

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

Jurģis Šuba\*

University of Latvia, Faculty of Biology, Department of Zoology and Animal Ecology, Kronvalda bulvaris 4, Rīga LV-1586, Latvia

\*Corresponding author, E-mail: jurgiss@imap.cc

## 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. Pennycuik 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<sup>-1</sup> (40.3 and 47.2 km h<sup>-1</sup>) 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.

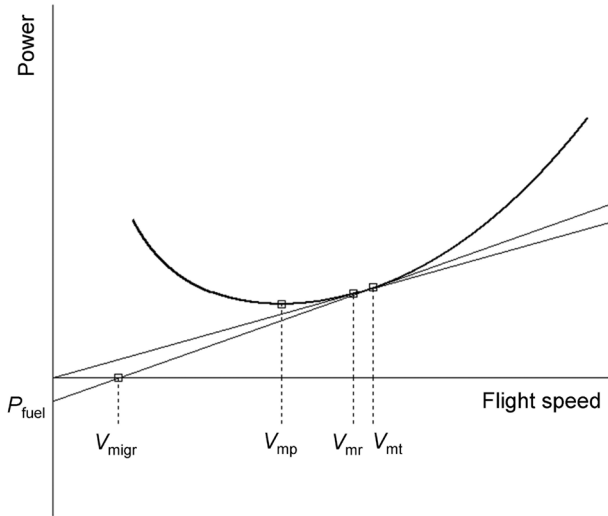
## Introduction

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 (Pennycuik 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  $\alpha$  and  $\beta$  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

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

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

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

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 ( $56^{\circ}09'57''N$   $21^{\circ}01'02''E$ ) 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 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 cm<sup>2</sup>). 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 cm<sup>2</sup> (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 (cm <sup>2</sup> )
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<sup>-1</sup> by intervals of 0.1 m s<sup>-1</sup>. 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 ( $P_{iner}$ )

$$P_{mech} = P_{ind} + P_{par} + P_{pro} + P_{iner} \quad (3)$$

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

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

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<sup>-2</sup>),  $\rho$  is the air density (1.2 kg m<sup>-3</sup>) and  $b$  is the wing span (in metres). The parasite power that overcomes the drag of the body was calculated as

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

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

$$S_f = 0.00813m^{0.666} \quad (6)$$

(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

$$P_{pro} \text{ (Norberg)} = \rho C_{Dpro} S V^3 / 2, \quad (7.1)$$

$$P_{pro} \text{ (Pennycuick)} = 8.4P_{am} S / b^2, \quad (7.2)$$

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

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

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),  $\eta$  is

the energy conversion efficiency (assumed to vary between 0.17 and 0.23 according to Rayner 1999; Pennycuick 2008) and  $P_{\text{BMR}}$  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

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

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

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

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  $V_{\text{mt}}$  (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

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

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

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

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

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<sup>-1</sup> or 47.2 km h<sup>-1</sup>. During the measurements, the wind speed varied from slow (0 to 2 m s<sup>-1</sup>,  $n = 85$ ) to moderate (3 to 4 m s<sup>-1</sup>,  $n = 12$ ). 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<sup>-1</sup>, 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  $V_{\text{mp}}$  for *P. nathusii* were 3.6 (SD = 0.1) and 5.8 m s<sup>-1</sup> (SD = 0.1), according to models by Norberg and Pennycuick respectively (Table 2). Negligible variation in the estimated  $V_{\text{mr}}$  (ca. 5 and 11 m s<sup>-1</sup>, 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<sup>-1</sup>, 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).

