

## RESEARCH ARTICLE

# Climbing flight performance and load carrying in lesser dog-faced fruit bats (*Cynopterus brachyotis*)

Leigh C. MacAyeal<sup>1,\*</sup>, Daniel K. Riskin<sup>1,†,‡</sup>, Sharon M. Swartz<sup>1,2</sup> and Kenneth S. Breuer<sup>2</sup>

<sup>1</sup>Department of Ecology and Evolutionary Biology, Brown University, Providence, RI 02912, USA and <sup>2</sup>School of Engineering, Brown University, Providence, RI 02912, USA

\*Present address: College of Veterinary Medicine, Cornell University, Ithaca, NY 14853, USA

†Present address: Department of Biology, City College of the City University of New York, New York, NY 10031, USA

‡Author for correspondence (driskin@ccny.cuny.edu)

Accepted 11 November 2010

### SUMMARY

The metabolic cost of flight increases with mass, so animals that fly tend to exhibit morphological traits that reduce body weight. However, all flying animals must sometimes fly while carrying loads. Load carrying is especially relevant for bats, which experience nightly and seasonal fluctuations in body mass of 40% or more. In this study, we examined how the climbing flight performance of fruit bats (*Cynopterus brachyotis*;  $N=4$ ) was affected by added loads. The body weights of animals were experimentally increased by 0, 7, 14 or 21% by means of intra-peritoneal injections of saline solution, and flights were recorded as animals flew upwards in a small enclosure. Using a model based on actuator disk theory, we estimated the mechanical power expended by the bats as they flew and separated that cost into different components, including the estimated costs of hovering, climbing and increasing kinetic energy. We found that even our most heavily loaded bats were capable of upward flight, but as the magnitude of the load increased, flight performance diminished. Although the cost of flight increased with loading, bats did not vary total induced power across loading treatment. This resulted in a diminished vertical velocity and thus shallower climbing angle with increased loads. Among trials there was considerable variation in power production, and those with greater power production tended to exhibit higher wingbeat frequencies and lower wing stroke amplitudes than trials with lower power production. Changes in stroke plane angle, downstroke wingtip velocity and wing extension did not correlate significantly with changes in power output. We thus observed the manner in which bats modulated power output through changes in kinematics and conclude that the bats in our study did not respond to increases in loading with increased power output because their typical kinematics already resulted in sufficient aerodynamic power to accommodate even a 21% increase in body weight.

Key words: bat, climbing flight, power.

### INTRODUCTION

Flight consumes energy at a higher rate than any other mode of locomotion, and its metabolic cost increases with the mass of the flying animal (Norberg, 1990). Thus, animals that fly possess a host of morphological characteristics that decrease body mass compared with terrestrial organisms. However, they must be able to tolerate increases in weight because all experience circumstances in which body mass is elevated from its baseline. In these instances, not only is the cost of flight increased, but certain aspects of flight performance, such as maneuverability, are also negatively affected. This is particularly relevant for bats, for which body mass can change substantially on nightly and seasonal time scales.

For all bats, natural changes in body weight can result from nightly feeding. In a single night, insectivorous bats have been known to increase their body mass by 20–30% (Kunz, 1974), and frugivorous species have been observed in flight carrying food items weighing more than 40% of their body weight (Jones, 1972). On longer time scales, many temperate bats hibernate, and pre-hibernation fat storage can add an additional 20–30% to total mass (Beer and Richards, 1956). Furthermore, female bats face the unique challenge of maintaining normal flight behavior while carrying pregnancies to full-term; at birth, a pup weighs roughly one quarter of its mother's body weight (Kurta and Kunz, 1987). Even after

parturition, lactating females may transport neonates short distances, sometimes doubling the weight that needs to be carried in flight (Bailey, 1937; Vonhof et al., 2004). This behavior is even more incredible when one takes into account that the body mass of a lactating female can be even greater than her mass during pregnancy (Speakman and Racey, 1987). Clearly, these feeding, hibernation, pregnancy and post-natal loads place exceptional demands on bats in flight. Such additional loading increases the aerodynamic power required to fly, but does not enhance the bat's ability to generate aerodynamic force or power (Pennycuik, 1975). Furthermore, to forage successfully, elude predators and land at overhanging roosts, bats must compensate for the deleterious effects of increased wing loading on flight maneuverability (Riskin et al., 2009).

