (T_{flight} + T_{fuel}), \qquad (1)$$

where VT_{flight} is equal to distance flown and $T_{flight} + T_{fuel}$ is equal to total time spent on migration (Hedenström, Alerstam 1995). It can be noted that the ratio T_{flight} / T_{fuel} is equal to P_{fuel} / P, where P_{fuel} is net energy accumulation rate (Hedenström, Alerstam 1995; Hedenström 2009). Hence the migration speed can be also calculated as

$$V_{migr} = VP_{fuel} / (P + P_{fuel}). \qquad (2)$$

Fast migration flight at optimal speed would therefore maximise the overall migration speed. The optimal flight speed, referred to as the minimum time speed (V_{mt}), depends on the fuelling rate and may exceed the maximum range speed to some extent (Hedenström, Alerstam 1995; Hedenström, Alerstam 1996; Hedenström 2008; Hedenström 2009).

The aim of this study was to measure the actual flight speed of migrating bats and test the hypothesis that bats optimise the speed of migration flight ($V \geq V_{mr}$). To the author's knowledge, this is the first observational study on the flight speed of migrating bats. Additionally, it was hypothesised that in a low migration flight, bats maintain acoustical contact with the ground. When flying low ($\leq$ 20 m), the range may fall within that of the bats' sonar perception (Lawrence, Simmons 1982). For example,

migrating *P. nathusii* and other insectivorous bats have been observed flying < 10 m above the surface of the Baltic Sea (Ahlén et al. 2009). To test this hypothesis, the flight altitude of migrating individuals was measured and compared with sonar sequences recorded simultaneously from the same individuals.

Materials and methods

Flight speed measurements and sonar recordings
The field work was conducted at Pape Ornithological Research Station (ORS) in SW Latvia (56°09'57"N 21°01'02"E) as part of a long-term research project on migrating bats (Pētersons 1990; Pētersons 2004). From mid-August to late September, many bats are typically observed flying more or less straight along the sea coast towards the south. Individual Nathusius's bats *Pipistrellus nathusii* (Keyserling & Blasius, 1839) caught and banded at Pape ORS in a Helgoland-type funnel trap have been recovered on the way to or within their hibernation area in Central, Western and Southern Europe (Pētersons 2004; Hutterer et al. 2005). Hence one can safely assume that the bats observed in Pape ORS flying to the south along the sea coast were indeed migrating.

Actual flight speeds of *P. nathusii* were measured on 13 to 18 August and 5 September 2011. Flight speed and altitude were measured within a 150 m wide and largely open area of sand dunes and grasses extending between the coastline and pine *Pinus sylvestris* woodland. For distance and altitude references, two poles (h = 10 and 7 m, respectively) were placed 20 meters apart along a frequently used migration flyway. The longest pole was was placed at the northernmost end of the flight path and fitted with light reflectors 1 m apart, to facilitate estimates of the flight height of the bats.

An ultrasound detector D-240x (Pettersson Elektronik AB, Uppsala, Sweden) was tuned to 40 kHz to detect approaching bats. This frequency roughly corresponds to the best listening frequency of *P. nathusii* sonar calls. Other species, e.g. northern bats *Eptesicus nilssonii*, noctules *Nyctalus noctula* and pygmy pipistrelles *P. pygmaeus* were distinguished from *P. nathusii* by differences in body size or relatively quiet and non-smacking sounds that passed through the heterodyne filtering.

The durations of the 20 m flights between the two poles were measured by a stopwatch (only passes of *P. nathusii* were measured, the passes of other species were ignored). All the measurements were made in a fixed location of the observer between the two reference poles at ca. 10 m distance. A similar approach, using natural reference objects, has been used to measure flight speed in free-ranging orange nectar bats *Lonchophylla robusta* (Tschapka 1998 cited from Winter 1999). All the bats were clearly seen as they passed by both reference poles. At several occasions (n = 7), it was possible to see the bats in the moonlight, but

in most cases ($n = 90$), a 100 W lamp was used to facilitate observation of the bats. The use of an ultrasound detector allowed noticing the bats ca. 1 s before they passed the first reference pole. It was impossible to determine the precise measurement error, but the mean time required to stop the watch immediately after its activation was 0.25 s (SD = 0.11, $n = 20$), which probably was at a slightly higher order of magnitude as the measurement error. Only measurements of straight and uninterrupted flights were registered and analysed ($n = 97$). Data on ambient temperature, wind speed and wind direction were collected between the measurements.

Sonar sequences of passing bats were recorded as they flew at various altitudes ($n = 20$). Using a time-expansion (10×) mode of the detector, 1.7 second fragments of the sonar sequences were recorded, providing 17 s long sequences suitable for analysis. These sequences were recorded by a digital recorder VN-550PC (Olympus Imaging America Inc., Pennsylvania, USA). Durations of pulses and inter-pulse intervals were measured by the sound editing software Sound Forge 9.0 (Sony Creative Software Inc., Middleton, UK). All the statistical analyses were performed by R version 2.13.0 (R Foundation for Statistical Computing, Vienna, Austria).

Theoretical considerations and calculation of characteristic flight speeds
Morphometric data used for calculating the power curves were obtained from individual bats captured occasionally in a Helgoland-type funnel trap at Pape ORS in September 2011 ($n = 8$). A permit for bat captures was granted by the Nature Conservation Agency. Measurements included body mass (to 0.1 g), wing span (to 0.1 cm) and wing area (to 0.25 cm²). The wing span and area were obtained from outlines drawn along the bat's body and spread wings, gently pressed and held on a sheet of millimetre paper (Pennycuick 2008). The mean body mass, wing span and wing area of captured individuals were 7.5 g (SD = 0.6), 23.5 cm (SD = 0.6) and 84.6 cm² (SD = 5.4), respectively (Table 1). All the bats were

Table 1. Morphometric data of *P. nathusii* captured occasionally at Pape Ornithological Research Station during the autumn migration season in year 2011

Age and sex	Body mass (g)	Wing span (cm)	Wing area (cm²)
Subadult male	6.4	23.3	80
Adult male	7.2	23	81
Adult female	7.4	22.8	79
Subadult female	7.4	24.2	88.5
Adult male	7.5	24	89
Adult male	7.6	23.8	84.5
Subadult male	7.7	22.6	81
Adult female	8.4	24	94

released at the place of capture immediately after the data collection was made.

