

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 south-eastern 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

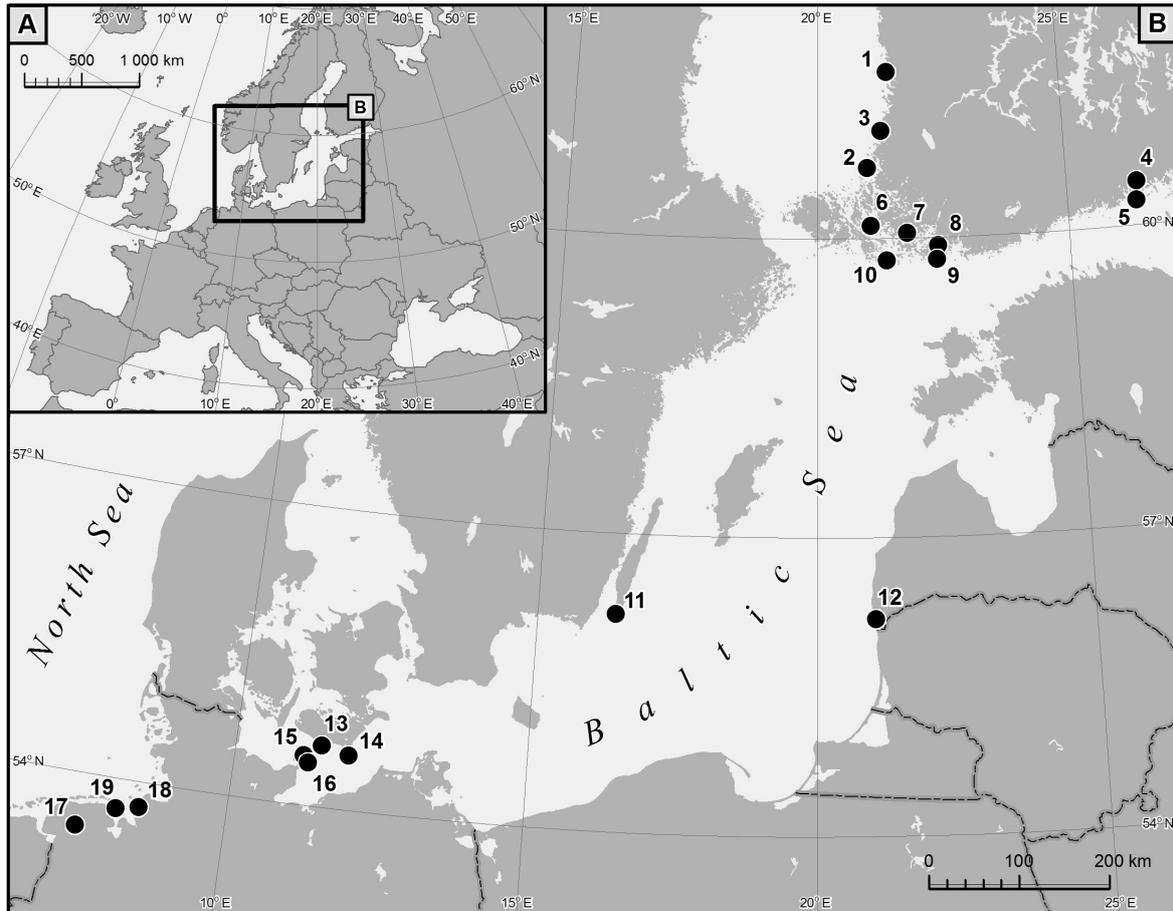


FIG. 1. Map showing the 19 localities included in this survey. Finland: 1 — Anttoora (61.67°N, 21.43°E); 2 — Isokari (60.71°N, 21.01°E); 3 — Rihntiemi (61.08°N, 21.30°E); 4 — Ruotsinpyhtää (60.44°N, 26.43°E); 5 — Aspskär (60.25°N, 26.40°E); 6 — Jungfruskär (60.13°N, 21.07°E); 7 — Berghamn (60.05°N, 21.79°E); 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 AnaloookW (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 <i>et al.</i> (2009), Frey <i>et al.</i> (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