When an animal carries a load, one aspect of flight performance that might be compromised is climbing flight, which we define here as the process of increasing the potential energy of the center of mass while flying at low speeds. This type of flight is required to take off from the ground and to navigate in highly cluttered environments, such as dense foliage or inside caves. Although flight-initiating jumps have been explored in a few bat species (Altenbach, 1979; Schutt et al., 1997; Siemers and Ivanova, 2004), climbing flight after take-off has received less attention. In one study of maximum lift production during take-off in a range of animals,

Marden (Marden, 1987) hung lead weights from the backs of three phyllostomid species of bats ranging from 6 to 43 g. He found that bats could carry approximately 60–80% added weight, and that the maximum lift per unit muscle mass for bats was similar to values for birds and insects that do not use clap-and-fling kinematics. Marden did not report the kinematics of flight in that study, nor did he estimate aerodynamic power production.

### Estimating the cost of climbing flight

Estimating the cost of flight for animals is always difficult, although there have been improvements in the sophistication of the techniques applied over the past several years (e.g. Ellington, 1984; Wakeling and Ellington, 1997; Askew et al., 2001). The minimum power estimate can be determined from actuator disk theory, in which we calculate the effective ('induced') velocity ( $v_f$ ) of an air jet generated by the motion of the wings and characterized by a 'disk area' ( $S$ ), which is typically chosen as the area swept out by the wing motion. For hovering flight, the thrust generated by the induced velocity must equal only the weight of the animal, and the induced hovering power ( $P_H$ ), is given by:

$$P_H = mgv_f, \quad (1)$$

where the induced velocity is given by:

$$v_f = k \sqrt{\frac{mg}{2\rho S}}, \quad (2)$$

where  $m$  is the animal mass,  $g$  is the acceleration due to gravity ( $9.81 \text{ m s}^{-2}$ ),  $\rho$  is the air density ( $1.204 \text{ kg m}^{-3}$ ) and  $k$  is an induced velocity correction factor to account for the simplicity of the actuator disk assumption being applied to the much more complex conditions of animal flight (Ellington, 1984). For climbing flight, the theory is more involved because the actuator disk is tilted with respect to the horizontal. For this case, the induced velocity is determined from the solution to the fourth-order polynomial (Johnson, 1980):

$$v_f^4 - 2Vv_f^3 \sin\phi + V^2v_f^2 - \left(\frac{T}{2\rho S}\right)^2 = 0, \quad (3)$$

where  $V$  and  $T$  are the animal's speed and thrust, respectively, and  $\phi$  is the angle between the thrust vector and the flight direction. The total induced power ( $P_T$ ) is then determined from the flow through the actuator disk:

$$P_T = -T(V \sin\phi - v_f). \quad (4)$$

This power estimate includes not only the power required to maintain flight but also contributions that can be explicitly identified, including the climbing power ( $P_{PE}$ ) associated with the increase in potential energy:

$$P_{PE} = mgV_z, \quad (5)$$

where  $V_z$  is the vertical velocity, as well as the kinetic power ( $P_{KE}$ ) associated with any acceleration contributing to an increase in kinetic energy:

$$P_{KE} = mV_z \frac{dV_z}{dt}. \quad (6)$$

The composite total induced power estimate is the minimum required for flight and includes all of the terms mentioned above (Eqns 1, 5 and 6) (Askew et al., 2001; Berg and Biewener, 2008), but does not include several other expenditures including: (1) profile power associated with viscous drag over the flapping wings; (2)

parasitic power due to viscous losses associated with other parts of the body, i.e. legs, ears, etc.; and (3) the inertial costs of accelerating the wings. At low speeds, the profile and parasitic power are generally thought to be smaller than the induced power, although the validity of this assumption has been questioned recently (e.g. Usherwood and Ellington, 2002). The inertial cost of flight is difficult to estimate because one doesn't know how much, if any, energy storage is employed during the wing stroke cycle. Nevertheless, in this study we are primarily interested in the relative changes of power that are required due to changes in mass. Under the assumption that flight kinematics do not change in a dramatic form, an assumption we address in the discussion of our results, profile, parasitic and inertial power losses do not change over all flights and all mass treatments. Hence, these three power terms can be treated as a constant offset to the total induced power expenditure.

