

Context-dependent flight speed: evidence for energetically optimal flight speed in the bat *Pipistrellus kuhlii*?

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Summary

1. Understanding the causes and consequences of animal flight speed has long been a challenge in biology. Aerodynamic theory is used to predict the most economical flight speeds, minimizing energy expenditure either per distance (maximal range speed, V_{mr}) or per time (minimal power speed, V_{mp}). When foraging in flight, flight speed also affects prey encounter and energy intake rates. According to optimal flight speed theory, such effects may shift the energetically optimal foraging speed to above V_{mp} .

2. Therefore, we predicted that if energetic considerations indeed have a substantial effect on flight speed of aerial-hawking bats, they will use high speed (close to V_{mr}) to commute from their daily roost to the foraging sites, while a slower speed (but still above V_{mp}) will be preferred during foraging. To test these predictions, echolocation calls of commuting and foraging *Pipistrellus kuhlii* were recorded and their flight tracks were reconstructed using an acoustic flight path tracking system.

3. Confirming our qualitative prediction, commuting flight was found to be significantly faster than foraging flight (9.3 vs. 6.7 m s⁻¹), even when controlling for its lower tortuosity.

4. In order to examine our quantitative prediction, we compared observed flight speeds with V_{mp} and V_{mr} values generated for the study population using two alternative aerodynamic models, based on mass and wing morphology variables measured from bats we captured while commuting. The V_{mp} and V_{mr} values generated by one of the models were much lower than our measured flight speed. According to the other model used, however, measured foraging flight was faster than V_{mp} and commuting flight slightly slower than V_{mr} , which is in agreement with the predictions of optimal flight speed theory.

5. Thus, the second aerodynamic model we used seems to be a reasonable predictor of the different flight speeds used by the bats while foraging and while commuting. This supports the hypothesis that bats fly at a context-dependent, energetically optimal flight speed.

Key-words: acoustic tracking, maximal range velocity, minimal power velocity, movement, power curve

Introduction

Movement is an important feature for most animals, facilitating resource use, danger avoidance and social interactions (Dingle & Drake 2007). Various considerations shape the movement pattern performed by animals, including external

factors such as resource and predator distribution and internal factors such as physiological constraints and energetic costs (e.g., Hedenström & Ålerstam 1995, 1996; Nathan *et al.* 2008). These factors can change between different contexts and, consequently, so do movement patterns. For actively flying vertebrates, energetic costs of flight are extremely high and may influence the selected flight pattern (Norberg 1990; Rayner 1999; Neuweiler 2000; Houston 2006). Since the power (energy per time) required for flight is a function of

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flight speed, flight speed is expected to be strongly affected by energetic considerations (e.g. Pennycuik 1975; Rayner 1999).

A power curve is the (U-shaped) function representing the relationship between power expenditure and forward flight speed (e.g. Pennycuik 1975; Rayner 1999), commonly used in the study of vertebrate flight (Norberg 1990; Hedenström & Ålerstam 1995; Rayner 1999; Houston 2006). Two alternative options for minimizing flight energy costs can be derived from this curve: V_{mp} (minimum power velocity), which minimizes power expenditure and V_{mr} (maximum range velocity), which is higher than V_{mp} and minimizes energy expenditure per distance travelled (Pennycuik 1975; Norberg 1990; Rayner 1999). Different ecological contexts may render either one of those (or other speeds) the most energetically effective (see Jones & Rayner 1991; Hedenström & Ålerstam 1995). For example, small migrating birds seem to fly at their predicted V_{mp} when the objective is to remain airborne (Bruderer & Boldt 2001), e.g. when skylarks (*Alauda arvensis*) perform song flight and are 'flying nowhere' (Hedenström & Ålerstam 1996). Much higher speeds, around V_{mr} , are used when trying to make best progress (Bruderer & Boldt 2001), e.g. when skylarks are migrating (Hedenström & Ålerstam 1996).

Given the uncertainties and assumptions of aerodynamic theory, with different models predicting different V_{mp} and V_{mr} values (see e.g. Pennycuik 1989; Norberg *et al.* 1993; Rayner 1999), comparing flight speeds of the same free-living population in different ecological context, for which different optimal flight speeds are predicted, provides the best way to date to test the predictions of optimal flight speed theory (Hedenström & Ålerstam 1995; Houston 2006). The term 'optimal' can be confusing (see Ydenberg, Brown & Stephens 2007), and we use it only to describe a flight speed that maximizes net energy intake rate (V_{mp} and V_{mr} are used when only energy expenditure is considered).

Bird flight speed has been studied extensively (e.g. McLaughlin & Montgomerie 1985; Hedenström & Ålerstam 1995, 1996; Bruderer & Boldt 2001; Blake & Chan 2006; Ålerstam *et al.* 2007). The flight speed of aerial-feeding bats, which is more technically difficult to measure, has been studied to a lesser extent (Jones & Rayner 1991; Sahley, Horner & Fleming 1993; Salcedo *et al.* 1995; Britton *et al.* 1997; Winter 1999; see also Holderied & Jones 2009, for a review), but may nevertheless provide valuable and testable predictions.

