

ENERGETIC CONSEQUENCES OF FLIGHT SPEEDS OF FORAGING RED AND HOARY BATS (*LASIURUS BOREALIS* AND *LASIURUS CINEREUS*; CHIROPTERA: VESPERTILIONIDAE)

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Summary

We used Doppler radar readings of the flight speeds of foraging, lactating female *Lasiurus borealis* ($N=826$) and *Lasiurus cinereus* ($N=544$) to test morphologically based predictions about their flight performance. Both species flew at speeds ($V=6.7$ and 7.7 ms^{-1} , respectively) that differed significantly from predicted minimum power speed (V_{mp} ; 4.0 and 5.08 ms^{-1} , respectively) or predicted maximum range speed (V_{mr} ; 5.25 and 6.69 ms^{-1} , respectively), perhaps reflecting the active pursuit of moths

performing evasive manoeuvres. Estimates of costs of flight and lactation are combined with data on prey size together with encounter and capture rates to illustrate the energetic benefits accruing to these species when they forage in concentrations of insects.

Key words: energy balance, costs of flight and lactation, food intake, bats, *Lasiurus borealis*, *Lasiurus cinereus*.

Introduction

The aerodynamic theory of vertebrate flight (e.g. Pennycuik, 1969, 1975, 1989; Rayner, 1979; Norberg, 1990) explains the forces that must be overcome to fly and predicts flight speeds that maximize, for a given amount of energy, either the time spent in the air (minimum power speed V_{mp}) or the distance flown (maximum range speed V_{mr}). Flight speeds are of ecological consequence for several reasons. They influence the energy budget for feeding offspring (R. Å. Norberg, 1981) and affect the daily energy balance, foraging efficiency (Blake, 1985) and endurance (Pennycuik, 1978; Carpenter, 1985). Differences in flight costs amongst species should be reflected in their flight speed distributions. When all other things are equal, species with higher flight costs should have smaller variance around their mean flight speed than species with lower flight costs. Owing to both the benefits of flying at the optimal speed for a given situation and the costs of flying at different speeds, species with higher flight costs should benefit more from more consistent flight speeds (i.e. with less variance).

Predicted flight speeds can be tested against real flight speeds provided that large numbers of accurate readings are available (e.g. Pennycuik, 1982, 1983; Blake *et al.* 1988) with which to investigate the effects of individual variation.

However, measurement of flight speeds during flapping flight has concentrated on population rather than on individual data (e.g. Blake *et al.* 1988; Gill, 1985; McLaughlin and Montgomery, 1985). Furthermore, many factors can affect flight speed. For example, insect abundance and patterns of distribution affect the patterns of habitat use by foraging bats (e.g. Barclay, 1985; Rydell, 1989; Hickey and Fenton, 1990; Aldridge and Brigham, 1991). Although flight speeds will directly affect the time and energy budgets of these predators, there are few published data on this topic.

In this study, we measured the flight speeds of two species of bats as they foraged and used these data (1) to test morphologically based predictions about flight performance, and (2) to examine the relationship between prey density and flight performance. We then used predictions of the costs of flight to examine the behavioural consequences of the energetic situation facing the bats we studied, namely the importance of flight time, prey density and the costs of lactation.

At a study site in southwestern Ontario, Canada, two species of aerial-feeding bats of the genus *Lasiurus* are sympatric (i.e. forage in the same places at the same time; Hickey and Fenton, 1990; Acharya and Fenton, 1992; Hickey, 1993). *Lasiurus borealis* (the red bat) is about half the body mass of *Lasiurus*

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cinereus (the hoary bat; Norberg and Rayner, 1987) and, at our study site, both feed mainly on moths. Over a 3 year period at our study site, the two species showed feeding niche overlaps of 0.261, 0.377 and 0.362 (Hickey *et al.* 1996), suggesting a degree of similarity in spite of size differences between the two species. We used morphological data from *L. borealis* and *L. cinereus* to generate predictions about their flight performance (see Table 1) and compared predicted flight speeds with values measured for foraging bats.