### Kinematics and power production

It is evident from the estimates presented above that it becomes more energetically expensive to climb as an animal becomes heavier. Hovering power is primarily dictated by the weight of the animal, but can be modified behaviorally through several possible kinematic changes, including changes in the wing extension during the downstroke, or flapping amplitude ( $A$ ), both of which will increase the swept wing area ( $S$ ). Total power is also highly dependent on both the net flight speed ( $V$ ) and the vertical velocity ( $V_z$ ). Thus, power can also be modified by kinematic changes, such as the stroke plane angle (SPA), that influence the overall direction of climbing velocity.

In this paper we explore how climbing power output changes under different loading regimes and how bats respond to the demands of increased body mass during flight. Specifically, we assess the degree to which bats are power-limited during the intensive requirements of near-vertical flight. To accomplish this, we examined the climbing flight performance of lesser dog-faced fruit bats carrying loads between 0 and 21% of their body mass. In the first part of the study, we focused on the changes in total induced power ( $P_T$ ) and its sub-components, hovering power ( $P_H$ ), climbing power ( $P_{PE}$ ) and kinetic power ( $P_{KE}$ ). If bats always use the same total induced power, independent of loading, we would expect a decrease in climbing performance with increased loading. If, however, bats can increase their power output to accommodate increased loads by recruiting more muscular power, total induced power should increase with loading, although climbing performance might still change.

Regardless of whether we find changes in power with loading treatment, we expect to find natural variability in power production among trials. In the second part of the study, we analyzed variation across all flights and loading levels to determine the kinematic changes associated with increases in total induced power production. Thus, this study provides the first quantitative examination of how the climbing flight performance of bats is influenced by the increased power requirements that result from an increased body mass, and sheds light on the kinematic mechanisms that increase power for climbing flight.

## MATERIALS AND METHODS

### Animals and experimental procedures

Captive-raised adult female lesser dog-faced fruit bats, *Cynopterus brachyotis* (Müller), on loan from the Lube Bat Conservancy (Gainesville, FL, USA) were tested in July 2008. The bats were housed in a large netted enclosure in the Animal Care Facility at Brown University (Providence, RI, USA) and were given food and

Table 1. Weight change (%) of *C. brachyotis* subjects by loading treatment and individual

Bat	0% Treatment	7% Treatment	14% Treatment	21% Treatment
A	0.5	7.2	14.7	21.3
B	0.5	8.0	14.7	20.8
C	0.7	8.0	14.5	21.5
D	0.8	6.8	14.5	21.6

Saline injection volumes were chosen based on the pre-injection mass of the animal and the percent difference was assigned to that treatment. Actual weight changes are listed.

water *ad libitum*. The subjects (body mass=32.5–41.1 g;  $N=4$ ) were selected from a colony of 15 individuals based on initial tests of repeatable climbing flight performance.

Before each experiment session, the bats were anesthetized with isoflurane gas, weighed and marked with high-contrast markers on the body and wing (Riskin et al., 2008). To experimentally change the mass of a bat, we injected the intra-peritoneal cavity of the bat with a volume of saline solution. Four different loading treatments were delivered to each bat: volumes amounting to 0 (control), 7, 14 or 21% of the bat's initial body mass. In the 0% treatment, the tip of the syringe pierced the abdomen of the bat, the plunger was depressed as slightly as possible and the syringe was then removed with little or no injection of saline. For each trial, the actual change in body mass was calculated from the difference in mass of the bat before and after saline injection (Table 1). Treatment order was randomized for each individual, and bats were given at least one rest day between experiments to prevent fatigue and ensure that excess saline from previous days had been excreted before each session.