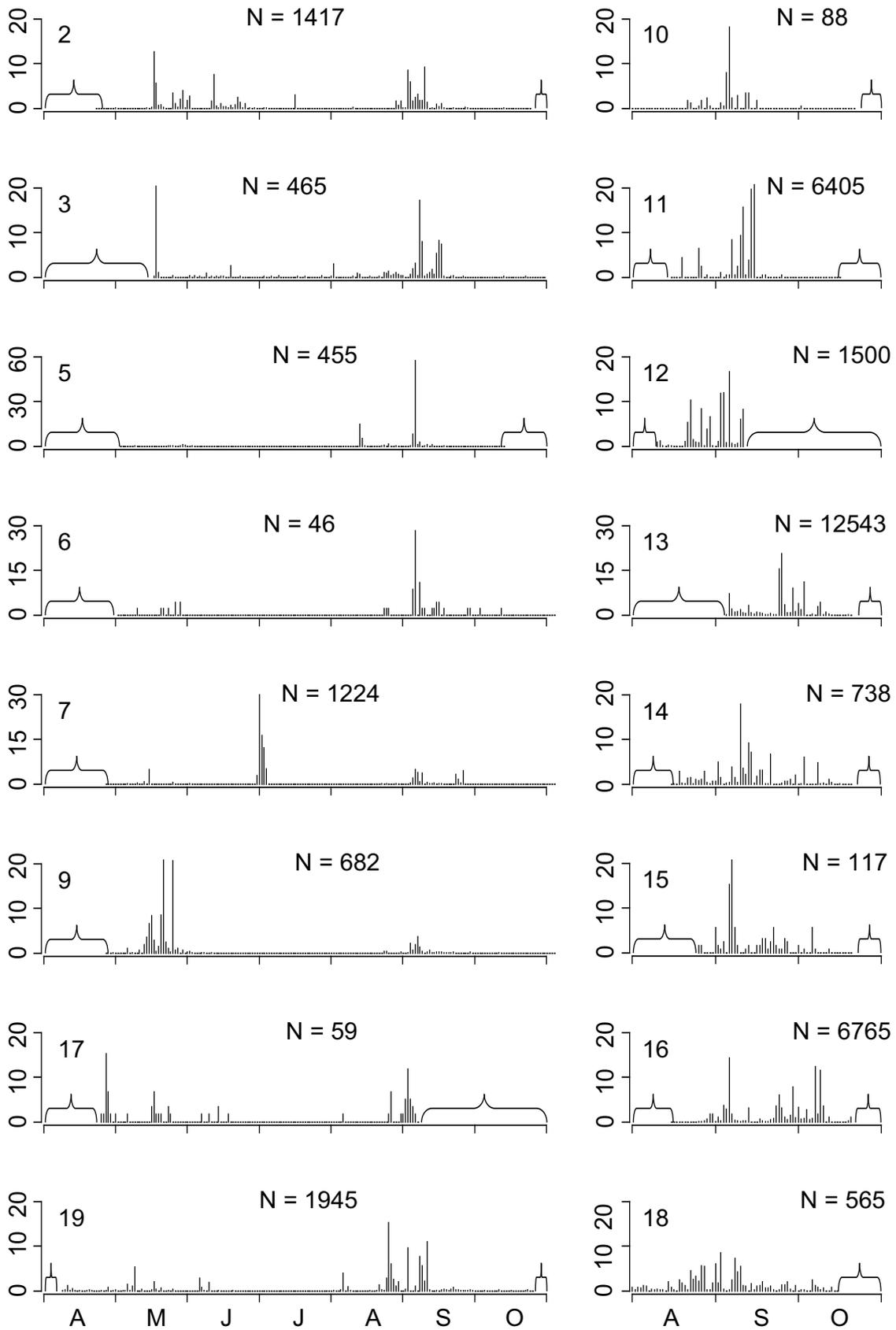


FIG. 2. Changes in occurrence (%) of *P. nathusii* throughout the season in 2009 at some of the localities monitored. The left column covers 1 April to 31 October, the right column covers 1 August to 31 October. Crochets denote periods without observations. The numbers refer to locality as in Fig. 1

(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

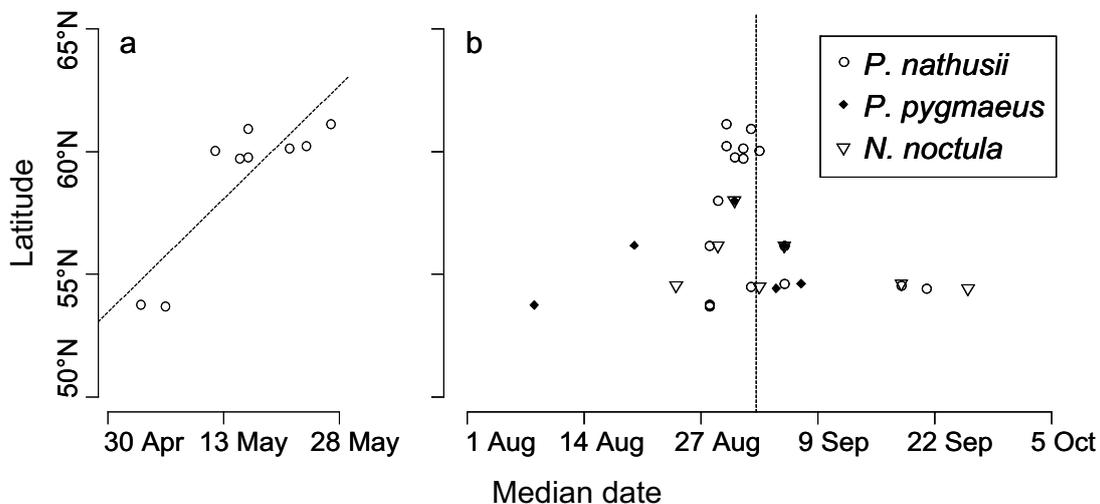


FIG. 3. Relationships between median dates of bat occurrence and latitude for the spring migration (a) and autumn migration (b) periods

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
<i>P. nathusii</i>	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)
<i>P. nathusii</i>	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)
<i>N. noctula</i>	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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