The relationships between the flight power and the flight speed including the minimum power and the maximum range speeds were predicted from aerodynamic theory of flapping flight (Norberg 1990; Pennycuick 1975; 2008; Hedenström 2002) using an approach similar to Grodzinski et al. (2009). The flight speed vector used for calculating the flight power and the lift to drag ratios ranged from 2 up to 26 m s⁻¹ by intervals of 0.1 m s⁻¹. The first model, used for estimating the flight power and the characteristic flight speeds, was introduced by Norberg and Rayner (1987) and modified by Norberg (1990). The second model, which appears to be more appealing (based on a recent study on bat flight speed by Grodzinski et al. 2009), was presented by Pennycuick (1975; 2008).

The total mechanical power required to fly (P_{mech}) consists of four main components (e.g. Rayner 1999): induced power (P_{ind}), parasite power (P_{par}), profile power (P_{pro}) and inertial power (P_{iner})

$$P_{mech} = P_{ind} + P_{par} + P_{pro} + P_{iner}. \tag{3}$$

No attempts were made to evaluate the inertial power, which is associated with wing inertia during strokes. It is probably small and insignificant at cruising speeds (Hedrick et al. 2004; Hedenström 2009). The induced power, which generates lift, was calculated as

$$P_{ind} = 2k(mg)^2 / (V\rho\pi b^2), \tag{4}$$

where k is the induced power factor (set to 1.2, a value typical for flapping flight Pennycuick 1989; Hedenström 2002; Morris, Askew 2010), m is the body mass (in kilograms), g is the acceleration due to gravity (9.81 m s⁻²), ρ is the air density (1.2 kg m⁻³) and b is the wing span (in metres). The parasite power that overcomes the drag of the body was calculated as

$$P_{par} = 0.5\rho C_{Dpar} S_f V^3, \tag{5}$$

where C_{Dpar} is the body drag coefficient (taken to be 0.1 according to Pennycuick 2008; Morris, Askew 2010; but see also Hedenström, Liechti 2001) and S_f is the body frontal area, which was estimated from the body mass as

$$S_f = 0.00813 m^{0.666} \tag{6}$$

(Pennycuick 2008).

According to models by Norberg (1990) and Pennycuick (2008), two different equations were applied to evaluate the profile power, which overcomes the drag of the wings

$$P_{pro} \text{ (Norberg)} = \rho C_{Dpro} S V^3 / 2, \tag{7.1}$$
$$P_{pro} \text{ (Pennycuick)} = 8.4 P_{am} S / b^2, \tag{7.2}$$

where C_{Dpro} is the profile drag coefficient (set to 0.02 according to Rayner 1979), S is the wing area (in square metres), and P_{am} is the absolute minimum power (min[$P_{ind} + P_{par}$]). The total metabolic power required to fly P was calculated as

$$P = R(P_{mech} / \eta + P_{BMR}), \tag{8}$$

where R is a respiration factor that represents the additional energy required by the heart and ventilation muscles in aerobic flight (set to 1.1 according to Pennycuick 2008), η is

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the energy conversion efficiency (assumed to vary between 0.17 and 0.23 according to Rayner 1999; Pennycuick 2008) and P_{BMR} is the basal metabolic rate calculated from the body mass (following Norberg et al. 1993) and based on McNab's (1988) regression equation for bats

$$P_{BMR} = 2.63m^{0.72}. \qquad (9)$$

The minimum power speed V_{mp} was found at the point of minimum flight power min(P). The maximum range speed Vmr was found at the point of maximum effective lift to drag ratio (N), calculated as

$$N = mgV / (\eta P). \qquad (10)$$

The migration speed and the net rate of fuel deposition can be estimated by constructing a tangent to the power curve at the flight speed value of V_{mt} (Hedenström, Alerstam 1995). The slope of the tangent to the power curve (s) is equal to dP / dV and hence was calculated by the following equations

$$s \text{ (Norberg)} = R(3P_{par} + 3P_{pro} \text{ [Norberg]} - P_{ind}) / (\eta V), \qquad (11.1)$$

$$s \text{ (Pennycuick)} = R(3P_{par} - P_{ind}) / (\eta V). \qquad (11.2)$$

Assuming that the observed speed of migration flight (if $V > V_{mr}$) corresponds to V_{mt}, the overall migration speed V_{migr} was calculated as

$$V_{migr} = (s_i V_i - P_i) / s_i, \qquad (12)$$

where V_i corresponds to the i-th value of the flight speed vector equal to the observed flight speed, and s_i and P_i are the corresponding i-th values of the slope of the tangent to the power curve and the flight power.

Calculations were performed by R. For Pennycuick's model, the results thus obtained were compared with those using software Flight 1.23 (developed by C.J. Pennycuick and available at http://www.bristol.ac.uk/biology/people/colin-j-pennycuick/index.html). No significant differences between the two methods were found, and therefore only calculations made by R are presented.

Results

Speed of migration flight

The mean duration of a 20 m flight was 1.5 s (SD = 0.4, $n = 97$), which corresponds to a flight speed of 13.1 m s^{-1} or 47.2 km h^{-1}. During the measurements, the wind speed varied from slow (0 to 2 m s^{-1}, $n = 85$) to moderate (3 to 4 m s^{-1}, $n = 12$). Only eastern, southern and western winds prevailed (Table 2). Differences in the 20 m flight durations according to wind speed, wind direction and the used illumination (moon light vs. artificial light) were statistically insignificant (ANOVA, $F_{6, 90} = 2.01$, $p = 0.073$). Therefore, it was assumed that the slow or moderate winds that prevailed during this study, as well as the artificial light source used to observe the bats, had a negligible effect on the flight speed. However, when moon light was used instead of artificial light, the mean flight duration and speed were 1.8 s and 11.2 m s^{-1}, respectively (see Table 2).

Estimates of characteristic flight speeds

Different estimates of characteristic flight speeds were obtained by the two models (Norberg 1990; Pennycuick 2008). The estimated V_{mp} for P. nathusii were 3.6 (SD = 0.1) and 5.8 m s^{-1} (SD = 0.1), according to models by Norberg and Pennycuick respectively (Table 2). Negligible variation in the estimated V_{mr} (ca. 5 and 11 m s^{-1}, according to Norberg's and Pennycuick's model respectively) resulted from assumed values (17 and 23%) of flight muscle efficiency (Table 3). The mean recorded flight speed of P. nathusii (13.1 m s^{-1}, see above), was considerably higher than the estimated minimum power speed and it also exceeded the maximum range speed as predicted based on either of the models (Fig. 2).