Materials and methods

We conducted our study at two sites within Pinery Provincial Park in southwestern Ontario, Canada (81°80'W, 43°15'N), where *Lasiurus borealis* Müller and *Lasiurus cinereus* (Palisot de Beauvois) hunt insects attracted to streetlights. On 6–10 July 1990, we measured flight speeds to the nearest 0.05 m s^{-1} using a Doppler radar system (see Blake *et al.* 1988, for details of calibration and use) at the entrance to the Riverside camp ground and at the Main Gate to the park. Blake *et al.* (1988) reported that readings of flight speeds could not be measured from bat-sized animals flying more than 10° outside the long axis of the radar. We noted flight speeds to the nearest 0.1 m s^{-1} from the radar digital output, also noting the time and the identity of bats previously marked using coloured bands. We used an Anemo anemometer (Germany) to measure wind speed to the nearest 1 m s^{-1} , 2.0–2.5 m above the ground during the experimental period. We also observed the bats visually as they flew in the lighted areas and monitored their echolocation calls on narrowband bat detectors tuned to 20 kHz (search phase calls of *Lasiurus cinereus*) and 40 kHz (calls of *Lasiurus borealis*). Flight speed data were obtained from both individually marked and unmarked bats at a time when females were lactating and before their young were volant. We used morphological data (see Table 1) obtained from the two species at the study site to generate predictions about their flight speed performance.

V_{mp} and V_{mr} were predicted using equations 2.29 and 2.30 from Norberg (1990), assuming a constant drag coefficient of 0.02 (Rayner, 1979) and an aerofoil efficiency constant k of 1.2 (after Pennycuik, 1975, 1989). Our calculations did not include inertial power components, which can be neglected as a significant factor in medium and fast forward flight (Norberg, 1990). R. Å. Norberg's (1981) model for predicting the optimal flight speeds of birds feeding young was modified to predict an optimal speed for maximal milk production as opposed to maximal delivery of food to nestlings (V_{gain}). The energy required for maximal milk production was calculated using the allometric equations of Hanwell and Peaker (1977). We used equation 6.5 (Norberg, 1990) to calculate turning radii and banking angle using the morphological data in Table 1.

The availability of prey was measured as the numbers of moths over 5 mm in length (corresponding to the size range eaten by the bats; Hickey and Fenton, 1990; Acharya and

Fenton, 1992; Hickey *et al.* 1995) taken hourly during the experimental period from an ultraviolet light trap consisting of a blacklight tube in the middle of four cross veins that directed the light away from the tube. This apparatus was held in place above a funnel which directed insects into a metal bucket containing ethanol. To avoid altering the distribution or abundance of prey where the bats foraged, this light trap was placed in a clearing along a high-voltage power line about 200 m from the study site.

We investigated possible correlations between flight speed, individual, food abundance and time of flight using linear and circular regressions and analysis of variance (ANOVA). All analyses of flight data were carried out by species and by individual. Since all bats whose flight speeds we measured were not always present, we carried out a the three-way ANOVA on data for individuals that were present on more than one night and at more than one time on these nights, to investigate the possible dependence of flight speed on date and time of flight. The times of night were taken as almost hourly distributions converted to radians to associate flight speeds with insect densities and perform the analysis with circular statistics. Correlations between flight speed, individual and date were assessed using linear procedures (Zar, 1983). Correlations between flight speed and time were calculated with non-parametric (rank) circular statistics (Batschelet, 1981, pp. 193–195). We used two-tailed *t*-tests to compare the observed mean speeds for each species with predicted speeds and performed an *F*-ratio test of speed distribution variances to detect any significant differences in speed distribution around the mean values between the two species. Values are given as means \pm 1 s.d. unless otherwise stated.

Results

The female bats whose flight speeds we measured were actively hunting, pursuing, attacking and sometimes catching insects (usually moths). We both observed chases and heard, using the bat detector, feeding 'buzzes'. These are echolocation calls produced at high pulse repetition rates associated with attacks on airborne targets (Griffin *et al.* 1960). Other studies have demonstrated that foraging *L. borealis* and *L. cinereus* catch insects on about 40–60% of their attacks (Hickey and Fenton, 1990; Acharya and Fenton, 1992; Hickey, 1993). Throughout our study, wind speeds were always less than 0.5 m s^{-1} and never appeared to influence the behaviour of the bats or their insect prey. There were no differences in wind conditions between the observation sites and the surrounding areas (within 1 km).