In order to minimize the energetic cost for the long search flights, aerial-feeding bats would need to fly at V_{mp} , making foraging a ' V_{mp} context' (Jones & Rayner 1991; Winter 1999; Holderied 2001; Holderied *et al.* 2005). However, optimal flight speeds during foraging depends also on energetic gain. Hedenström & Ålerstam (1995) discuss a variety of situations where foraging birds are expected to maximize either net energy intake rate (the difference between energy gain from consumed food and energy expenditure during foraging; see also Jones & Rayner 1991; Bautista, Tinbergen & Kacelnik 2001; Houston 2006) or foraging gain ratio (the quotient of energy gain and the energetic cost of foraging). In both cases, they predict optimal foraging flight speeds somewhat above V_{mp} (see figure 1 in Hedenström & Ålerstam 1995; also see

figure 10 in Jones & Rayner 1991). This prediction is based on the power curve and the notion that energy intake rate increases with speed (because encounter rate rises) at a decelerating rate before it decreases at higher speeds (due to difficulties to notice or catch prey). Thus, considering the cost of flying and reasonable assumptions regarding gains from foraging, it is predicted that foraging bats should fly somewhat faster than V_{mp} . How much above V_{mp} depends on what 'currency' is maximized (Bautista *et al.* 2001) and on the exact effect of flight speed on energy intake rate (Jones & Rayner 1991; Hedenström & Ålerstam 1995).

At nightfall, some bat species commute along relatively constant routes from their roost to foraging sites (Lewis 1995; Britton *et al.* 1997; Robinson & Stebbings 1997; Holderied, Jones & von Helversen, 2006). This may represent a ' V_{mr} context' in which bats minimize energy expenditure per travelled distance by flying at V_{mr} (Hedenström & Ålerstam 1995, 1996; Sahley *et al.* 1993). Thus, we predict that bats will fly faster (close to V_{mr}) when leaving their roost than when foraging. Commuting speed may be shifted to be even faster than V_{mr} by energy intake considerations (as discussed for foraging speed), if resources deplete rapidly or when feeding young (Hedenström & Ålerstam 1995; Houston 2006).

To test our predictions of context-dependent flight speed, accurate speed measurement is essential, something in which previous studies may have suffered from methodological limitations. For instance, Sahley *et al.* (1993) used radiotelemetry to estimate speed by calculating time required to pass a 25-km commuting track, likely underestimating actual flight speed if the path was not a perfectly straight 25-km line. In this report, we use the powerful method of acoustic 3D tracking of echolocating bats to measure their speeds in different contexts. Echolocation calls of flying bats were recorded using an array of microphones that enabled us to reconstruct their flight trajectories and calculate speed and other flight characteristics. Commuting and foraging flight speeds of the bat *Pipistrellus kuhlii* (Kuhl 1817) were measured in this manner. Like other aerial-feeding bats, *P. kuhlii* hunts flying insects, with the search phase of foraging consisting of long periods of flight (Barak & Yomtov 1989). The observed commuting and foraging flight speeds were then compared with V_{mr} and V_{mp} values generated from morphological parameters of bats captured at the field site, using two aerodynamic models.

Materials and Methods

Field observations were conducted at Midreshet Ben-Gurion in the Negev desert highlands, southern Israel (30°52' N, 34°47' E) where *P. kuhlii* is common (Korine & Pinshow 2004). The study population comprised ~100–150 individuals, consisting mostly of females and sub-adults (no mature males were caught), which roost in an isolated building (a gym) and forage at various sites in the village and its surroundings (around vegetation, street lights and over water; for further information regarding the species and its echolocation calls see Korine & Pinshow 2004; Berger-Tal *et al.* 2008).

Bat echolocation calls were recorded on six nights in summer 2007, between 19:30 h and 23:00 h, at four distinct foraging sites

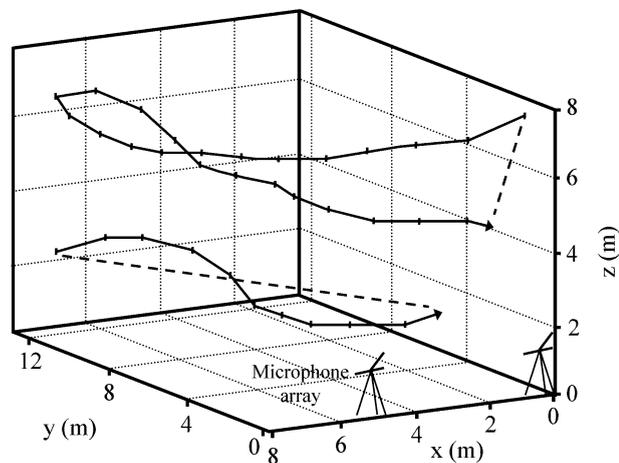


Fig. 1. Two examples of flight trajectories of *Pipistrellus kuhlii*. Each point represents the location of a bat (in spatial coordinates x , y and z) at the time of emitting a single echolocation call. Localization was based on time-of-arrival differences between eight microphones arranged as symmetrical stars in two T-shaped arrays on tripods. Straight lines between consecutive localizations are termed segments. Trajectory flight speed was calculated as the average segment speed, and tortuosity was calculated as the ratio of travelled distance (sum of segment lengths) and the displacement (dashed lines). In this example, the upper trajectory has a higher tortuosity value than the lower one.

(100–500 m from the roost) differing in spatial structure: Ben-Gurion tomb (29/07, 01/08; hereafter ‘Tomb’), Guesthouse (02/08), Road (02/08, 05/08, 07/08) and Lawn (06/08). One of these sites, a street nearby the roost (Road), also constitutes a commuting route that bats use to reach their foraging areas.

MEASURING FLIGHT SPEED

The recording system consisted of two microphone arrays placed ~5 m apart [with four Knowles BT1759 microphones (Maplewood Drive, Itasca, IL, USA) each, arranged in a symmetrical star]. This system allows localization of the bat every time it emits an echolocation call, based on the difference in the propagating signal’s arrival time at the different microphones. Exact measurements of air temperature and relative humidity (affecting sound propagation velocity) and the system’s spatial configuration are a prerequisite for accurate localization, and were obtained for each night.