Assuming the minimum time speed V_{mt} to be equal to the mean observed flight speed (13.1 m s^{-1}) and 17 to 23% flight muscle efficiency, the predicted migration speed V_{migr} was 8.3 to 8.4 and 4.1 to 4.6 m s^{-1} (ca. 30 and 16 km h^{-1}), according to Norberg's and Pennycuick's model respectively. The flight speed of 11.2 m s^{-1}, observed when moon light was used instead of artificial light (Table 2), corresponded to a considerably lower migration speed of 6.9 to 7.0 (Norberg's model) and 0.8 to 1.5 m s^{-1} (Pennycuick's model) or ca. 25 and 4 km h^{-1}.

Table 2. Summary of the time used to cross 20-metre distance by P. nathusii during migration flight in relation to wind direction and wind speed. In most cases, an artificial 100 W illumination was used to observe the bats; the cases when moon light was used instead are marked by *

Wind	Mean distance time (s)	Estimated mean flight speed (m s^{-1})
E 0 to1 m s^{-1}	1.443 (SD = 0.338, n = 16)	14.8 (SD = 4.2)
E 1 to 2 m s^{-1}	1.562 (0.456, 21)	13.9 (3.9)
E 1 to 2 m s^{-1}*	1.843 (0.353, 7)	11.2 (2.2)
SE 0 to 1 m s^{-1}	1.627 (0.395, 15)	13.0 (3.4)
SE 3 to 4 m s^{-1}	1.717 (0.434, 7)	12.3 (2.9)
SW 0 to 1 m s^{-1}	1.385 (0.295, 25)	15.2 (3.7)
W 2 to 4 m s^{-1}	1.45 (0.5, 6)	14.9 (3.8)

Table 3. Estimated characteristic flight speeds (± SD) for P. nathusii according to morphometric data (n = 8) and two aerodynamic models (Norberg 1990; Pennycuick 2008), assuming flight muscle efficiency to be 17 and 23%

| Flight muscle efficiency	Norberg's model		Pennycuick's model	
	V_{mp} (m s^{-1})	V_{mr} (m s^{-1})	V_{mp} (m s^{-1})	V_{mr} (m s^{-1})
17%	3.6 ± 0.1	5.3 ± 0.1	5.8 ± 0.1	10.5 ± 0.3
23%	3.6 ± 0.1	5.4 ± 0.1	5.8 ± 0.1	10.7 ± 0.2
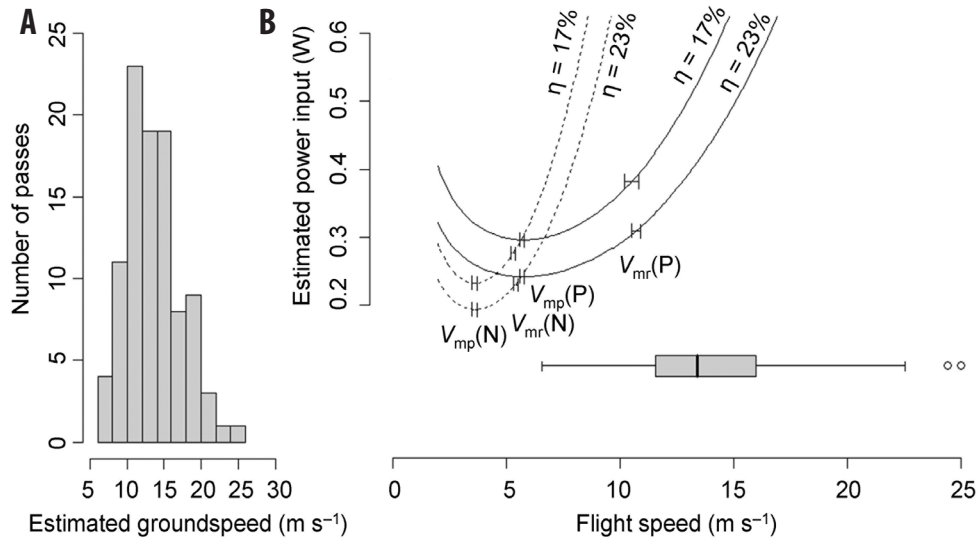
Fig. 2. Estimated speed of *P. nathusii* migration flight (A) and comparison with predictions based on aerodynamic models (B) by Norberg (1990, dashed line) and Pennycuick (2008, solid line). The flight muscle efficiency was assumed to be 17 and 23%, whiskers indicate one standard deviation of estimated characteristic flight speeds. The box plot indicates the 10th, 25th, 75th and 90th percentiles as well as the median flight speed as measured.

Changes in sonar properties according to flight altitude
The mean height of the observed flights was 11.5 m (SD = 2.4, n = 26). The mean duration of sonar pulses and pulse intervals was 6.6 (SD = 1.50, n = 116) and 103.7 ms (SD = 25.6, n = 116), respectively. The duration of the inter-pulse intervals was significantly correlated with the flight altitude (Pearson's product-moment correlation, $r = 0.66$,