Flight speeds for *L. borealis* ($N=826$) and *L. cinereus* ($N=544$) ranged from 3.8 to 10 m s^{-1} and from 4.0 to 12 m s^{-1} , respectively, and showed truncated normal distributions (Fig. 1). The differences between mean and median flight speeds were not significant, allowing the use of parametric statistics in further analyses. A one-way ANOVA revealed statistically significant differences between the flight speeds of

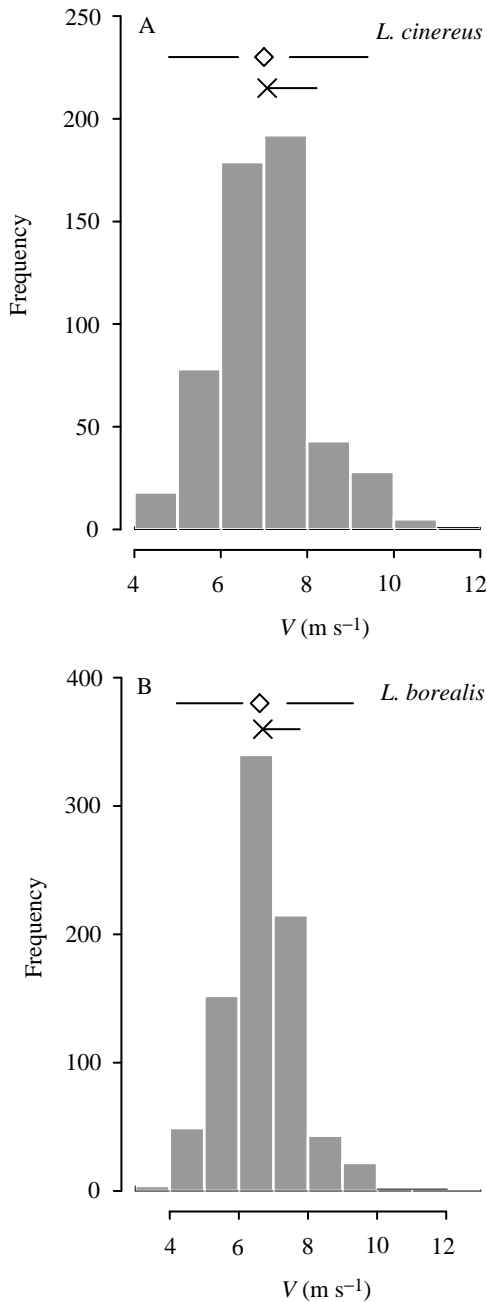


Fig. 1. Histograms, giving mean, standard deviation and quartile distribution, of the flight speeds of female *Lasiurus cinereus* (A) and *Lasiurus borealis* (B). The \times marks the mean speed and the attached horizontal line is the standard deviation. The \diamond is the median speed, the line to its left the first quartile, the line to its right the fourth quartile (cf. Tufte, 1983).

individuals of both species (for *L. cinereus*, $F=3999.13$, d.f.=1, 4, $P<0.001$; and for *L. borealis*, $F=1327.4$, d.f.=1, 8, $P<0.001$). The individual differences were not significant if the measurements for individuals recorded on less than 10 occasions were eliminated from the analyses ($N=13$ for *L. borealis* and $N=12$ for *L. cinereus*). There was no significant correlation between mean flight speeds and time of flight for