The temporal resolution of this method is dictated by bat echolocation rate, which in this study was 10 Hz (with 25th and 75th percentiles of 9.1 and 11.6 Hz, respectively), corresponding with published results for the species (Schnitzler *et al.* 1987). The system is unable to track bats flying at wind conditions of more than 1 m s^{-1} , and data were therefore recorded under near-windless conditions. For further information regarding this method, see Holderied & von Helversen (2003) and Aubauer (1994).

Flight trajectories were reconstructed from these single call locations using BatSonar (Technical University of Darmstadt, Darmstadt, Germany and University of Erlangen, Erlangen, Germany) (Fig. 1). Trajectories consist of segments, i.e. straight 3D connections between two consecutive locations. Three measures were calculated for each trajectory using MatLab scripts (version 6.5 The Mathworks, Natick, MA, USA): (i) trajectory height above-ground (by averaging location heights), (ii) trajectory speed (by averaging all segment speeds, i.e. segment length divided by segment duration),

and (iii) tortuosity value (travelled distance divided by net displacement; see Fig. 1). To ensure that all trajectory means are based on sufficient data, trajectories with less than seven segments ($n = 120$) were excluded from the data set. From the foraging data, all trajectories containing an approach phase ($n = 28$) were also excluded to ensure that the data reflect speeds during the search phase only. The remaining 58 commuting and 479 foraging flight trajectories were included in our data analyses.

The localization error of the recording system is less than 0.2% of the distance from the arrays for 45% of the localizations, less than 2% for 80% of the localizations and larger than 2% for 20% of the localizations (Aubauer 1994). Large localization errors (over 2%) are easily apparent as they distinctively perturb from the trajectory, and these were manually deleted before data analyses. Therefore, our ranging error was no more than 2% and less than 0.2% for the majority (56%) of the localizations. To assess the effect of these measurement errors on the calculated trajectory flight speed, we repeated speed calculations after randomly assigning errors of relevant size and probability (this procedure was repeated 20 times). As foraging trajectories were recorded at greater distances ($8.39 \pm 2.22 \text{ m}$) than commuting trajectories ($5.71 \pm 1.82 \text{ m}$), error introduction resulted in a larger effect on foraging speeds: introduced errors increased mean foraging speed by $1.72\% \pm 0.36\%$, and the standard deviation by $12.03\% \pm 9.43\%$ as compared to the measured speed. For commuting flight, mean speed and standard deviation increased only by $0.22\% \pm 0.16\%$ and $0.45\% \pm 1.32\%$, respectively. The order of magnitude of the errors compared to the measurement size, and especially compared with the difference between commuting and foraging speeds (see below), suggests that our main results are robust to the system’s localization errors (Bradshaw, Sims & Hays 2007).

TRAJECTORY DATA ANALYSIS

To avoid pseudo-replication of data points taken from the same trajectory, we treated each trajectory as a single value (the mean of its segments’ values). For commuting bats, light conditions allowed visually counting 71 different individuals leaving the roost in the direction of our recording area, at least 32 of which were sampled within one session (07/08). Our foraging data set comprises 479 trajectories, of which many are probably repeated recordings of the same bats. Assigning trajectories to individual bats is impossible once they leave and then re-enter the recording zone. Therefore, and due to the structure of the data set with respect to dates and sites, each trajectory was treated as an independent data point for the statistical analyses, following previous studies (e.g., Schnitzler *et al.* 1987; Britton *et al.* 1997; Holderied *et al.* 2005). However, at least five foraging bats were counted simultaneously, during recording, at each of the foraging sites, consistent with numbers of *P. kuhlii* reported to forage together (Barak & Yomtov 1989). Altogether, our data comprise at least 21 different foraging bats whose flight speed is compared with at least 32 commuting bats. This sets a minimal sample size of different individuals on which generalization from our results can be based.

SELECTING COMMUTING FLIGHTS

Commuting flight was defined as bats using the route at the Road site within the first 15 min after the first bat had emerged from the roost (around 19:35 h). We chose this cut-off (before performing any flight speed calculations) because (i) light conditions (with sunset at 19:31) enabled clear observations of the bats leaving the roost, (ii) all recorded trajectories within these 15 min (58/58) were in the expected commuting direction (i.e. away from the roost), and (iii) the

bats flew in remarkably straight lines (tortuosity mean \pm SD was 1.062 ± 0.069). Subsequent trajectories (from 15 min after start of emergence until 1 h later), on the other hand, were characterized by varied directionalities (only 16/45 flew from the direction of the roost) and by higher tortuosity values (1.821 ± 1.654), and were regarded as foraging flight.

We acknowledge that the foraging data from this site ($n = 45$ trajectories) might thus include some commuters, but this is only conservative when testing for differences between commuting and foraging flight speeds. In fact, these 45 trajectories provide a unique opportunity to compare commuting and foraging flight which occurred at the same location and at the same time (see below).

GENERATING V_{mr} AND V_{mp}

Using the actual morphological data relevant to the time, site and population of the study (as well as air-density data, see below) maximizes the quality of input used for aerodynamic modelling and the quality of its predictions. Therefore, during one of the recording nights (05/08) 15 commuting bats were captured after they had passed through our recording zone, using mist nets (under permit from the Israel Nature and National Parks Protection Authority No. 2008/91373). All bats were measured and released within 90 min from capture time of the first bat. Body mass (mean \pm SD: 5.25 ± 0.49 g) of all bats was measured to the nearest 0.1 g (using ScoutII, Ohaus electronic scales, Pine Brook, NJ, USA) and the right wing was digitally photographed, stretched against a white background. The images were analysed (using ImageJ 1.38x, NIH, USA) to produce the wingspan (0.24 ± 0.006 m) and wing area (0.0082 ± 0.0006 m²), following the definitions of morphological quantities in Norberg & Rayner (1987). These values, together with basal metabolic rate (BMR) and atmospheric conditions were used to calculate the chemical power (*i.e.* the rate of energy consumption) as a function of flight speed for each individual bat. Measurement errors of mass, wing span and wing area were less than 2, 4% and 1% of the mean, respectively (C. Korine, unpublished data).