$t = 2.5$, $df = 8$, $p = 0.04$; Fig. 3). Also, there was an almost significant relationship between the pulse duration and the flight altitude ($r = 0.60$, $t = 2.1$, $df = 8$, $p = 0.07$). As expected, the distance a sound wave could travel during the shortest recorded inter-pulse intervals closely corresponded to the distance from the bat to the ground and back (i.e. to the flight altitude doubled, Table 4).
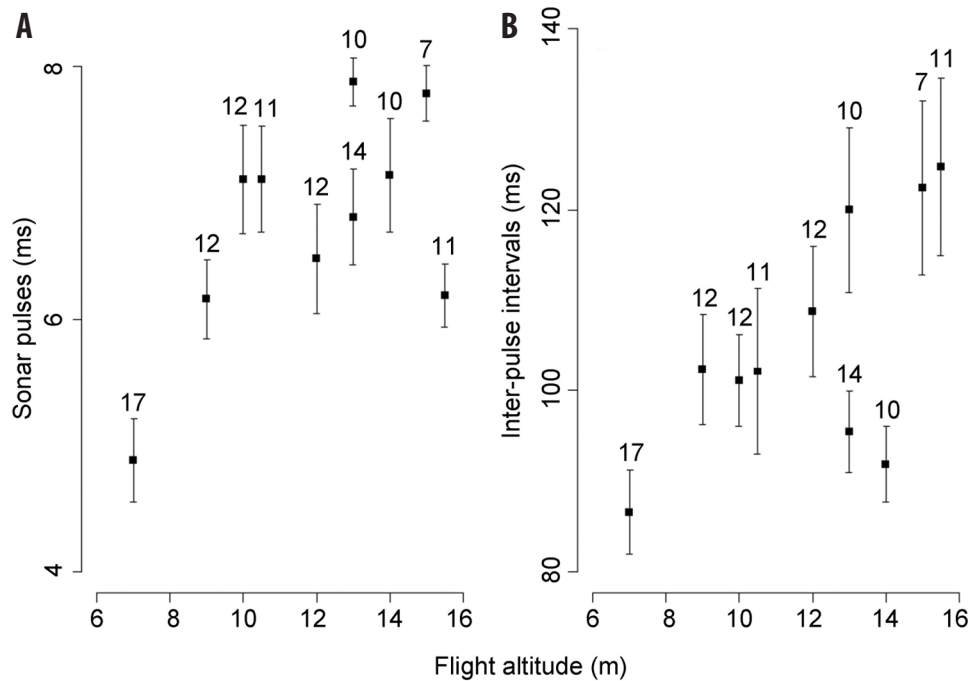
Fig. 3. Duration of recorded sonar pulses (A) and inter-pulse intervals (B) in relation to flight altitude of migrating *P. nathusii*. The error bars indicate one standard deviation and the numbers refer to sample sizes.

Table 4. Flight altitude and duration of shortest recorded inter-pulse intervals between sonar impulses of migrating *P. nathusii*. The speed of sound through the air used for calculating the achievable distance of a sound wave was assumed to be 343.2 m s^{-1}

Individual No	Flight altitude (m)	Three selected minimum intervals (ms)	Corresponding distance achievable by sound wave (m)
1	7	44.1, 49.5, 73.3	15.1, 17, 25.2
2	9	86, 91.2, 91.3	29.5, 31.3, 31.3
3	10	67.9, 79.3, 85.4	23.3, 27.2, 29.3
4	10.5	71.6, 79.7, 86.4	24.6, 27.4, 29.7
5	12	86.4, 93.6, 94.6	29.7, 32.1, 32.5
6	13	97.3, 98.5, 103.8	33.4, 33.8, 35.6
7	13	70.5, 75.3, 76	24.2, 25.8, 26.1
8	14	66.3, 79.5, 80.5	22.8, 27.3, 27.6
9	15	95.7, 105.5, 111.4	32.8, 36.2, 38.2
10	15.5	89.4, 93.4, 95.3	30.7, 32.1, 32.7

Discussion

This study provides the first flight speed estimates of *P. nathusii* during migration. The observed migrating *P. nathusii* crossed the 20 m distance between the poles in 1.5 s on average and the mean flight altitude was 11.5 m. Commuting and migration flights are predicted to be faster than foraging flights (Norberg 1981; Houston 2006), and this has demonstrated for common pipistrelles *P. pipistrellus* (Jones, Rayner 1989) and Kuhl's pipistrelles *P. kuhlii* (Grodzinski et al. 2009). On average, foraging *P. nathusii* fly at 5.6 (range 5.1 to 6.0) m s^{-1} (Baagøe 1987). Thus, the present estimate of 13.1 m s^{-1} during migration flight agrees with this prediction. However, most observations of the bats were made using an artificial 100 W light source. Although no statistically significant effects were found, the observed flight speed was lower when natural moon light was used (11.2 m s^{-1}) instead of artificial illumination (13.2 m s^{-1}) Ambient illumination probably has an impact on flight speed of bats (Winter 1999). More precise three-dimensional methods exist for measuring flight speed of the bats (e.g. Grodzinski et al. 2009), which should be applied in further studies.

The results of this study also support the hypothesis that *P. nathusii* adjust sonar parameters according to flight height in a low-altitude migration flight. The duration of the intervals between consecutive sonar pulses was correlated with the flight height, which would be expected if bats aim the sonar towards the ground. There are published examples of bats showing this behaviour (e.g. Rydell 1990). The reason why the bats maintain contact with the surface while flying low over water during migration over the sea (Ahlén et al. 2009) may seem quite obvious, but why they do so also when flying at several metres over land is not clear at all. It may be hypothesised that bats routinely check the

substrate of the ground by maintaining contact. Potential landmark recognition by sonar may also be considered. However, homing experiments on displaced blind-folded and untreated bats suggest that vision is essential for successful homing (Smith, Goodpaster 1958; Williams et al. 1966; Layne 1967; Williams, Williams 1967; 1970) and hence may be more important for landmark recognition than sonar.

Generally, aerodynamic models for flapping flight appear to describe correctly the physical processes involved in the generation of aerodynamic force (Rayner 1999). The major problems, however, lie in estimates of appropriate values for the model coefficients and their possible dependence on flight speed, which still needs examination (Rayner 1999; Hedenström 2009). The differences in the estimates of characteristic flight speeds based on the two models were caused by different approaches in evaluation of the profile drag (see Materials and Methods). In Pennycuick's (1975; 2008) model, it is assumed that the profile power is almost constant between V_{mp} and V_{mr}, whereas in Norberg's (1990) model the drag caused by wings is considered to be proportional to the flight speed cubed. It appears that Pennycuick's estimate agrees more closely with observed and predicted speeds of foraging and commuting flights (Grodzinski et al. 2009). Comparing predicted V_{mp} and V_{mr} to observed flight speed, Pennycuick's model was found more suitable for *P. nathusii*. Hence predictions from this model will be discussed further.