To record the climbing flight performance of a bat, we placed it on the floor of a clear Lexan® flight enclosure with a floor and walls but no ceiling ( $0.60 \times 0.60 \times 0.86$  m, length  $\times$  width  $\times$  height). Upon release, the bat launched from the floor and flew out of the column. The dimensions of the flight column were such that the maximum wing span of the bat ( $\sim 0.4$  m) was not inhibited, but there was little opportunity for horizontal flight. Several trials, each consisting of at least five consecutive wingbeats, were recorded for each bat in each treatment. All flights were recorded at  $1000 \text{ frames s}^{-1}$  with three phase-locked high-speed Photron 1024 PCI digital cameras ( $1024 \times 1024$  pixel resolution; Photron USA, San Diego, CA, USA). These cameras were placed  $\sim 0.4$  m from the column, below the height of its floor, and captured simultaneous ventrolateral views of the bat (Fig. 1A). Because the four walls and floor of the flight

column were fully enclosed, there was some confinement of the air flows generated by the wing motion. However, the effect of this on the flight performance was estimated to be minimal, and because it was constant across all trials, we did not include any possible corrections due to this in our estimates for power consumption. The wingbeats used in the analysis were sampled from motion occurring after the bat was sufficiently far from the ground such that the wing motion had settled into a relatively repeatable pattern. This also ensured that ground effect forces, which are minimal when the subject is more than one wingspan above the ground (Betz, 1937), could be neglected.

### Three-dimensional coordinate mapping

Each day, the test section volume was calibrated using the Direct Linear Transformation method based on a 40-point calibration cube ( $0.35 \times 0.35 \times 0.28$  m). Three anatomical markers – two ventral midline points on the anterior and posterior margin of the sternum, and one at the left wingtip (Fig. 1B) – were digitized for five consecutive wingbeat cycles in a trial, using custom tracking software written in MATLAB R2008b (MathWorks Inc., Natick, MA, USA). Three-dimensional (3-D) trajectories for each marker were calculated when it was visible from two or more cameras simultaneously. For gaps resulting from frames in which an individual point was not visible from at least two cameras, its spatial position was interpolated using a third-order overconstrained polynomial fit of the 3-D positional data (Riskin et al., 2008). Trajectory analyses were performed using custom scripts in MATLAB.

### Kinematic recordings

Two coordinate systems, one global and one body-referenced, were established to calculate the wing kinematics in this study. In each system, the  $x$  and  $y$  directions defined the horizontal plane, and  $z$  was positive in the upward vertical direction. The global coordinate system ( $x_g, y_g, z_g$ ) described the positions of markers with respect to still air, and the body-referenced coordinate system ( $x_b, y_b, z_b$ ) described marker positions relative to the body (Fig. 1). The two coordinate systems were aligned at the start of the wingbeat cycle, with the  $x$ -axes aligned with the horizontal projection of the line through both sternum markers, anterior facing positive  $x$ , with the anterior sternum marker positioned at (0, 0, 0). Over the course of the wingbeat cycle, the bat moved relative to the global coordinate system. Meanwhile, the body-referenced coordinate system moved with the bat, always centered with (0, 0, 0) at the anterior sternum marker, and with  $x_b$  pointing forward through the horizontal projection of the two sternum markers. Thus, the body-referenced coordinate system translated and rotated with respect to the global

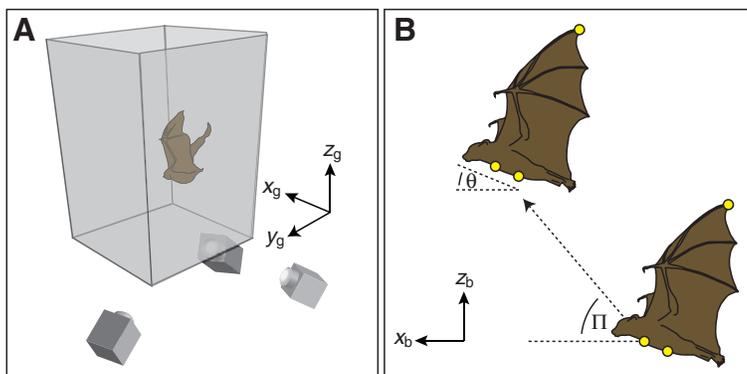


Fig. 1. (A) Bats were placed in a Lexan® enclosure and then recorded with three phase-locked high-speed cameras as they flew toward the open top of the enclosure. The global coordinate system ( $x_g, y_g, z_g$ ) remained fixed with respect to the enclosure. (B) Three body markers (yellow circles) were attached to the sternum and left wingtip of each bat. The body-referenced coordinate system ( $x_b, y_b, z_b$ ) was fixed with respect to the bat's heading. As the bat flew, the climbing angle ( $\Pi$ ) was calculated on the basis of the angle of travel of the anterior sternum marker above horizontal from the beginning to the end of the wingbeat cycle, and body pitch ( $\theta$ ) was measured on the basis of the average angle between horizontal and a line through the two sternum markers through a wingbeat cycle.

coordinate system over the course of the wingbeat cycle, but  $z_g$  and  $z_b$  were always parallel.