The most energetically economical flight speeds, V_{mr} and V_{mp} , are a product of the overall chemical power curve (P_{chem}). We used two alternative aerodynamic models to calculate the P_{chem} , Pennycuik's model (FLIGHT software V1.18; covered in detail in Pennycuik 2008; V1.20 is available at www.bio.bris.ac.uk/research/pennycuik/flight120.zip) and Norberg's model (Norberg 1990; see eq. 2.15), a modification of the model by Norberg & Rayner (1987) (see Formulas 4.1 for Pennycuik and 4.2 for Norberg below). Parameters for the models include local air density, morphological data and BMR.

Local air density (ρ) was calculated for each recording hour as:

$$\rho = (p - p_v) / (R_d T) + p_v / (R_v T) \quad \text{eqn 1}$$

Where p is the air pressure, p_v is water vapour pressure and T is the air temperature in K (all kindly provided by the Sede-Boqer

meteorological station). (R_d is the specific gas constant for dry air, $287.05 \text{ J kg}^{-1} \text{ K}^{-1}$ and R_v is the specific gas constant for water vapour, $461.495 \text{ J kg}^{-1} \text{ K}^{-1}$). The calculated local air density ranged between 1.095 and 1.103 kg m^{-3} , and therefore a value of $\rho = 1.1 \text{ kg m}^{-3}$ was used in all subsequent calculations.

The components of the P_{chem} (induced power P_{ind} , parasite power P_{par} and profile power P_{pro}) were calculated as follows:

$$P_{ind} = 1.2 m^2 g^2 / (\rho \pi b^2 V / 2) \quad \text{eqn 2}$$

where m is mass (in kg), b is the wing span (in m) and g is Earth's gravity (in m s^{-2}) and V is flight speed (in m s^{-1}).

$$P_{par} = \rho S_b C_{Db} V^3 / 2 \quad \text{eqn 3}$$

where C_{Db} is the body drag coefficient (set at 0.1), V is speed (in m s^{-1}) and S_b , the body frontal area (in m²), is estimated using an empirical formula:

$$S_b = 0.00813 m^{0.666}$$

$$P_{pro} (\text{Pennycuik}) = 8.4 P_{am} S / b^2 \quad \text{eqn 4.1}$$

where S is wing area (in m²) and P_{am} is the 'absolute minimum power', calculated as the minimum value of the sum of P_{ind} and P_{par} , found with the speed set to V_{mp} .

$$P_{pro} (\text{Norberg}) = \rho S 0.02 V^3 / 2 \quad \text{eqn 4.2}$$

BMR (basal metabolic rate) was calculated following Norberg *et al.* (1993), based on McNab's (1988) regression data for bats:

$$\text{BMR} = 2.63 m^{0.72} \quad \text{eqn 5}$$

All of these components were used to calculate the overall chemical power:

$$P_{chem} = 1.1 [(P_{ind} + P_{par} + P_{pro}) / 0.23 + \text{BMR}] \quad \text{eqn 6}$$

The most energetically economical flight speeds, V_{mr} and V_{mp} , were derived from P_{chem} for each of the 15 individuals independently.

Results

Our analysis is based on 8524 independent single call localizations, which correspond to 7987 speed measurements (segments between each two localizations). These comprise 537 flight trajectories, 58 of which (with 572 segments) were from commuting bats while the remaining 479 trajectories (7415 segments) were from bats foraging at the four foraging sites (Table 1). The mean (\pm SD) number of independent speed

Table 1. Total number of trajectories and segments, as well as number of segments per trajectory, segment duration and segment length (mean \pm SD) for commuting flight and for flight at the four different foraging sites (Lawn, Road, Guesthouse and Tomb)

Site	Trajectories	Segments	Segments per trajectory	Mean segment duration (s)	Mean segment length (m)
Commuting	58	572	9.86 ± 2.58	0.11 ± 0.07	1.04 ± 0.67
Lawn	98	2513	25.64 ± 18.84	0.14 ± 0.09	0.70 ± 0.50
Road	45	652	14.49 ± 6.43	0.15 ± 0.09	0.77 ± 0.47
Guesthouse	83	961	11.58 ± 4.85	0.17 ± 0.12	1.02 ± 0.76
Tomb	253	3289	13.00 ± 5.24	0.16 ± 0.09	1.13 ± 0.69

measurements (segments) per trajectory was 9.86 ± 2.58 for commuting trajectories and between 11.58 ± 4.85 and 25.64 ± 18.84 for foraging trajectories at the different foraging sites. The mean distance between consecutive localizations (mean segment length) ranged from 0.70 to 1.13 m at the different recording sites (Table 1).