According to Pennycuick's model, V_{mp} and V_{mr} for the migrating *P. nathusii* were 5.8 and ca. 11 m s^{-1}, respectively. The mean speed of migration flight recorded in this study (11 to 13 m s^{-1}) slightly exceeded the predicted V_{mr} and would result in a migration speed of ca. 4 to 16 km h^{-1}. In a previous capture-recapture study by Pētersons (2004), it was documented that two individual *P. nathusii*, for which the time of capture and recapture were known exactly, migrated at 5.1 and 10.2 km h^{-1}, which is in rough agreement with the present estimate (4 to 16 km h^{-1}). Assuming that the bats are active for 7.3 hours each night (Šuba et al. 2012), the predicted average migration speed from the data of this study would be ca. 30 to 120 km per night. The analysis of capture-recapture data by Pētersons (2004) suggests that *P. nathusii* migrate on average 47 km per night (range 32 to 77 km per night). Assuming that the bats were active during the entire night, the average migration speed of recovered bats would have ranged between 1.2 and 2.9 m s^{-1}, which corresponds to a flight speed between 11 and 12 m s^{-1} and agrees with the estimates of this study. Another prediction of migration speed for *P. nathusii* (46 km per night, Hedenström 2009) agrees very closely with the mean migration speed calculated from ringing recoveries (Pētersons 2004). However, it is generally assumed that bats have flown the shortest distance between ringing and recovery sites, which may not be the case in practice. The migrating bats may follow landscape structures (e.g.

rivers, Furmankiewicz, Kucharska 2009) and thus may have travelled longer distances between banding and recovery sites.

This study indicates that the speed of *P. nathusii* migration flight is close to the predicted V_{mr}, which supports the hypothesis that the bats do optimise the speed of migration flight by minimising energy expenditure. A time minimisation strategy would require a faster flight at V_{mt} which exceeds V_{mr}. The data of this study does not provide a strong support for a time minimisation strategy. The migrating *P. nathusii* also engage in mating activities during the autumn migration (Lundberg 1989), hence longer overall duration of migration may be expected.

In migratory birds, the difference between V_{mr} and V_{mt} is hard to distinguish due to relatively low fuelling rates (Hedenström 2008). Insectivorous bats, however, are probably able to achieve higher net fuelling rates than birds due to energy savings by daily torpor (McGuire et al. 2012). Additionally, insectivorous bats are capable of aerial refuelling (Voigt et al. 2010), and migrating *P. nathusii* may forage quite frequently during migration flight (Šuba et al. 2012). Bats are capable of catching 1 to 3 g of insects per hour (Gould 1955) and the consumable energy content of insects is ca. 8.6 kJ g^{-1} wet mass (Finke 2002; Voigt et al. 2010). Assuming that the flight metabolic rate of *P. nathusii* is 1.2 W (calculated according to Speakman, Thomas 2003) or 4.3 kJ h^{-1}, three grams of insects could fuel the flight of *P. nathusii* for six hours. Additional energy requirements are met by consuming a fraction of the stored fat reserves (Voigt et al. 2012).

The data of this study were collected under slow wind conditions (0 to 2 m s^{-1}), which probably had little effect on the flight speed. It is expected, however, that wind speed and wind direction affect the speed and perhaps the direction of migration flights, since the wind speed may be similar or even higher than the bat's (or bird's) flight speed (Hedenström 2002; Hedenström 2009). For instance, V_{mr} is supposed to decrease in tail-winds and increase in head-winds (Pennycuick 1978; Hedenström 2002). In order to maintain a constant track over the ground, the flight speed should increase with increasing angle of the side wind (Liechti et al. 1994). The current situation may force a bat to delay its migration flight (Weber et al. 1998) or apply wind drift for compensation (Alerstam 1979; Hedenström 2009). The impact of wind on bat migration needs to be investigated in further studies.

Acknowledgements

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Paper VI

J. Eklöf, Šuba J., Petersons G., Rydell J. 2014. Visual acuity and eye size in five European bat species in relation to foraging and migration strategies. *Environmental and Experimental Biology,* **12: 1–6.**

Visual acuity and eye size in five European bat species in relation to foraging and migration strategies

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Abstract

Optomotor response tests provided visual acuity thresholds in five species of north European insectivorous bats of the family Vespertilionidae. Individuals of three species of predominantly aerial-hawking and trawling *Myotis* (*M. brandtii, M. mystacinus* and *M. daubentonii*) responded only to a stripe pattern equivalent to 5 degrees of arc, whereas the long-distance migrant *Pipistrellus nathusii*, another aerial-hawking species, responded to 1 degree. In contrast, *Plecotus auritus*, which is a gleaner and capable of detecting prey using vision alone, responded to a pattern equivalent to 0.5 degrees. The visual acuity was positively correlated with eye diameter, which varied from 0.9 mm in *M. mystacinus* to 1.7 mm in *P. auritus*. The results are consistent with earlier findings on related species in other parts of the world. The variation in eye size and visual acuity among insectivorous bats reflect differences in foraging techniques and perhaps also in migrating behavior, thus illustrating how vision is used as a complement to ultrasonic echolocation in various navigation and foraging situations.

Key words: Chiroptera; optomotor response; orientation; navigation; night vision; spatial resolution.

Introduction

The eyes of insectivorous bats are adapted to nocturnal conditions, and, although they are small, they have relatively large corneal surfaces and lenses and large receptor fields, which provide good light gathering capacity. However, this partly occurs at the expanse of acuity, the ability to resolve fine spatial detail (Suthers 1970; Suthers, Wallis 1970). Generally, bat eyes are best suited for long-range operation, and considering the short effective range of ultrasonic echolocation (Lawrence, Simmons 1982), vision is probably of major importance in guidance over longer distances (Griffin 1970; Boonman et al. 2013).

Nevertheless, some bats use vision over short distances as well, such as during escape and obstacle avoidance experiments (Chase 1981; Chase, Suthers 1969; Bradbury, Nottebohm 1969). Bats may even use vision to find prey under some conditions, a task that requires relatively fine detail discrimination at a very short range (Bell 1985; Grant 1991; Vaughan, Vaughan 1986; Surlykke et al. 1993; Eklöf et al. 2002a; Eklöf, Jones 2003). Vision and hearing are closely integrated in bats (Horowitz et al. 2004; Boonman et al. 2013), as in other animals, but visual information usually takes precedence over echolocation in situations when sufficient light is available (Eklöf et al. 2002b; Orbach, Fenton 2010). In view of the relatively recent findings

that bats possess color vision (Wang et al. 2004; Müller, Peichl 2005; Zhao et al. 2009), including sensitivity for UV (Winter et al. 2003; Müller et al. 2009; Xuan et al. 2012) and specializations for dim light vision (Shen et al. 2010), bat eyes are clearly much more complicated and versatile than previously anticipated.