All wingbeat cycles were isolated based on the vertical movement of the wingtip in the body-referenced coordinate system ( $z_b$ -axis). Reversals in that vertical trajectory were determined, and the period of a wingbeat cycle was defined as the time between two consecutive upper reversal points. Wingbeat frequency ( $f$ ) was defined as the inverse of wingbeat period. Within a wingbeat cycle, the downstroke was defined as the time from the first upper reversal point to the lower reversal point, and the upstroke was defined as the time from the lower reversal point to the second upper reversal point.

#### Movement of the bat in the global coordinate system

The forward and vertical velocity of the body over the wingbeat cycle ( $V_x$  and  $V_z$ , respectively) were calculated as the distance traveled by the anterior sternum marker from the beginning to the end of the wingbeat cycle multiplied by wingbeat frequency. This is a better approximation for the average velocity of the body's center of mass than tracking the sternum throughout the wingbeat cycle, because inertial effects are avoided by measuring the sternum position when wing posture is consistent. The climbing angle ( $\Pi$ ) was defined as the arctangent of the ratio of  $V_z$  to  $V_x$ .

The velocity of the wingtip during downstroke ( $V_{tip}$ ) was calculated as the mean of the first derivative of the global position vector of the wingtip during the downstroke in the 3-D global coordinate system.

The power estimates were calculated according to Eqns 1–6. The net thrust ( $T$ ) was computed as the magnitude of the vector sum of gravitational acceleration and the mean body acceleration. For the purposes of this experiment, the induced velocity correction factor ( $k$ ) was set at 1.56 to account for the periodic pulses of the generated wake (see Norberg et al., 1993).

#### Kinematics of the bat with respect to the body-referenced coordinate system

Yaw ( $\psi$ ) was defined as the change in the  $x_b$ -axis between the start and end of a wingbeat cycle. Body pitch ( $\theta$ ) was defined as the mean angle of the line between the two sternum markers in the  $x_b$ - $z_b$  plane over the course of the wingbeat cycle (Fig. 1B). Wing extension ( $R$ ) was defined as the maximum distance between the wingtip and the sagittal ( $x_b$ - $z_b$ ) plane over the course of the wingbeat cycle, and wingspan ( $b$ ) was calculated as  $2R$ .

The amplitude of the wingbeat cycle ( $A$ ) was the maximum 3-D angle between any two positions of the wingtip relative to the anterior sternum marker within the wingbeat cycle. Amplitude is usually calculated using a shoulder marker instead of the sternum marker used here, but we used the sternum marker in order to reduce the number of markers that needed to be digitized. Using data from another study (Riskin et al., 2010), we have found that, for *C. brachyotis* flying forward in a wind tunnel, amplitude calculations based on the sternum are offset  $10.7 \pm 2.26$  deg lower than those using the shoulder, but the offset is extremely consistent, with amplitude calculations using those two methods linearly correlated with an  $r^2$  value of 0.993 ( $N=25$  wingbeat cycles across five individuals). We therefore feel justified in our use of the sternum marker for calculation of amplitude, especially where changes in amplitude are of interest.

SPA was defined by projecting the path of the wingtip onto the  $x_b$ - $z_b$  plane, as though the bat were viewed laterally in the body-referenced coordinate system with its head facing to the right. The wingtip trajectory in that plane was fitted using a least-squares orthogonal linear regression, and the arctangent of the slope of that

regression line was multiplied by  $-1$  to give SPA as a negative number. As SPA approaches  $-90$  deg, the wings are moving vertically, and as it becomes less negative, the wings move in a more horizontal plane; at  $-45$  deg they move anteroventrally and posterodorsally. This method does not account for movement of the body relative to the global frame, which might influence the area swept by the wingtip, but as the velocity of the wingtip relative to the body was much greater than the velocity of the body relative to the enclosure (see 'Results'), we believe that this error can be safely ignored.