FLIGHT SPEED OF COMMUTING AND FORAGING BATS

P. kuhlii flight (trajectory) speed measured ranged between 3.4 m s^{-1} and 11.6 m s^{-1} . Commuting trajectories were significantly faster than foraging trajectories ($9.30 \pm 1.22 \text{ m s}^{-1}$ vs. $6.74 \pm 1.16 \text{ m s}^{-1}$, respectively, $F_{1,535} = 248.3$, $P < 0.001$, Fig. 2a), had lower tortuosity values (1.06 ± 0.07 vs. 2.51 ± 4.17 , respectively, $F_{1,535} = 7.1$, $P = 0.008$, Fig. 2b) and a lower height above-ground ($2.7 \pm 0.9 \text{ m}$ vs. $4.7 \pm 1.7 \text{ m}$, respectively, $F_{1,535} = 73.4$, $P < 0.001$, Fig. 2c). Displacement values were similar for the two groups ($10.19 \pm 4.64 \text{ m}$ vs. $9.8 \pm 3.08 \text{ m}$, respectively, $F_{1,535} = 0.25$, $P = 0.61$) confirming that commuting and foraging trajectories were traced over similar ranges.

To rule out the possibility that commuting flight speed was faster only because foraging flight incorporated more turns (suggested by its higher tortuosity values), a comparison was made between the commuting flight trajectories and a subset of 'equivalently straight' foraging flight trajectories. To create this subset, the foraging trajectories with the highest tortuosity values (i.e. those including turns) were filtered out so that the mean tortuosity value of the foraging subset was equal to the mean commuting tortuosity (1.062 ± 0.048 and 1.062 ± 0.069 , respectively). While the subset's flight speed ($n = 318$, $7.11 \pm 1.08 \text{ m s}^{-1}$) was slightly faster than the original foraging flight speed ($n = 479$, $6.74 \pm 1.16 \text{ m s}^{-1}$), it was still very low compared to the measured commuting speed ($9.30 \pm 1.22 \text{ m s}^{-1}$; $F_{1,374} = 193.0$, $P < 0.001$), ruling out lower tortuosity as the cause of the difference between both contexts. Furthermore, had tortuosity been the reason for this difference, one might expect it to explain a large amount of the variation in flight speed among foraging trajectories. However, tortuosity does not explain much of the variance in speed, neither over all foraging trajectories ($r_p^2 = 0.09$, $P < 0.001$) nor within sites (Guesthouse: $r_p^2 = 0.032$, $P = 0.108$, Road: $r_p^2 = 0.053$, $P = 0.125$, Lawn: $r_p^2 = 0.018$, $P = 0.190$, Tomb: $r_p^2 = 0.02$, $P = 0.024$). A similar analysis is inapplicable for commuting trajectories since their tortuosity level is relatively constant (ranging between 1.01 and 1.38).

DIFFERENCES BETWEEN FORAGING SITES

In addition to the differences between foraging and commuting flight, flight trajectories in the four foraging sites differed in speed ($F_{3,475} = 94.0$, $P < 0.001$, Fig. 2d), tortuosity ($F_{3,475} = 38.7$, $P < 0.001$, Fig. 2e) and height above-ground ($F_{3,475} = 204.4$, $P < 0.001$, Fig. 2f). Among the foraging sites, the Lawn was characterized by exceptionally high tortuosity and relatively slow speeds (see Fig. 2d,e). Speed was positively correlated with height above-ground over all foraging trajectories ($r_p^2 = 0.26$, $P < 0.001$). However, since commuting flight was

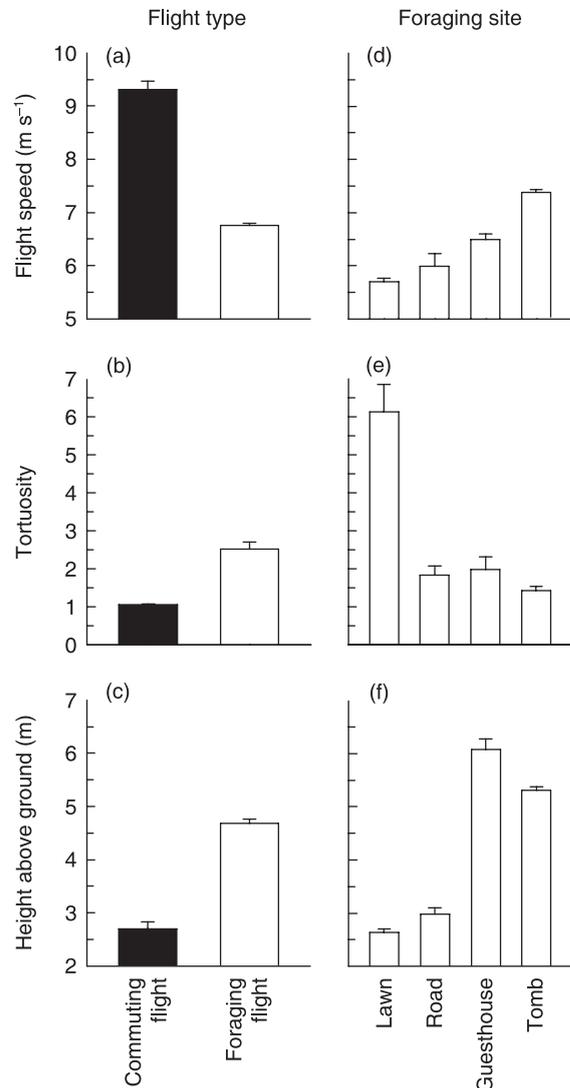


Fig. 2. (a)–(c) Analysis of flight trajectories of *Pipistrellus kuhlii* bats during commuting ($N = 58$) and foraging ($N = 479$) flight. (a) Mean trajectory speed, (b) tortuosity and (c) height above-ground. Differences between foraging and commuting are significant for all three variables (all P values < 0.009). (d)–(f) Differences in flight behaviour of *Pipistrellus kuhlii* among all four foraging sites. (d) flight speed, (e) tortuosity and (f) height above-ground. Effect of foraging site on all three variables is significant (all P values < 0.001). Means + 1 SE error bars are shown.

lower than foraging flight (Fig. 2c), height cannot explain the higher speed of commuting flight (Fig. 2a).