The potential visual acuity can be estimated theoretically, based on counts of retinal ganglion cells, and this has been done in several species of bats (Marks 1980; Pettigrew et al. 1988; Heffner et al. 2001). Estimates based on this technique show a large range of variation, from 16 minutes of arc in the gleaning and partly carnivorous *Macroderma gigas* and *Megaderma lyra* (Megadermatidae), two species with unusually large eyes, to 1.4 degrees in the strictly insectivorous flutter-detector *Rhinolophus rouxii* (Rhinolophidae), which has very small eyes (Pettigrew at el. 1988). Behavioural observations such as optomotor response tests, where the visual acuity is tested directly, generally agree with the theoretical predictions, and confirm that the visual acuity varies considerably from species to species and to some extent is related to behavioral characters such as the typical foraging technique (Suthers 1966; Manske, Schmidt 1976; Bell, Fenton 1986).

Generally, gleaners, species able to detect and catch non-flying insects and other animals, seem to have better visual capacity than other bats, i.e. aerial-hawking species,

those that normally detect and catch insects in the air. This is probably because the search for food is to some extent guided by vision in gleaners, maintaining strong natural selection on this trait (Bell, Fenton 1986; Eklöf, Jones 2003).

It also seems possible that bats that perform long-distance migrations may require relatively sharp vision, assuming that orientation and navigation partly rely on visual cues on the night sky such as single bright stars or stellar constellations (Childs, Buchler 1981; Buchler, Childs 1982) or perhaps the moon. This has not been examined as far as we know.

Hence, the main purpose of this study was to test the hypothesis that visual acuity varies across bat species according to their foraging and migration strategies, and that gleaning species show better visual acuity than aerial hawking ones. We also investigated the possibility that migrating bats apply stellar or possibly lunar navigation, and perhaps show better visual acuity than stationary (non-migratory) species. Long-term data on migration flight activity of Nathusius' pipistrelle *Pipistrellus nathusii*, a known long-distance migrant (Hutterer et al. 2005), were analyzed, testing the hypothesis that migration intensity increases on clear as compared to cloudy nights, i.e. with and without stellar (and lunar) cues, respectively.

Materials and methods

The behavioural experiments were made at (a) the old magnetite mine at Taberg, 13 km south of Jönköping in south-central Sweden (57°41´N, 14°05´E), and (b) Pape Ornithological Station at the Baltic coast in southernmost Latvia (56°10´N, 21°01´E). For descriptions of these localities in some detail, we refer to Karlsson et al. (2002), Pētersons (2004) and Šuba et al. (2012), respectively. At Taberg, bats (eight *Plecotus auritus*, three *Myotis mystacinus*, two *M. brandtii* and three *M. daubentonii*) were caught in mist nets outside one of the mine entrances, while at Pape the bats (21 *Pipistrellus nathusii*, of which 13 were tested) were captured in a large Helgoland-type funnel trap placed near the shoreline, as described previously (Pētersons 2004). At Taberg the tests were made in the evening from August to November 2002 and from March to April 2003. The tests at Pape were made in August and September 2011 and 2012, while bats were on migration.

The bats were tested for optomotor responses immediately after capture or as soon as they had come to rest. To achieve the responses, we used two devices (one at each site) similar to those used by Suthers (1966) and Bell and Fenton (1986). Each of the devices consisted of a 30 cm high and 60 cm diameter revolving drum with a 20 cm high and 10 cm diameter plexiglass cylinder in the centre with the experimental bat inside. The drum could be rotated freely and independently of the cylinder by hand in both directions. Inside the drum and visible from its center, we attached a paper with a sinusoidal grating

pattern of varying fineness. A sinusoidal pattern means that the luminance varied continuously from black to white. We used sinusoidal pattern instead of discrete black and white stripes to reduce the risk of optical illusions, which could otherwise elicit responses from the bats and thus make the results harder to interpret (as suggested by D. Nilsson and E. Warrant at Lund University, Sweden). Six gratings with different width (distance from white to white) were used; 2.84, 1.42, 0.57, 0.43, 0.28 and 0.14 cm, respectively, equivalent to subtending angles of 5, 2.5, 1, 0.75, 0.5 and 0.25 degrees of arc, as seen from the bat's point of view (i.e. from the center of the plexiglass cylinder). When a response was recorded the grating was switched to a finer pattern until no response was recorded, indicating that the bat could no longer resolve the pattern. At this point a wider pattern was reintroduced, to make sure that the bat still responded to the moving stripes. This also served as a control for responses to stimuli other than the stripes, such as, for example, noise originating from the drum and our own movements. Of the bats captured at Taberg, two *M. mystacinus* individuals and one *M. daubentonii* individual did not respond to the widest pattern (5 degrees) and they were therefore released and not tested further. These individuals are not included in the results table (Table 1).

Natural light was usually insufficient for direct unaided observation of the bats' responses. Therefore, dim artificial light conditions were maintained during the experiments. At Taberg, the study setup was placed outdoors ca 5 m from a 40 W light bulb that permanently illuminated the entrance to a building (the "Mining Office"). This measure provided us with sufficient light to see what happened inside the cylinder. The light intensity inside the drum was thus 0.1 to 0.7 lux (Photometer IL 1400A, International Light Inc., USA). At Pape, the tests were made inside a small lab facility and the light intensity inside the drum was 3 to 7 lux (Lutron YK-2001 TM with aYK-200PLX light meter probe; Lutron Electronics Enterprise Co. Ltd., USA).

At Taberg, the faces of the bats were photographed after testing the optomotor responses, using a high quality macro lens and a flash, to achieve an estimate of the eye diameter. We held the bats by hand so that the face of the bat was perpendicular to the lens (bat seen in profile) with a ruler next to the bat, providing a cm scale. At Pape, photos from other individuals than those tested for optomotor response were used. The eye sizes of individual bats were later estimated on a computer screen, using only bats that had eyes fully open and where the bat and the ruler were in focus. The bats were released at the site of capture immediately after the experiments and the photographs.