#### Statistical analyses

We recorded multiple trials for each individual in each treatment, but the number of successful trials varied among them, with a minimum of two. To make sample sizes equal for all individuals, we thus limited our analysis to two trials for each individual in each treatment. In cases where excess trials were available for an individual in a treatment, only the two trials with the lowest mean body yaw rotation over the course of the wingbeat cycle were used. This resulted in a total of 32 trials. Within each trial, five consecutive wingbeat cycles were digitized and analyzed, resulting in a total of 160 wingbeat cycles.

We addressed two distinct questions in our analysis, and because what constituted an independent sample of kinematic data differed for each, the sample sizes differ in the two parts of the study. In the first part of the study, we investigated how wing loading influenced power production, and considered a trial to be an independent sample. For this part of the analysis, we used mean summary statistics from across the five wingbeat cycles within each trial, resulting in a sample size of 32 trials. For the second part of the study, we investigated the kinematic correlates of power output. Because each wingbeat cycle consisted of an independent set of kinematics resulting in its own power output, we included all 160 wingbeat cycles in that analysis.

To determine the effect of loading treatment on total induced power, induced hovering power, climbing power, kinetic power, horizontal velocity, vertical velocity and climbing angle ( $P_T$ ,  $P_H$ ,  $P_{PE}$ ,  $P_{KE}$ ,  $V_x$ ,  $V_z$  and  $\Pi$ , respectively), seven separate standard least-squares regressions were performed, with  $N=32$  trials for each. Loading treatment (0, 7, 14 or 21% loading) and individual bat as a random effect were used as model effects in all seven models.

To evaluate which kinematic parameters changed with increasing power production, we examined changes in total induced power production with wing kinematics. Standard least-squares regression analysis was performed on the 160 wingbeat cycles, using amplitude ( $A$ ), wing extension ( $R$ ), wingbeat frequency ( $f$ ), SPA and downstroke wingtip velocity ( $V_{tip}$ ) as effects, with individual bat as a random effect. We report adjusted restricted maximum likelihood  $r^2$ -values for all models. All statistical analyses were performed using JMP IN 8.0 (SAS Institute, Cary, NC, USA). All values are reported as means  $\pm$  s.d.

## RESULTS

### General description of flights

All four bats were able to push off the ground and initiate climbing flight in all treatments, even when loaded with an additional 21% of their body mass. Not all trials resulted in the bat leaving the enclosure successfully, but all individuals flew with a non-zero vertical speed for at least five wingbeat cycles before either leaving the enclosure or colliding with an enclosure wall (Table 2).

Bats flew upward at a variety of climbing angles, usually with a small forward or backward horizontal velocity component. Climbing

Table 2. Vertical velocity ( $V_z$ ;  $\text{m s}^{-1}$ ) of *C. brachyotis* by loading treatment and individual ( $N=160$  wingbeat cycles)

Bat	0% Treatment	7% Treatment	14% Treatment	21% Treatment
A	0.84±0.11	0.41±0.22	0.32±0.16	0.50±0.05
B	0.60±0.23	0.66±0.17	0.53±0.15	0.46±0.20
C	0.47±0.06	0.50±0.08	0.33±0.22	0.15±0.16
D	0.70±0.13	0.43±0.22	0.66±0.07	0.27±0.11
Overall	0.65±0.20	0.50±0.20	0.46±0.21	0.35±0.20

Values are means ± s.d.

Table 3. Climbing angle ( $\Pi$ ; deg) of *C. brachyotis* by loading treatment and individual ( $N=160$  wingbeat cycles)

Bat	0% Treatment	7% Treatment	14% Treatment	21% Treatment
A	103.5±22.4	117.1±29.4	93.1±43.7	75.7±40.8
B	93.6±10.9	98.5±12.7	63.9±23.8	55.0±22.3
C	129.2±26.6	136.3±21.7	148.5±28.1	76.6±50.9
D	92.1±14.5	110.7±35.0	106.9±9.6	103.8±44.9
Overall	117.1±29.4	103.5±22.4	93.1±43.7	75.7±40.8

Values are means ± s.d.

angles were  $97.3\pm 38.0$  deg ( $N=160$ ; Table 3), with forward speeds close to zero ( $-0.1\pm 0.4$   $\text{m s}^{-1}$ ) and vertical velocities of  $0.5\pm 0.3$   $\text{m s}^{-1}$ . Wingbeat amplitude was  $91.7\pm 17.1$  deg, maximum wingtip extension was  $19.6\pm 0.9$  cm, wingbeat frequency was  $10.8\pm 0.7$  Hz and SPA was  $-25.6\pm 10.0$  deg. The velocity of the wingtip during the downstroke was  $8.0\pm 0.6$   $\text{m s}^{-1}$ , and body pitch was  $39.9\pm 11.6$  deg.