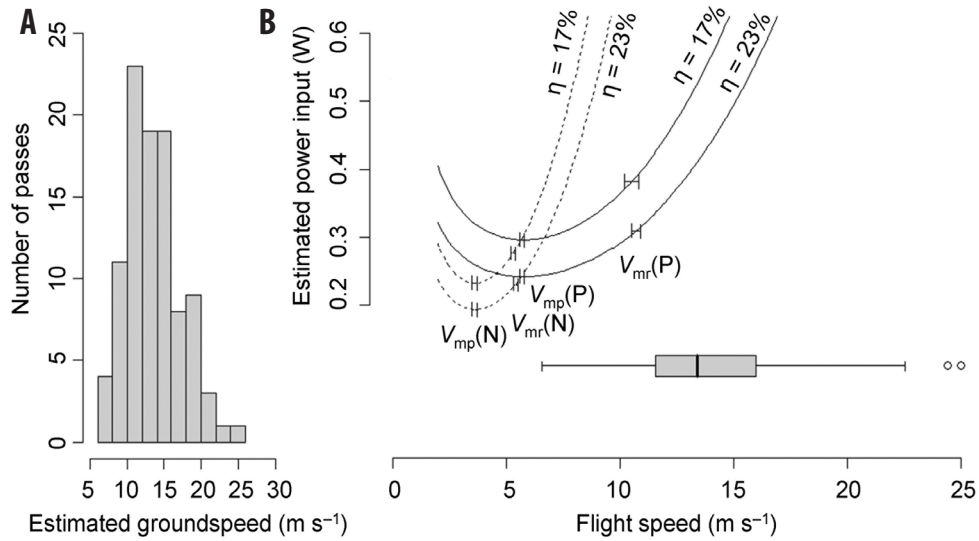
Assuming the minimum time speed  $V_{\text{mt}}$  to be equal to the mean observed flight speed (13.1 m s<sup>-1</sup>) and 17 to 23% flight muscle efficiency, the predicted migration speed  $V_{\text{migr}}$  was 8.3 to 8.4 and 4.1 to 4.6 m s<sup>-1</sup> (ca. 30 and 16 km h<sup>-1</sup>), according to Norberg's and Pennycuick's model respectively. The flight speed of 11.2 m s<sup>-1</sup>, 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<sup>-1</sup> (Pennycuick's model) or ca. 25 and 4 km h<sup>-1</sup>.

**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 <sup>-1</sup> )
E 0 to 1 m s <sup>-1</sup>	1.443 (SD = 0.338, $n = 16$ )	14.8 (SD = 4.2)
E 1 to 2 m s <sup>-1</sup>	1.562 (0.456, 21)	13.9 (3.9)
E 1 to 2 m s <sup>-1</sup> *	1.843 (0.353, 7)	11.2 (2.2)
SE 0 to 1 m s <sup>-1</sup>	1.627 (0.395, 15)	13.0 (3.4)
SE 3 to 4 m s <sup>-1</sup>	1.717 (0.434, 7)	12.3 (2.9)
SW 0 to 1 m s <sup>-1</sup>	1.385 (0.295, 25)	15.2 (3.7)
W 2 to 4 m s <sup>-1</sup>	1.45 (0.5, 6)	14.9 (3.8)

**Table 3.** Estimated characteristic flight speeds ( $\pm$  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	
	$V_{\text{mp}}$ (m s <sup>-1</sup> )	$V_{\text{mr}}$ (m s <sup>-1</sup> )	$V_{\text{mp}}$ (m s <sup>-1</sup> )	$V_{\text{mr}}$ (m s <sup>-1</sup> )
17%	3.6 $\pm$ 0.1	5.3 $\pm$ 0.1	5.8 $\pm$ 0.1	10.5 $\pm$ 0.3
23%	3.6 $\pm$ 0.1	5.4 $\pm$ 0.1	5.8 $\pm$ 0.1	10.7 $\pm$ 0.2