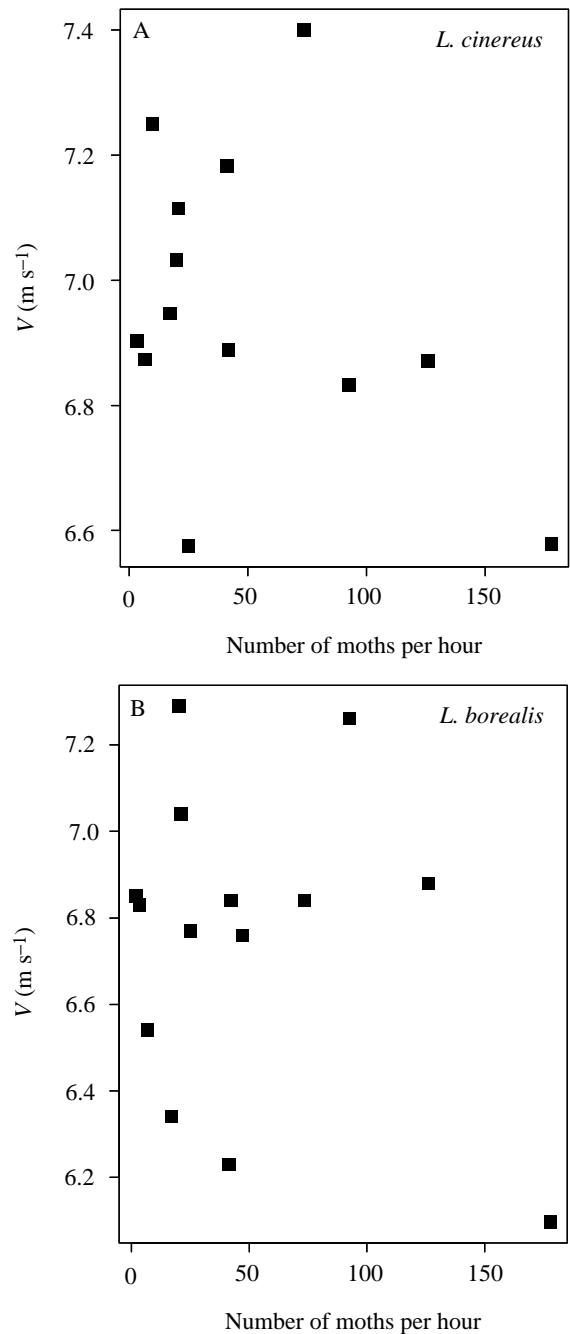


Fig. 2. Relationship between hourly measures of insect numbers and bat flight speeds from 6 to 10 July 1990 for *Lasiurus borealis* and *Lasiurus cinereus*.

either species (*L. borealis*, $N=813$, $r=0.06$, $U_n=0.18$, $U_{0.05}=4.89$, $P>0.05$; *L. cinereus*, $N=532$, $r=0.14$, $U_n=0.97$, $U_{0.05}=4.90$, $P>0.05$; Batschelet, 1981). Mean flight speeds were not significantly different for date or site, and we found no significant interaction between individual, time and date for either species. There were significant inter-individual differences between two *L. borealis* ($F=370.852$; d.f.=1, 1; $P=0.037$) and two *L. cinereus* ($F=9660.935$; d.f.=1, 1; $P=0.037$). *Lasiurus borealis* showed significantly more

variance in flight speed than *L. cinereus* ($F=1.157$; d.f.=544,826; $P=0.05$), $1.34(\text{m s}^{-1})^2$ and $1.31(\text{m s}^{-1})^2$, respectively.

The numbers of moths trapped per hour was not significantly correlated (Zar, 1983) with the mean hourly flight speeds of foraging *L. borealis* or *L. cinereus* (Fig. 2), for *L. borealis*, $r=-0.24$, $t=-0.88$, $P=0.40$; for *L. cinereus*, $r=0.35$, $t=-1.25$, $P=0.24$.

The mean flight speeds we measured (Table 1) differed significantly from the predicted values for V_{mp} and V_{mr} . The two species will differ in the cost of transport, C , which is the power (P) required to transport a unit of body weight (mg), where m is body mass and g is the acceleration due to gravity, over a unit of distance ($C=P/mgV$; Tucker, 1970; Norberg, 1990). Our data indicate that the cost of transport is lower for *L. borealis* than for *L. cinereus* at some speeds, but not at others (Table 1; Fig. 3). The calculated turning radii of the two

Table 1. Morphological parameters measured for female *Lasiurus borealis* and *Lasiurus cinereus* caught at the study site