#### Effect of loading on climbing performance

Total induced power ( $P_T$ ) did not change with loading ( $t=1.33$ , d.f.=27,  $P=0.19$ ; Fig. 2A), despite an increase in the hovering power ( $P_H$ ;  $t=6.92$ , d.f.=27,  $P<0.0001$ ; Fig. 2B). Climbing power ( $P_{PE}$ ) decreased slightly with loading, though not significantly ( $t=-1.11$ , d.f.=27,  $P=0.28$ ; Fig. 2C), and kinetic power ( $P_{KE}$ ) did not change with loading ( $t=-0.36$ , d.f.=27,  $P=0.73$ ; Fig. 2D).

There was considerable variance among individual means with loading, but statistically significant trends emerged. Forward flight velocity increased with loading ( $t=3.83$ , d.f.=27,  $P=0.0007$ ; Fig. 2E) and vertical velocity decreased ( $t=-2.11$ , d.f.=27,  $P=0.044$ ; Fig. 2F). As a result, climbing angle decreased with loading ( $t=-3.40$ , d.f.=27,  $P=0.002$ ; Fig. 2G). Amplitude, wing extension, frequency, wing tip velocity and body pitch did not change with loading, but SPA became more horizontal ( $t=2.46$ , d.f.=27,  $P=0.021$ ).

#### Changes in wing kinematics with increased power output

Our multiple regression model explained 27.3% of the variability in  $P_T$  output based on the kinematic parameters included. Wingbeat frequency was the most significant predictor of  $P_T$  when the influences of the other kinematic parameters were held constant,