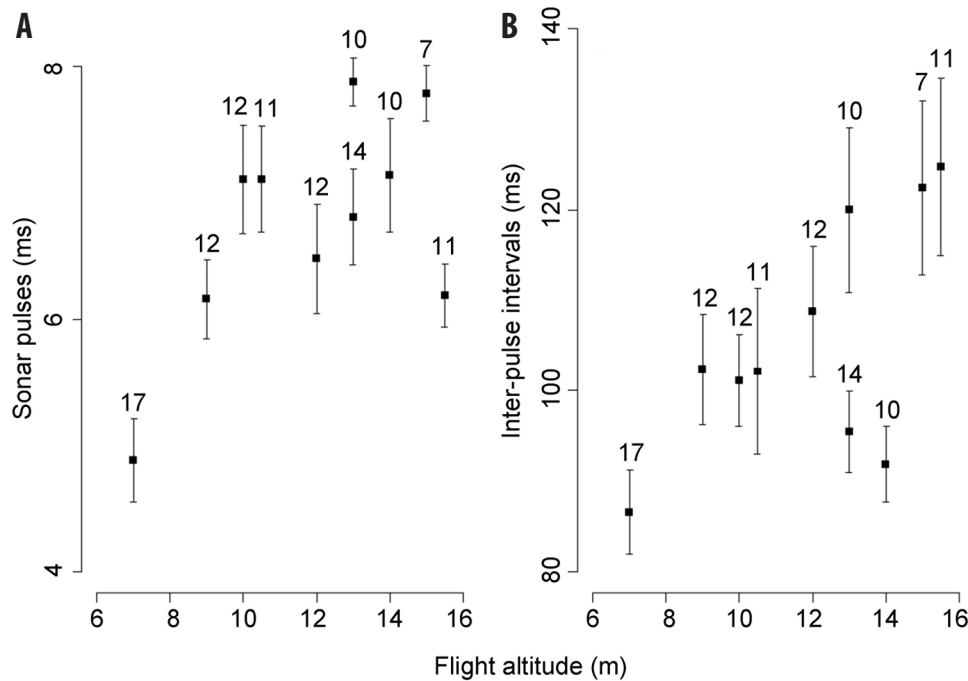


**Fig. 2.** Estimated speed of *P. nathusii* migration flight (A) and comparison with predictions based on aerodynamic models (B) by Norberg (1990, dashed line) and Pennycuik (2008, solid line). The flight muscle efficiency was assumed to be 17 and 23%, whiskers indicate one standard deviation of estimated characteristic flight speeds. The box plot indicates the 10<sup>th</sup>, 25<sup>th</sup>, 75<sup>th</sup> and 90<sup>th</sup> 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<sup>-1</sup>

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 been 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<sup>-1</sup> (Baagøe 1987). Thus, the present estimate of 13.1 m s<sup>-1</sup> 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<sup>-1</sup>) instead of artificial illumination (13.2 m s<sup>-1</sup>). 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<sup>-1</sup>, respectively. The mean speed of migration flight recorded in this study (11 to 13 m s<sup>-1</sup>) slightly exceeded the predicted  $V_{mr}$  and would result in a migration speed of ca. 4 to 16 km h<sup>-1</sup>. 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<sup>-1</sup>, which is in rough agreement with the present estimate (4 to 16 km h<sup>-1</sup>). 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<sup>-1</sup>, which corresponds to a flight speed between 11 and 12 m s<sup>-1</sup> 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<sup>-1</sup> 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<sup>-1</sup>, 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<sup>-1</sup>), 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 (Pennycuik 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

This work was supported by the European Social Fund within the project "Support for Doctoral Studies at University of Latvia - 2". D. Spalis, M. Briedis, K. Čehoviča, I. Dinsbergs, J. Āboltiņš, K. Reinis, K. Ritums, U.N. Urbāne and Z.J. Ziemeļis helped with the preparation and completing the field work. G. Pētersons, J. Rydell, R.Å. Norberg, C.C. Voigt, M.W. Holderied and A. Hedenström contributed by providing literature, valuable comments and corrections during manuscript preparation.

### References

- Ahlén I., Baagøe H.J., Bach L. 2009. Behavior of Scandinavian bats during migration and foraging at sea. *J. Mammal.* 90: 1318–1323.
- Alerstam T. 1979. Wind as selective agent in bird migration. *Ornis Scandinavica* 10: 76–93.
- Alerstam T. 1991. Bird flight and optimal migration. *Trends Ecol. Evol.* 6: 210–215.