COMMUTING AND FORAGING AT THE SAME SITE

In addition to our main analysis, our data for the Road site enables us to compare between commuting and foraging behaviour performed during the same time at the same site, thereby controlling for possible time or site-specific differences. Figure 3 shows the data for one recording session (05/08) split into its first 15 min (which was defined as commuting flight; left panels A–C) and the following hour of recording (right

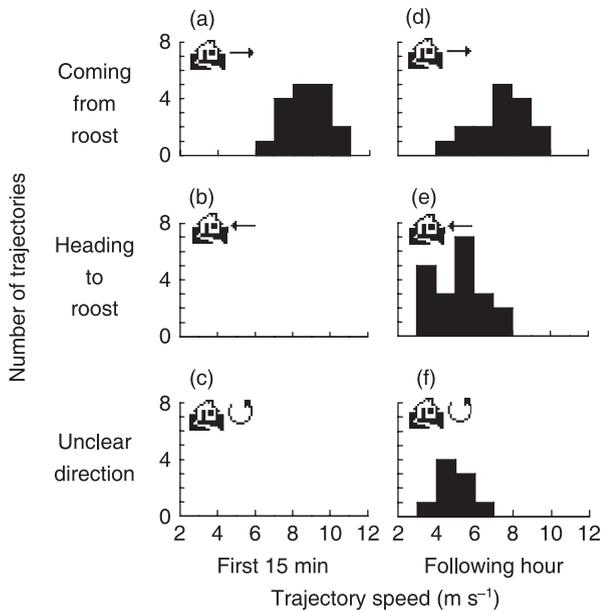


Fig. 3. The flight-speed distribution of trajectories recorded on one night at the commuting site (Road) during the first 15 min of commuting from the roost (left panels a–c) and the following hour of recording (right panels d–e). Trajectories are divided according to their directionality: (a) and (d) in the direction corresponding to leaving the roost. (b) and (e) in the opposite direction (i.e. heading towards the roost). (c) and (f) – trajectories with an unclear direction, including turning.

panels D–F). Recall that our 15-min cut-off time was chosen because all of the trajectories were in the commuting direction (i.e. from the roost, Fig. 3a) and rather straight (see above), while subsequent trajectories were characterized by variable directionality (Fig. 3e–f) and higher tortuosity (see above). The flight speed distribution shown in Fig. 3 corroborates our choice of a 15-min cut-off, with trajectories which are in the general direction of the roost (Fig. 3e) and circling trajectories (Fig. 3f) being slower than commuting flight (Fig. 3a). Importantly, even among post-cut-off trajectories, those heading away from the roost (Fig. 3d; $7.38 \pm 1.48 \text{ m s}^{-1}$) are faster than those heading in the general direction of the roost (Fig. 3e; $5.27 \pm 1.25 \text{ m s}^{-1}$; $t_{34} = 4.64$, $P < 0.0001$). Given the early time of recording (~20:00), trajectories in the general direction of the roost are more likely to be foraging flights than bats commuting back to the roost (Fig. 3e). Apparently, these individuals were already foraging at the site while others were still commuting, showing that commuting flight speed is higher than foraging flight speed regardless of site, time, or light conditions. Indeed, the last trajectory leaving the roost at high speed occurred 42 min after the cut-off.

COMPARING MEASURED AND PREDICTED FLIGHT SPEED

Predictions according to Pennycuik. Measured foraging flight speed was higher than V_{mp} and measured commuting flight speed was slower than V_{mr} (see Table 2, Fig. 4). Whereas mean

Table 2. Comparison of aerodynamic model predictions based on 15 bats captured *in situ*, with *Pipistrelle* flight speed measured in the field during foraging (V_{mp} context) and commuting (V_{mr} context). Means (m s^{-1}) \pm SD are presented

	Pennycuik	Norberg	Field measurement
V_{mp}	5.30 ± 0.14	3.18 ± 0.10	Foraging: 6.75 ± 1.16
V_{mr}	10.32 ± 0.18	5.03 ± 0.12	Commuting: 9.31 ± 1.22

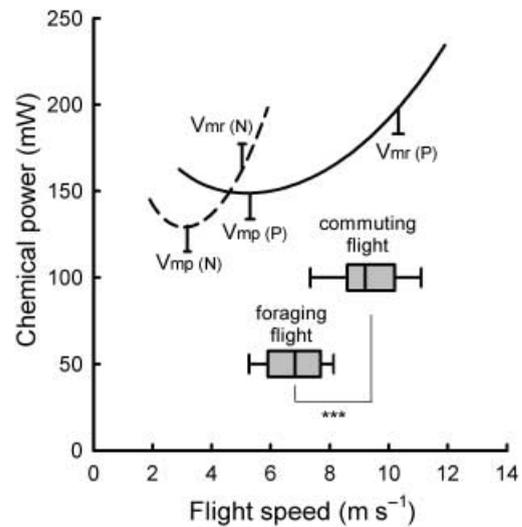


Fig. 4. Chemical power curves for *Pipistrellus kuhlii* generated using the mean values of wing morphology and body mass of the study population, following aerodynamic models by Pennycuik (solid line, $V_{mp(P)}$ and $V_{mr(P)}$) and Norberg (dashed line, $V_{mp(N)}$ and $V_{mr(N)}$). Mean predicted values of V_{mp} (minimal power speed) and V_{mr} (maximal range speed) are indicated for each model by a vertical line and the population SD with horizontal lines. Box plots indicate the 10th, 25th, 75th and 90th percentiles as well as the median flight speed of all commuting and foraging trajectories.

foraging speed was $6.75 \pm 1.16 \text{ m s}^{-1}$, the predicted V_{mp} (for our 15 captured bats) was $5.30 \pm 0.14 \text{ m s}^{-1}$ (range: 5.02 to 5.50 m s^{-1}). Mean commuting speed was $9.31 \pm 1.22 \text{ m s}^{-1}$ while predicted V_{mr} was $10.32 \pm 0.18 \text{ m s}^{-1}$ (range: 9.88 to 10.60 m s^{-1}).