To test whether the intensity of *P. nathusii* autumn migration increases on clear nights, assuming that a clear sky provides the best conditions for stellar and/or lunar navigation, we used data from a long term census of migrating bats at Pape Ornithological Station, collected from 10 August to 10 September 2003 – 2012 by one of

us (GP). At this site, bats migrate in large numbers at low altitude along the coast of the Baltic Sea (Pētersons 2004; Šuba et al. 2012). Passes of migrating bats were counted manually in 15-min intervals during the first two hours after sunset (n = 300), aided by an ultrasound detector (model D-200 or D-240X, Pettersson Elektronik AB, Uppsala, Sweden). Relative cloud cover was assessed on a four-class scale: clear sky, some clouds (< 50% cloud cover), cloudy (50 to 80% cloud cover) and overcast (> 80% cloud cover). Other factors, such as ambient temperature, wind speed and wind direction were also recorded and included in the analysis. Records that contained fog, rain or strong wind (> 6 m s⁻¹; *n* = 122) were not included in the analysis, because much fewer bats migrate in such conditions (Pētersons, unpublished data). A multi-way analysis of covariance (ANCOVA) was used to test for the impact of cloud cover, wind direction and wind speed on the number of bat passes, using ambient temperature as covariate. The data on bat passes were log transformed to fit the normal distribution. The analysis was made using R version 2.13.0 (R Foundation for Statistical Computing, Vienna, Austria).

Results

When put in the cylinder the bats typically moved about for a few minutes and they sometimes continued to do so during the test. However, most of them unambiguously responded to the rotating pattern by moving their heads in a snappy, stereotyped manner, either following the direction of the rotating drum or in the opposite direction, as described earlier by others (Suthers 1966; Bell, Fenton 1986).

The results (Table 1) were consistent within a species and genus but differed considerably and consistently between the genera. Individuals of the three species of *Myotis* were similar in performance and responded only to the largest pattern, equivalent to 5° of arc. In the brown long-eared bat *Plecotus auritus* all individuals except one responded down to the pattern equivalent to 1 – 0.5°. Nathusius' pipistrelle *Pipistrellus nathusii* was intermediate, individuals of this species usually responded down to 1° (Table 1).

The eye size varied with visual capacity as expected (Table 1). The *Myotis* spp. had the smallest eyes (ca. 1 mm

diameter) and *P. auritus* the largest (ca. 1.7 mm). *P. nathusii* was intermediate (ca. 1.3 mm).

The migration intensity of *P. nathusii* at Pape varied considerably in relation to cloud cover (Fig. 1). On average, more passes were registered under a clear sky, and the effect of cloudiness was statistically significant. However, considerable migration activity still occurred on cloudy nights. Wind direction and ambient temperature also had significant impacts on migration intensity (Table 2). On average most bat passes were recorded when the wind blew from the east and from the southwest (headwind).

Discussion

Visual acuity differs considerably among bats in general and this is also the case within the Vespertilionidae, the family to which the species tested here belong. The variation presumably reflects the extent to which the bats make use of vision and what they do with it. As expected, the relatively big eyed gleaner *Plecotus auritus* did much better than the three predominantly aerial-hawking and trawling *Myotis* species that we tested, and which also had much smaller eyes (Fig. 2).
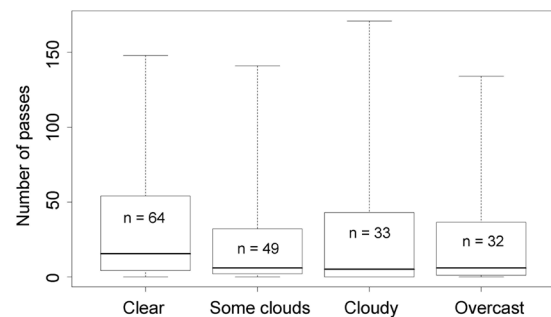
Fig. 1. Box-whisker plots of the number of passes of migrating *P. nathusii* in relation to the cloud cover. Passes were recorded during 15-minute intervals at Pape Ornithological Station during autumn migration (10 August to 10 September 2003 – 2012). Stripes indicate the medians, whickers indicate the maximum and minimum numbers and the boxes show the inter quartiles; n is the number of observations in each class.

Table 1. Eye diameter and optomotor responses to patterns of different fineness in five European bat species. The n-values under the minimum separable angle refer to the number of individuals showing the modal value and the number of responding individuals, respectively

Species	Eye diameter (mm)	Ambient light (lux)	Minimum separable angle	
			Modal value	Range
Plecotus auritus	1.7 ± 0.1 (*n* = 4)	0.1 – 0.7	45′ (*n* = 3)	30′ – 2.5° (*n* = 8)
Myotis mystacinus	1.0 and 0.9 (*n* = 2)	0.1 – 0.6	5° (*n* = 1)	
Myotis brandtii	Not measured	0.1 – 0.6	5° (*n* = 2)	
Myotis daubentonii	1.2 and 1.3 (*n* = 2)	0.1 – 0.3	5° (*n* = 2)	
Pipistrellus nathusii	1.3 ± 0.1 (*n* = 21)	3 – 7	1° (*n* = 7)	45′ – 5° (*n* = 13)

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Table 2. A multi-way ANCOVA table showing the number of passes of migrating *P. nathusii* at Pape in Latvia in August and September 2003 to 2012 in relation to cloud cover and other weather factors (wind direction, wind speed and temperature)

Factor	Values	SS	d.f.	F	p
Cloud cover	Clear (*n* = 64)	16.0	3	3.4	0.019
	Some clouds (*n* = 49)				
	Cloudy (*n* = 33)				
	Overcast (*n* = 32)				
Wind direction	No wind (*n* = 21)	104.2	4	16.6	< 0.001
	North (*n* = 29)				
	East (*n* = 49)				
	South (*n* = 32)				
	West (*n* = 47)				
Wind speed	0 m s^{-1} (*n* = 21)	1.6	1	1.0	0.32
	1–2 m s^{-1} (*n* = 96)				
	3–5 m s^{-1} (*n* = 61)				
Ambient temperature	15.5 °C (SD = 3.1)	24.5	1	15.6	< 0.001
Residuals		263.0	168		
Total	*n* = 178	409.1	177		

The response to the 5° but not to the 2.5° pattern by the *Myotis* spp. used in our tests was consistent across the three species and our result was also consistent with an earlier test of the American conspecific *M. lucifugus*, which responded down to 3 – 6° patterns (Suthers 1966). Because of this consistency, we believe that our results are robust with respect to *Myotis* spp., despite the fact that only five individuals were tested successfully. A visual acuity in this range suggests that these bats can detect a 5 to 9 cm object at 1 m at best. Therefore, it seems very unlikely that they can visually detect the insects that they eat, which are mostly chironomids and other small flies (e.g. Swift, Racey 1983). Insects must therefore be detected by echolocation alone. Nevertheless, vision may be used to detect large objects at distances beyond the range of echolocation and may therefore be important in navigation and orientation. Indeed, the loss of vision drastically reduces the homing performance in other *Myotis* species such as *M. sodalis* (Hassell 1966; Davis, Barbour 1970) and *M. austroriparius* (Layne 1967), as well as in many other bats (Hassell 1966; Williams et al. 1966; Davis, Barbour 1970; Holland 2007).