- Baagøe H.J. 1987. The Scandinavian bat fauna: adaptive wing morphology and free flight in the field. In: Fenton M.B., Racey P.A., Rayner J.M.V. (eds) *Recent Advances in the Study of Bats*. Cambridge University Press, Cambridge, pp. 57–74.
- Britton A.R.C., Jones G., Rayner J. M.V., Boonman A.M., Verboom B. 1997. Flight performance, echolocation and foraging behaviour in Pond bats, *Myotis dasycneme* (Chiroptera: Vespertilionidae). *J. Zool.* 241: 503–522.
- Finke M.D. 2002. Complete nutrient composition of commercially raised invertebrates used as food for insectivores. *Zoo Biol.* 21: 269–285.
- Fleming T. H., Eby P. 2003. Ecology of bat migration. In: Kunz T.H., Fenton M.B. (eds) *Bat Ecology*. Chicago University Press, Chicago, pp. 156–208.
- Furmankiewicz J., Kucharska M. 2009. Migration of bats along a large river valley in southwestern Poland. *J. Mammal.* 90: 1310–1317.
- Gould E. 1955. The feeding efficiency of insectivorous bats. *J. Mammal.* 36: 399–407.
- Griffin D.R. 1970. Migrations and homing of bats. In: Wimsatt W.A. (ed) *Bat Biology and Conservation*. Vol. 1. Academic Press, New York, pp. 233–264.
- Grodzinski U., Spiegel O., Korine C., Holderied M. W. 2009. Context-dependent flight speed: evidence for energetically optimal flight speed in the bat *Pipistrellus kuhlii*? *J. Anim. Ecol.* 78: 540–548.
- Hedenström A. 2002. Aerodynamics, evolution and ecology of avian flight. *Trends Ecol. Evolut.* 17: 415–422.
- Hedenström A. 2008. Adaptations to migration in birds: behavioural strategies, morphology and scaling effects. *Phil. Trans. Royal Soc. B* 363: 287–299.
- Hedenström A. 2009. Optimal migration strategies in bats. *J. Mammal.* 90: 1298–1309.
- Hedenström A., Alerstam T. 1995. Optimal flight speed of birds. *Phil. Trans. Royal Soc. B* 348: 471–487.
- Hedenström A., Alerstam T. 1996. Skylark optimal flight speeds for flying nowhere and somewhere. *Behav. Ecol.* 7: 121–126.
- Hedenström A., Alerstam T. 1998. How fast can birds migrate? *J. Avian Biol.* 29: 424–432.
- Hedenström A., Liechti F. 2001. Field estimates of body drag coefficient on the basis of dives in passerine birds. *J. Exp. Biol.* 204: 1167–1175.
- Hedrick T.L., Usherwood J.R., Biewener A.A. 2004. Wing inertia and whole-body acceleration: an analysis of instantaneous aerodynamic force production in cockatiels (*Nymphicus hollandicus*) flying across a range of speeds. *J. Exp. Biol.* 207: 1689–1702.
- Houston A.I. 2006. The flight speed of parent birds feeding the young. *J. Avian Biol.* 37: 545–554.
- Hutterer R., Ivanova T., Meyer-Cords C., Rodrigues L. 2005. *Bat Migrations in Europe: A Review of Banding Data and Literature*. Naturschutz und Biologische Vielfalt, Bonn, 176 p.
- Jones G. 1995. Flight performance, echolocation and foraging