Predictions according to Norberg. Predicted V_{mp} was $3.18 \pm 0.10 \text{ m s}^{-1}$ (range: 2.97 to 3.34 m s^{-1}) and the predicted V_{mr} was $5.03 \pm 0.12 \text{ m s}^{-1}$ (range: 4.77 to 5.25 m s^{-1}). All these values are markedly below the observed commuting speeds ($9.31 \pm 1.22 \text{ m s}^{-1}$) and also well below the foraging speed ($6.75 \pm 1.16 \text{ m s}^{-1}$).

Discussion

Our results show that bats fly at different speeds in different behavioural contexts, flying faster when commuting than when foraging. This supports our first (qualitative) prediction, and may occur because commuting presents a context where flying at a higher speed is energetically more efficient as was also suggested by Houston (2006).

Our results are comparable with previous studies of bat flight speed that used methods such as videogrammetry, photogrammetry, Doppler radar and acoustic tracking (e.g. Schnitzler *et al.* 1987; Salcedo *et al.* 1995; Holderied 2001; Holderied *et al.* 2005; see Holderied & Jones 2009, for a review). Schnitzler *et al.* (1987) reported that foraging *P. kuhlii* in Yugoslavia, measured using multi-exposure photography, flew at 3.5–5 m s⁻¹. The disagreement with our foraging flight speed (6.74 ± 1.16 m s⁻¹) could arise from morphological (different subspecies) or methodological differences. First, using one camera (Schnitzler *et al.* 1987) gives a 2D projection of the 3D flight track (see Holderied & Jones 2009) which might underestimate travelled distance and result in lower speed estimation relative to a 3D trajectory produced by acoustical flight-tracking (this study). Second, flight speed differences may be attributed to site-specific factors, as observed in this study (see Fig. 2d) and in other studies (e.g. Britton *et al.* 1997; Jacobs 1999). Site structure and local prey composition and abundance will determine how bats manoeuvre through the site and in particular the need for making sharp turns, which affects their flying speed at each site (Jacobs 1999). Using modern technology to track 3D movement was recently used to measure swimming speeds of foraging short-finned pilot whales based on their echolocation calls (Soto *et al.* 2008), broadening the range of taxa and physical environments of 3D speed measurements to test optimal speed theory.

To the best of our knowledge, despite the growing recognition of the need to test aerodynamic predictions on a given species in more than one ecological context (Hedenström & Ålerstam 1995; Houston 2006), predictions comparing commuting and foraging flight speed in free-ranging bats were directly tested only twice (Jones & Rayner 1989; Britton *et al.* 1997). Similar to our results, in both cases the measured commuting speed was faster than foraging speed. Nevertheless, even the measured foraging speeds in both studies were higher than the V_{mr} values predicted from aerodynamic models (see also Jones & Rayner 1991). Such substantial differences between predictions and measurements raise questions about the relevance of power curves alone as a useful predictor of flight speed of free-ranging bats (see in particular Britton *et al.* 1997).

In contrast to the disagreements highlighted in the previous paragraph, the data presented here seems to be remarkably consistent with quantitative predictions from Pennycuik's aerodynamic model, supporting our prediction that energetic considerations lead bats to energetically optimal flight speeds as predicted by aerodynamic models. However, before discussing how well flight speed in different behavioural contexts is predicted by aerodynamic models, correct identification of these contexts must be established and influences on flight speed other than energetic considerations need to be ruled out.

Foraging flight. Attacks on insects are accompanied by characteristic changes in the echolocation sequence (feeding buzzes). Trajectories containing such sequences were

identified and excluded from the analysis, but their occurrence is a clear indicator of active foraging. Social interactions or displays are unlikely to have influenced foraging speeds, because, while several individuals were present at all times, bats chasing each other were not observed and, in addition, no advertisement calls, typically emitted by male pipistrelles for mate attraction, were recorded. Other factors influencing foraging speed might be: (i) the extra energy needed for curved search flights, which will affect the power curve (reducing the optimal speed); (ii) the available manoeuvring space at the foraging site; (iii) the need to be able to initiate abrupt narrow pursuit turns (reducing foraging speed); (iv) the density and type of prey (e.g. by affecting prey encounter rate; see Gerritsen & Strickler 1977; Speakman & Bryant 1993). All of these will affect the function of flight speed on energy intake rate, and therefore the optimal foraging speed (see Hedenström & Ålerstam 1995).

In this study, foraging flight speed, tortuosity and height above-ground differed significantly among sites (Fig. 2d,e and f), reflecting perhaps site structure, environmental clutter and prey community differences (Jacobs 1999). The 'Lawn' site, for instance, was characterized by exceptionally high tortuosity and relatively slow trajectories, probably because flight was confined by surrounding houses and vegetation more than at other foraging sites. The design of our study, however, limits our data in this respect and prevents us from drawing strong conclusions.

Commuting flight. Commuting flight, (emerging bats recorded at a distance of ~90 m from their roost) was straight, fast and relatively low above-ground. When bats need a surplus energy net gain, beyond maintenance, they might fly faster than V_{mr} (Hedenström & Ålerstam 1995; Houston 2006). In contrast, bats in our study were already after breeding and probably not yet building fat reserves for migration or hibernation, and therefore our data very likely represents a case where energy is needed only for maintenance, predicting V_{mr} (and not a higher speed) as the commuting speed.