	<i>Lasiurus borealis</i>	<i>Lasiurus cinereus</i>
<i>N</i>	9	3
Mass (kg)	0.013±0.001	0.031±0.001
Wing span, <i>B</i> (m)	0.293±0.001	0.356±0.002
Wing area, <i>S</i> (m ²)	0.013±0.001	0.019±0.001
Wing loading, <i>Q</i> (N m ⁻²)	10.55±0.584	15.62±0.361
Aspect ratio	6.7±0.70	8.1±1.16
Mean flight speed, <i>V</i> (m s ⁻¹)	6.7±1.07	7.7±1.14
Total observations	826	544
<i>P</i> (W)	0.150	0.375
V_{mp} (m s ⁻¹)	4.0* ¹	5.08* ²
P_{mp} (W)	0.068	0.223
V_{mr} (m s ⁻¹)	5.25* ³	6.69* ⁴
P_{mr} (W)	0.109	0.373
V_{gain} (m s ⁻¹)	10.0* ⁵	13.0* ⁶
P_{gain} (W)	0.224	0.746

*Indicates a significant difference from mean flight speed at $P<0.001$ (Student's *t*-test).

¹ $t = 72.896$; ² $t = 40.479$; ³ $t = 38.896$; ⁴ $t = 7.709$; ⁵ $t = 89.281$; ⁶ $t = 120.124$.

V_{mp} is the minimum power speed, V_{mr} the maximum range speed and V_{gain} is the optimal speed for maximum milk production. P_{mp} , P_{mr} and P_{gain} are the predicted power requirements for these speeds. V_{mr} is calculated from equation 2.30 in Norberg (1990) and P_{mr} by substituting V_{mr} for V in equation 2.18 (Norberg, 1990). V_{mp} was calculated from equation 2.29 (Norberg, 1990) and P_{mp} by substituting V_{mp} for V in equation 2.18 (Norberg, 1990). Inertial power, which can be neglected at medium and fast forward speeds (Norberg, 1990) is not included. Calculations for V_{gain} and P_{gain} were made from a modified version from the model described by R. Å. Norberg for predicting the flight speeds of birds feeding young.

Mean flight speeds (V) recorded using Doppler radar are shown along with predicted flight speeds (V_{mp} , V_{mr} , V_{gain}).

The predicted power requirements for flight (P) are also shown and are used to calculate expected flight speed values.

Means are shown ± 1 S.E.M.

species (Fig. 4) predict that *L. borealis* has a narrower turning radius than *L. cinereus*.

Discussion

Our values for the flight speeds of *Lasiurus borealis* (mean $6.7\pm 1.1 \text{ m s}^{-1}$) and *L. cinereus* ($7.7\pm 1.1 \text{ m s}^{-1}$) are higher than others reported in the literature. Patterson and Hardin (1969) found that *L. borealis* flew at $2.8\text{--}6.04 \text{ m s}^{-1}$ (mean 3.5 m s^{-1}), and Hayward and Davis (1964) reported a range of