- behaviour in noctule bats *Nyctalus noctula*. *J. Zool.* 237: 303–312.
- Jones G., Rayner J.M.V. 1989. Optimal flight speed in pipistrelle bats, *Pipistrellus pipistrellus*. In: Hanák V., Horáček I., Gaisler J. (eds) *European Bat Research*. Charles University Press, Prague, Czechoslovakia, pp. 247–253.
- Lawrence B.D., Simmons J.A. 1982. Measurement of atmospheric attenuation at ultrasonic frequencies and the significance for echolocation by bats. *J. Acoust. Soc. Am.* 71: 585–590.
- Layne J.N. 1967. Evidence for the use of vision in diurnal orientation of the bat *Myotis austroriparius*. *Anim. Behav.* 15: 409–415.
- Liechti F., Hedenström A., Alerstam T. 1994. Effects of sidewinds on optimal flight speed of birds. *J. Theor. Biol.* 170: 219–225.
- Lundberg K. 1989. Social organization and survival of the pipistrelle bat (*Pipistrellus pipistrellus*), and a comparison of advertisement behaviour in three polygynous bat species. Lund University, Lund, 88 p.
- McGuire L.P., Guglielmo C.G. 2009. What can birds tell us about the migration physiology of bats? *J. Mammal.* 90: 1290–1297.
- McGuire L.P., Guglielmo C.G., Mackenzie S.A., Taylor P.D. 2012. Migratory stopover in the long-distance migrant silverhaired bat, *Lasionycteris noctivagans*. *J. Anim. Ecol.* 81: 377–385.
- McNab B.K. 1988. Complications inherent in scaling the basal rate of metabolism in mammals. *Quart. Rev. Biol.* 63: 25–54.
- Morris C.R., Askew G.N. 2010. Comparison between mechanical power requirements of flight estimated using an aerodynamic model and in vitro muscle performance in the cockatiel (*Nymphicus hollandicus*). *J. Exp. Biol.* 213: 2781–2787.
- Norberg R.Å. 1981. Optimal flight speeds in birds when feeding young. *J. Anim. Ecol.* 50: 474–477.
- Norberg U.M. 1990. *Vertebrate Flight: Mechanics, Physiology, Morphology, Ecology and Evolution*. Springer Verlag, Berlin, Heidelberg, New York, 291 p.
- Norberg U.M., Kunz T.H., Steffensen J.F., Winter Y., von Helversen O. 1993. The cost of hovering and forward flight in a nectar-feeding bat, *Glossophaga soricina*, estimated from aerodynamic theory. *J. Exp. Biol.* 182: 207–227.
- Norberg U.M., Rayner J.M.V. 1987. Ecological morphology and flight in bats (Mammalia; Chiroptera): wing adaptations, flight performance, foraging strategy and echolocation. *Phil. Trans. Royal Soc. B* 316: 335–427.
- Pennycuik C.J. 1975. Mechanics of flight. In: Farner D.S., King J.R., Parkes K.C. (eds) *Avian Biology*. Vol. 5. Academic Press, New York, pp. 1–75.
- Pennycuik C.J. 1978. Fifteen testable predictions about bird flight. *Oikos* 30: 165–176.
- Pennycuik C.J. 1989. *Bird Flight Performance: A Practical Calculation Manual*. Oxford University Press, New York, 170 p.
- Pennycuik C.J. 2008. *Modelling the Flying Bird*. Elsevier Science, Academic Press Inc, San Diego, 496 p.
- Petersons G. 1990. Die Rauhhauffledermaus, *Pipistrellus nathusii* (Keyserling u. Blasius, 1839), in Lettland: Vorkommen, Phänologie und Migration. *Nyctalus* 3: 81–98.
- Petersons G. 2004. Seasonal migrations of north-eastern populations of *Nathusius' bat Pipistrellus nathusii* (Chiroptera). *Myotis* 41/42: 29–56.
- Popa-Lisseanu A.G., Voigt C.C. 2009. Bats on the move. *J. Mammal.* 90: 1283–1289.
- Rayner J.M.V. 1979. Vortex theory of animal flight 2. Forward flight of birds. *J. Fluid Mech.* 91: 731–763.
- Rayner J.M.V. 1994. Aerodynamic corrections for the flight of birds and bats in wind tunnels. *J. Zool.* 234: 537–563.
- Rayner J.M.V. 1999. Estimating power curves of flying vertebrates. *J. Exp. Biol.* 202: 3449–3461.
- Rydell J. 1990. Behavioural variation in echolocation pulses of the Northern Bat, *Eptesicus nilssonii*. *Ethology* 85: 103–113.
- Sahley C.T., Horner M.A., Fleming T.H. 1993. Flight speeds and mechanical power outputs of the nectar-feeding bat, *Leptonycteris curasoae* (Phyllostomidae: Glossophaginae). *J. Mammal.* 74: 594–600.
- Smith E., Goodpaster W. 1958. Homing in nonmigratory bats. *Science* 127: 644.
- Speakman J.R., D.W. Thomas D.W. 2003. Physiological ecology and energetics of bats. In: Kunz T.H., Fenton M.B. (eds) *Bat Ecology*. Chicago University Press, Chicago, pp. 430–490.
- Šuba J., Petersons G., Rydell J. 2012. Fly-and-forage strategy in the bat *Pipistrellus nathusii* during autumn migration. *Acta Chiropterol.* 14: 379–385.
- Thomas S.P. 1975. Metabolism during flight in two species of bats, *Phyllostomus hastatus* and *Pteropus gouldii*. *J. Exp. Biol.* 63: 273–293.
- Thomas S.P., Suthers R.A. 1972. The physiology and energetics of bat flight. *J. Exp. Biol.* 63: 273–293.
- Tobalske B.W., Hedrick T.L., Dial K.P., Biewener A.A. 2003. Comparative power curves in bird flight. *Nature* 421: 363–366.
- Tschapka M. 1998. Coexistence and resource utilization in a community of nectar-feeding bats (Phyllostomidae: Glossophaginae) in the Atlantic lowland rainforest of Costa Rica. Doctoral thesis, Universität Erlangen. [in German]
- Voigt C.C., Sörgel K., Dechman D.K.N. 2010. Refuelling while flying: foraging bats combust food rapidly and directly to power flight. *Ecology* 91: 2908–2917.
- Voigt C.C., Sörgel K., Šuba J., Petersons G., Keišs O. 2012. The insectivorous bat *Pipistrellus nathusii* uses a mixed-fuel strategy to power autumn migration. *Proc. Royal Soc. B* 279: 3772–3778.
- Ward S., Moller U., Rayner J.M.V., Jackson D.M., Bilo D., Nachtigall W., Speakman J.R. 2001. Metabolic power, mechanical power and efficiency during wind tunnel flight by the European starling *Sturnus vulgaris*. *J. Exp. Biol.* 204: 3311–3322.
- Weber T.P., Alerstam T., Hedenström A. 1998. Stopover decisions under wind influence. *J. Avian Biol.* 29: 552–560.
- Williams T.C., Williams J.M. 1967. Radio tracking of homing bats. *Science* 155: 1435–1436.
- Williams T.C., Williams J.M. 1970. Radio tracking of homing and feeding flights of a neotropical bat, *Phyllostomus hastatus*. *Animal Behav.* 18: 302–309.
- Williams T.C., Williams J.M., Griffin D.R. 1966. Visual orientation in homing bats. *Science* 152: 677–679.
- Winter Y. 1999. Flight speed and body mass of nectar-feeding bats (Glossophaginae) during foraging. *J. Exp. Biol.* 202: 1917–1930.