Reasons for fast emergence flight, other than minimizing energetic expenses, might be: (i) minimizing the risk of predation by visually guided predators during dusk (Jones & Rayner 1989; Britton *et al.* 1997); (ii) a need for timely arrival due to a (potential) short-lived peak in prey abundance during dusk (Jones & Rayner 1989; Britton *et al.* 1997; Houston 2006); or because (iii) prey resources are exhaustible. However, bat emergence behaviour (Fig. 3) does not support these three competing explanations: First, emergence with high flight speeds lasted for about 1 h, while predation avoidance (alternative i) predicts that late commuters (Fig. 3d) will fly slower. More importantly, fast emerging bats flew together with slow foraging individuals for 42 min, under the same predation pressure (if any). Alternatives (ii) and (iii) would result in a race towards feeding grounds, but the drawn-out emergence lasting 1 h speaks against that. Although we do not have direct estimation of prey depletion rate, bats foraging activity lasted (with a similar apparent intensity) long after we stopped measuring, suggesting prey

depletion is not the explanation for the fast commuting speed.

Therefore, considerations of energy expenditure seem to be the most plausible explanation to the fast flight speed of the late-emerging bats. Consequently, we conclude that emerging bats were indeed commuting in a ' V_{mr} context'. It is also valuable to compare the observed commuting and foraging flight speed with the quantitative predictions made by the aerodynamic models in order to test their predictive accuracy.

ENERGETIC CONSEQUENCES OF DEVIATION FROM PREDICTED FLIGHT SPEED

Flight speeds predicted by Norberg's model were half an order of magnitude slower than measured speeds, rejecting this model as an accurate predictive tool for our system (see below) and potentially in other systems as well (Jones & Rayner 1989; Winter 1999). The deviations from Pennycuick's predictions were markedly smaller and we refer to this model exclusively hereafter. In agreement with the prediction from optimal flight theory that flight speed is selected to maximize either net energy gain per unit time or the foraging gain ratio (Blake 1985; Hedenström & Ålerstam 1995), foraging flight speed was close to but faster than the predicted V_{mp} (6.7 vs. 5.5 m s⁻¹; see Fig. 4). This 18% (of measured speed) difference is robust to measurement errors, which are an order of magnitude smaller (1.72% ± 0.36% for foraging flight). As can be intuitively deduced from the chemical power curve's flat shape in the vicinity of V_{mp} (Fig. 4), the energetic costs of the observed deviations of foraging flight from V_{mp} are small, allowing energetic intake consideration to play a role (Winter 1999). Indeed, the deviation in measured foraging flight speed from Pennycuick's V_{mp} results in 4 mW of extra expenditure (calculated for chemical power at mean speed), increasing power by a mere 2%. In contrast, foraging at the measured flight speed of commuting bats would have caused a much higher energetic cost (an increase in power of 19% relative to V_{mp}).

While the range of the population V_{mr} values overlaps the observed commuting flight speed, the mean V_{mr} value is higher than the mean commuting speed. However, the energetic costs of this deviation are rather low: For any given commuting distance, the additional cost of covering that distance at the observed commuting flight speed (9.3 m s⁻¹), instead of at the calculated V_{mr} for the population (10.32 m s⁻¹) is only 1.2% of the cost at V_{mr} . In contrast, covering the commuting distance while flying at the observed foraging speed (6.75 m s⁻¹) would have resulted in a much higher additional cost (19% of the cost at V_{mr}), due to a 1.5-fold flight duration. For example, a bat commuting at V_{mr} will cover 4 km in 388 s at 196 mW, a bat commuting at the observed commuting speed in 430 s at 179 mW and a bat commuting at the measured foraging speed in 593 s at 153 mW. Four kilometres is roughly 10-fold the distance between the roost and our most distant foraging site (Tomb), and is probably an overestimation even if bats intermittently returned to the roost during the night (although all adult female bats caught

were post-lactation). Even if we assume such a large commuting distance, flying at the observed commuting speed (instead of at V_{mr}) would only result in an extra 0.9 J per night (increase in commuting costs of 1.1%), so it is reasonable to conclude that observed commuting flight was energetically similar to flying at V_{mr} . Some possible explanations for a flight speed lower than V_{mr} are the low flight height (< 3 m), the presence of obstacles close to the commuting corridor and the fact that the corridor was not linear, all of which might result in a slightly slower speed compared to commuting at greater height and in the absence of obstacles.

CONCLUSIONS

Taken together, our data show that *P. kuhlii* bats seem to use flight speeds similar to the energetically optimal flight speed predicted for the two contexts studied here. While there is remarkable agreement between the predictions derived from Pennycuick's aerodynamic model and our results, Norberg's model (1990) predicts much slower flight speeds and is not supported by our data (see Rayner 1999, for a detailed discussion on the limitations of the different models). When possible, generating and testing distinct predictions for flight speed of the same population in different contexts may assist researchers to overcome an inherent challenge in this field. Namely, when trying to explain discrepancies between measured and predicted speed, it is difficult to distinguish between the effect (on flight speed) of factors external to aerodynamic models and inadequacies in the models themselves (Hedenström & Ålerstam 1995). Testing a set of context-dependent quantitative predictions against the different measured speed values can yield a qualitative conclusion about the relevance of aerodynamic theory for the studied organism. This may be essential for understanding the ecological relevance of an organism's flight speed, as well as for validating and improving existing models. Our analysis of two ecological flight contexts supports the notion that the Pennycuick's aerodynamic model can indeed make reasonable predictions about context-dependent flight speed of flying vertebrates.

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