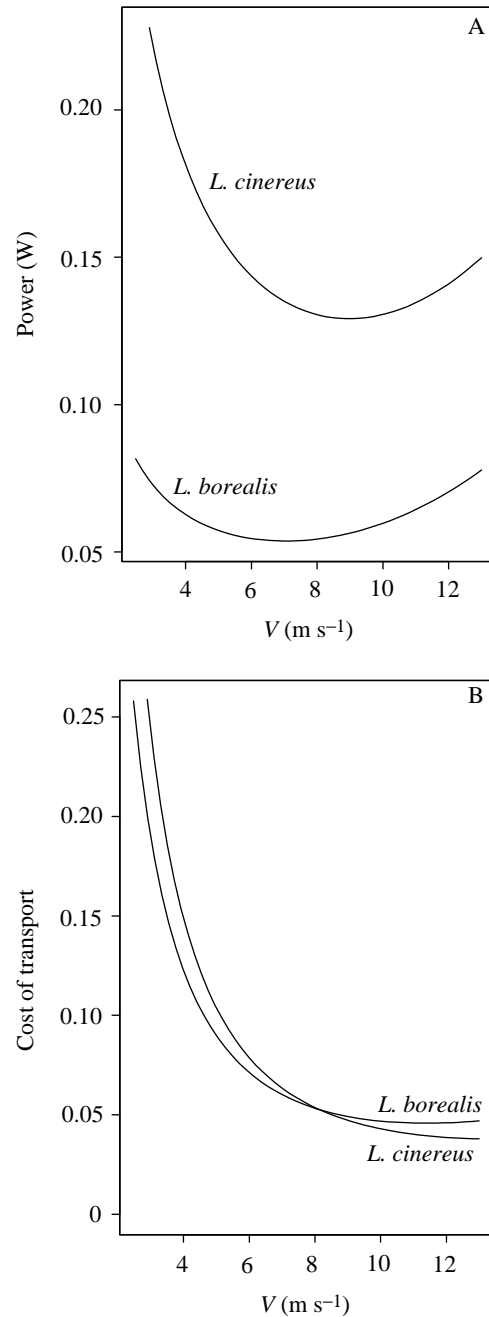


Fig. 3. The power required for flight (A) and cost of transport (B) for female *Lasiurus cinereus* (Hoary) and *Lasiurus borealis* (Red) flying at a range of speeds.

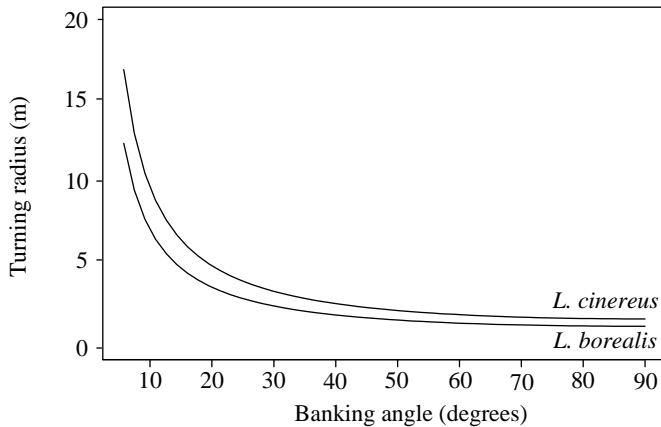


Fig. 4. The turning performance of *Lasiurus borealis* and *Lasiurus cinereus* as a function of banking angle.

4.3–5.9 m s⁻¹ (mean 5.02 m s⁻¹) for *Lasiurus cinereus* both flying down enclosed corridors. We suspect that these discrepancies reflect the settings in which the bats were studied. Our radar equipment permitted us to obtain many accurate readings under natural conditions, whereas these slower speeds were from captive animals flying in artificial settings. This is supported by an average estimate of 7.2 m s⁻¹ for *L. cinereus* foraging for insects attracted to lights in Hawaii (Belwood and Fullard, 1984). Our data for *L. borealis* and *L. cinereus* differ from those used by Norberg and Rayner (1987; for *L. borealis* they used 0.0167 kg, 0.281 m wingspan, and 6.7 aspect ratio; for *L. cinereus*, they used 0.0330 kg, 0.398 m wingspan, and 8.1 aspect ratio) but fall within the range of values reported for the two species (e.g. Shump and Shump 1982a,b). Our data support the predicted relationship between variance in flight speed and cost of flight; with lower flight costs, *L. borealis* showed significantly higher variance in flight speed than *L. cinereus* (Fig. 1).

Different biomechanical models may give different results for the same data set. For example, our data on the morphology of *L. borealis* (Table 1) gave a predicted V_{mr} of 7.1 m s⁻¹ using Pennycuick's (1989) program, compared with 5.25 m s⁻¹ from equation 2.30 in Norberg (1990). There were similar discrepancies in V_{mr} for *L. cinereus* and also in V_{mp} , P_{mp} and P_{mr} for both species. The values presented in Table 1 are based on calculations from the appropriate equations given in Norberg (1990).

Biomechanical predictions often do not agree with measured values. Speakman and Racey (1991) provide physiological measurements of the energy consumption by *Pipistrellus pipistrellus* (mass 5.4–9.4 g) in flight which, at 1.43±0.51 W, are much higher than our estimated costs for the larger *L. cinereus*. In our study, the comparison of measured flight speeds with those predicted from aerodynamic models allows us to test these models. Furthermore, our findings can be placed in a broader biological perspective by considering other available information on foraging *L. borealis* and *L. cinereus*.