In contrast to *Myotis* spp. the brown long-eared bat *Plecotus auritus* responded to a pattern equivalent to 30′ of arc, which means that this species should be able to see objects as small as 0.9 cm diameter at a distance of 1 m. Among the Vespertilionidae only the pallid bat *Anthrozous pallidus*, which also is a gleaner, has been shown to have a better resolving power, namely 15′ (Bell, Fenton 1986). *P. auritus* typically feeds on relatively large prey items (Swift, Racey 1983; Rydell 1989), including many moths and beetles, and can detect at least some prey items, e.g. mealworms, by the use of vision alone (Eklöf, Jones 2003).

The visual acuity of Nathusius' pipistrelle *Pipistrellus nathusii* was intermediate between those of *Myotis* spp. and *Plecotus auritus*. In contrast to the other four species,

P. nathusii is a long-distance migrant (Hutterer et al. 2005), and as such it may perhaps be expected to show a visual acuity of sufficient quality for perception of stars or other objects on the night sky, cues which may possibly be used during nocturnal orientation and navigation. Its visual acuity is similar to that of some other aerial-hawking bats that typically forage in open air, such as the big brown bat *Eptesicus fuscus* in North America and the northern bat *E. nilssonii* in Europe, species considered to be non-migratory (Bell, Fenton 1986; Rydell, Eklöf 2003). Optomotor responses provided similar acuity thresholds (0.9 to 1.5°) for aerial-hawking vespertilionid bats in Africa (*Neoromicia capensis, N. zuluensis, N. nana, Scotophilus dinganii, Pipistrellus rueppelii* and *Nycticeius schlieffeni*), and also in aerial-hawking species of other families from the same area [e.g. *Miniopterus natalensis* (Miniopteridae), *Chaerophon pumila* and *Mops midas* (Molossidae); using the nomenclature in Monadjem et al. (2010); M.B. Fenton and C. Portfors, unpublished results, cited in Eklöf 2003]. Hence, the visual acuity of *P. nathusii* is by no means exceptional, but rather typical for open air foragers among aerial-hawking bats, presumably including both migratory and more stationary species.

The big brown bat *E. fuscus* seems to use visual cues for nocturnal orientation and navigation purposes (Buchler, Childs 1982) and there is indeed experimental evidence that it can see single bright stars against the night sky (Childs, Buchler 1981). The northern bat *E. nilssonii* occasionally uses vision in prey detection under exceptional circumstances, provided that the prey is large, slow moving and visually conspicuous (Eklöf et al. 2002a). Our analysis demonstrated that the migration activity of *P. nathusii* increased considerably on clear nights, although relatively high activity was also observed on overcast nights. This suggests that *P. nathusii* may use stars and/or other
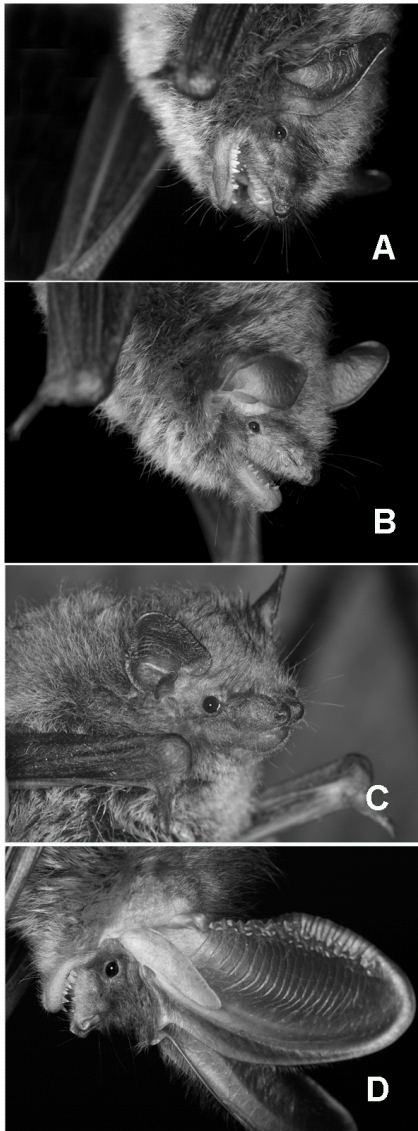
Fig. 2. Portraits of four of the species used in this study, illustrating the differences in eye size. A, *Myotis brandtii*; B, *Myotis daubentonii*; C, *Pipistrellus nathusii*; D, *Plecotus auritus*. The pictures are not exactly to scale; *M. brandtii* and *P. nathusii* are somewhat smaller than the other two species. Photo by J. Rydell.

cues on the night sky for navigation purposes, but also that such cues are by no means the only ones used. Other potential cues include, for example, the earth´s magnetic field (Holland et al. 2006).

The visual acuity in bats varies with the ambient light intensity and also with the contrast between the object and the background. In the common vampire bat *Desmodus rotundus*, for example, the acuity drops from 48´ at a light intensity of 31 mL (ca. 310 lux) to about 2° at 4×10^{-4} mL (ca. 0.004 lux; Manske, Schmidt 1976). Other bats, such as *Macrotus californicus* (Phyllostomidae) and *Anthrozous pallidus* (Vespertilionidae), both of which are gleaning insectivores or carnivores, retain visual acuity down to light levels as low as 2×10^{-4} mL (ca. 0.002 lux; Bell, Fenton

1986). For comparison, a light level of 0.1 lux is roughly equivalent to the light under full moon and similar to the experimental conditions in this study.

The best optomotor response does not necessarily occur at high or even moderate light intensity. Rather, bats tend to perform best in dim light (Bradbury, Nottebohm 1969). For example, individuals of *E. fuscus* respond optimally to brightness discrimination at ambient light levels of about 10 lux, a condition roughly equivalent to that prevailing at dusk and dawn, but perform well down to 0.001 lux (Ellins, Masterson 1974). As the ambient illumination increases towards daylight, the visual sensitivity generally declines, although the tolerance varies between species (Hope, Bhatnagar 1979). The ambient light level and the way it was measured differ strongly between the tests reported in the literature, sometimes making the results a bit hard to compare.

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