Data about flight speed and predicted power requirements

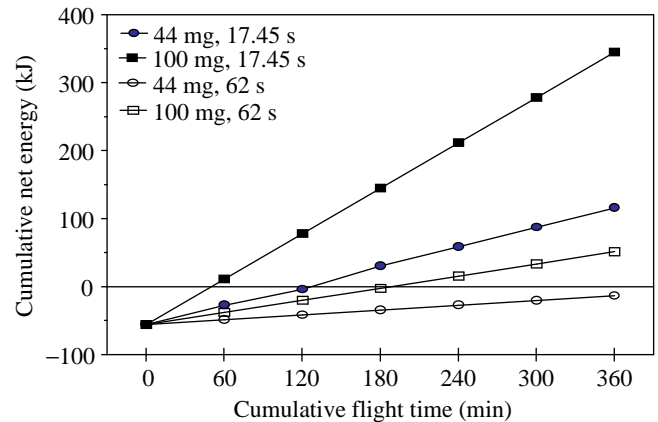


Fig. 5. The cumulative net energy of a lactating female *Lasiurus cinereus* foraging at V_x showing the influence of attack rate and insect size. The attack rates were obtained from our study site (Hickey, 1993) and Barclay's (1985) site in southern Manitoba, and the moth sizes (moths without wings) represent average prey size for this species at our study site (44 mg) and some of the larger moths the bats take (100 mg). We used the following equation to calculate the net cumulative energy:

$$\text{Net energy gain} = \left[\left(\frac{T_f \times 60}{\lambda} \right) \times S \times E_m \right] - [(T_f \times 60 \times P_x) + C_l],$$

where T_f is flight time in min ($\times 60$ to convert to s), S is success rate (51%), λ is encounter rate (attack every 17.45 s or every 62 s), E_m (in kJ) is the energy in a 44 mg or 100 mg moth (from Barclay *et al.* 1991), P_x the power required to fly at V_x (0.375 W) and C_l is the cost of lactation (in kJ) (corrected to *L. cinereus* mass from Kurta *et al.* 1990).

can be combined with information about flight times (t_f) to predict the power consumption associated with these flights. Hickey (1993), using data from *L. cinereus* carrying radiotransmitters, demonstrated that, at our study site over 73 bat nights, $t_f = 222 \pm 101$ min. Hickey and Fenton (1990), using observation of marked *L. borealis* at the same study site, including some with radiotransmitters, found $t_f = 127 \pm 36$ min ($N = 20$ bat nights). At the flight speeds we observed, these flight times translate into average flight energy costs of 1.14 kJ for *L. borealis* and 5.00 kJ for *L. cinereus*. These values would have been lower if the bats had flown at V_{mp} .

Information about t_f , attack frequency (λ ; Stephens and Krebs, 1986) and success rates, moth size and the energetic value of prey allows us to estimate the bats' energy intake. Hickey (1993) observed that *L. cinereus* attacked a moth every 17.45±5.75 s, succeeding on 51% of its attacks. Comparable values for *L. borealis* are 20.3 s and 39% (Hickey and Fenton, 1990). While *L. cinereus* usually captures 44 mg moths (Hickey, 1993), *L. borealis* captures 30 mg moths (L. Acharya, personal communication). Barclay *et al.* (1991) found an average of 24.0 kJ g⁻¹ moth dry mass, which translates into 6.48 kJ g⁻¹ wet mass of useful energy. Following Kurta *et al.* (1989, 1990), we used these data to estimate the daily energy

intake of the lactating female bats we studied as 111.00 ± 139.38 kJ for *L. cinereus* and 30.04 kJ for *L. borealis*.

We could find no published data on the costs of milk production in *Lasiurus*, but Kurta *et al.* (1989) estimated that lactating *Myotis lucifugus* required 41.3 kJ day^{-1} , of which 13.2 kJ (32%) was for milk production, the equivalent of 1.67 kJ g^{-1} . Comparable figures for *Eptesicus fuscus* were similar ($1.69 \text{ kJ g}^{-1} \text{ day}^{-1}$; Kurta *et al.* 1990) even though *E. fuscus* females feed twins compared with the single young of *M. lucifugus*. If the mass-specific costs of lactation are equivalent between *E. fuscus* and the two *Lasiurus* species we studied (which also have litters of two or more), *L. cinereus* would require $55.90 \text{ kJ day}^{-1}$ for milk production and *L. borealis* would require $22.02 \text{ kJ day}^{-1}$. The average values of energy intake from Hickey (1993) suggest that the *L. cinereus* we studied consumed more than enough energy per day (111.00 kJ) to cover the energy costs of flight (5.00 kJ) and lactation (55.90 kJ). The *L. borealis* also consumed more than enough energy (30.04 kJ) for flight (1.14 kJ) and lactation (20.02 kJ). These balances do not cover the costs of thermoregulation and maintenance, nor do they account for changes in the cost of lactation as the young grow. When the range of energy input is considered, on any given night, a bat may have operated significantly above or below its combined costs of flight and lactation. On cooler nights when insects were less abundant, some radio-tagged *L. cinereus* entered torpor, apparently to conserve energy (Hickey, 1993), although this strategy would depend on the level of milk production required, in turn reflecting the stage of development of the young (Kurta *et al.* 1989).

We propose that the bats we studied flew faster than V_{mp} because they were attacking prey attracted to the lights. Flying faster than V_{mp} may have been necessary to counter the evasive behaviour of moths, a factor influencing the bats' foraging success (Acharya and Fenton, 1992). Although the rate at which *L. cinereus* attacked moths was independent of moth density at the lights (Hickey, 1993), two lines of evidence suggest that the insects attracted to the lights were important to the bats we studied. First, marked individuals returned night after night (both species) and season after season (both species, but mainly *L. cinereus*) to the same lights and concentrated their foraging there (Hickey and Fenton, 1990; Hickey, 1993). Most radio-tagged bats of both species roosted within 500 m of the foraging sites (Hickey and Fenton, 1990; Hickey, 1993). At 500 m, the two-way commuting costs are 58.73 J for *L. cinereus* and 33.13 J for *L. borealis* at the V and P values we obtained (Table 1); both values are much lower than the useful energy in a medium-sized moth. Second, monitoring bats using their echolocation calls repeatedly demonstrated that both species were rarely encountered away from the lights and feeding buzzes in unlighted areas were extremely uncommon (Hickey and Fenton, 1990; Hickey, 1993). We predict that bats foraging in lower prey-density situations will fly at speeds closer to predicted V_{mp} and spend more time foraging (=flying).

There are no published data about flight speeds in other natural situations, but Barclay (1989) found that, in southern

Manitoba, radio-tagged lactating *L. cinereus* foraged for between 250 and 375 min per night, longer than the mean time spent in flight by the bats in our study area. At V_{mp} , these flight times correspond to energy costs of 3.35 kJ (250 min) and 4.68 kJ (350 min) compared with our P values of 5.62 kJ and 8.45 kJ. The differences between the costs at V versus V_{mp} are approximately equivalent to the assimilatable energy in 7–12 moths weighing 44 mg (minus wings), the average prey size that Hickey (1993) found for *L. cinereus*. At inter-attack intervals of 17.45 s and with a success rate of 51%, these energetic differences would be covered in 244–408 s of hunting around the lights in our study area. Longer flight times also coincide with lower rates of attack; in our study, mean inter-feeding buzz intervals were 17.45 ± 5.75 s (Hickey, 1993) compared with 62 ± 0.76 s (Barclay, 1985). The differences between these estimated costs and attack rates emphasize the importance of patches of prey to the foraging bats and demonstrate the impact of prey size on their energy budgets (Fig. 5). The picture is probably more complicated than depicted in Fig. 5, since female *L. cinereus* successfully reproduced in southern Manitoba (Barclay, 1989).

Our data, combined with aerodynamic predictions (e.g. Norberg, 1990) and energetic information (Kurta *et al.* 1989, 1990), suggest that foraging lactating *L. borealis* and *L. cinereus* operate on positive energy budgets. Discrepancies between observed and predicted flight speeds may reflect the situation in which we collected our data, namely bats hunting in concentrations of insects around street lights. We predict that clumped prey will have similar effects on the foraging times of other insectivorous bats that exploit rich patches (Fenton, 1990).

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