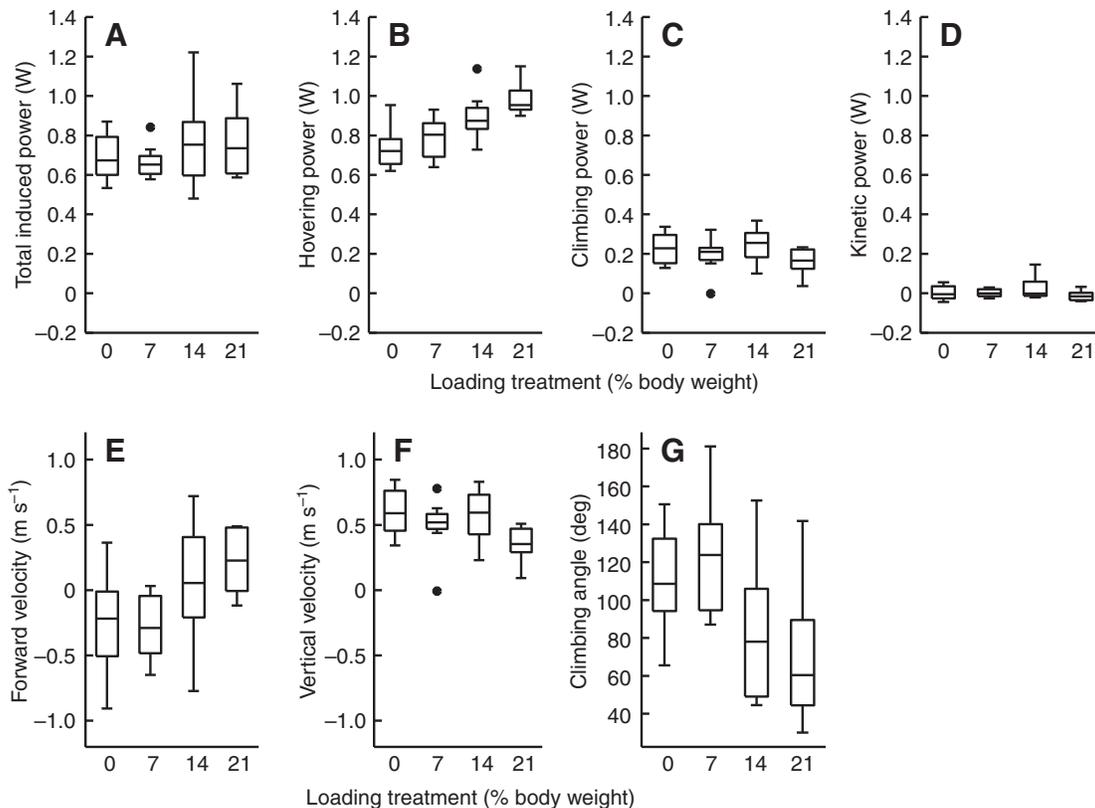


Fig. 2. Boxplots of power and flight performance for  $N=32$  flight trials across four different treatments of added weight (0, 7, 14 and 21% mass added). Total induced power ( $P_T$ ) did not change with loading (A;  $t=1.33$ , d.f.=27,  $P=0.19$ ), despite an increase in the hovering power ( $P_H$ ) (B;  $t=6.92$ , d.f.=27,  $P<0.0001$ ). Climbing power ( $P_{PE}$ ) decreased slightly with loading, though not significantly (C;  $t=-1.11$ , d.f.=27,  $P=0.28$ ), and kinetic power ( $P_{KE}$ ) did not change with loading (D;  $t=-0.36$ , d.f.=27,  $P=0.73$ ). Forward flight velocity ( $V_x$ ) increased with loading (E;  $t=3.83$ , d.f.=27,  $P=0.0007$ ), and vertical velocity ( $V_z$ ) decreased (F;  $t=-2.11$ , d.f.=27,  $P=0.044$ ). As a result, climbing angle ( $\Pi$ ) decreased with loading (G;  $t=-3.40$ , d.f.=27,  $P=0.002$ ).

and it increased with increased power production ( $t=4.41$ , d.f.=151,  $P<0.0001$ ). Total induced power became significantly greater as amplitude decreased ( $t=-2.68$ , d.f.=151,  $P=0.008$ ). No other kinematic parameters had a significant influence on  $P_T$ , although there were trends towards increasing  $P_T$  with increased extension ( $t=0.96$ , d.f.=151,  $P=0.34$ ), decreased stroke angle ( $t=-0.85$ , d.f.=151,  $P=0.40$ ) and increased tip velocity ( $t=0.41$ , d.f.=151,  $P=0.41$ ).

## DISCUSSION

When faced with the mechanical challenge posed by ascending flight with elevated body mass, the bats in this study did not increase the total induced power spent on climbing flight. Because of their increased mass, there was a significant increase in the power required for weight support, accompanied by reduced metrics of climbing performance, including vertical velocity and climbing angle.

Given that the total induced power did not change with loading (and that the kinetic power was minimal and did not change with loading), it seems at first glance surprising that the increase in hovering power appeared to outpace the decrease in climbing power. However, this can be attributed to the fact that the hovering power overestimates the demands of weight support, since it doesn't include any benefit from forward flight. However modest at these low speeds, forward flight decreased the power demands from that predicted by the pure hovering condition,  $P_H$ .

We found that variation in power production among trials was correlated with variation in wing kinematics. Bats produced more power chiefly by increasing wingbeat frequency.

### Changes in performance with increased loading

The decrease in vertical flight velocity with increased loading is consistent with previous studies of load carrying and climbing flight in birds (Videler et al., 1988; Pennycuik et al., 1989; Hughes and Rayner, 1991; Nudds and Bryant, 2002; Berg and Biewener, 2008), and marks the first demonstration of this trend in bats. In addition, like birds, bats in this study showed lower climbing angles when loaded. In the climbing flight of pigeons, climbing angle is correlated with changes in vertical velocity (Berg and Biewener, 2008), and we observed the same trend for bats here.

The ability of the bats in this study to continue ascending flights even while carrying the maximum loads employed in these experiments reveals that these loads did not exceed the performance limits of these animals. At some point, if the loads continued to rise, they would reach a point at which the bats would be unable to fly. It is not clear how close our experimental conditions came to this maximum possible load, and future tests would be needed to determine this limit. Our maximum load (21%) is well within the range of additional loads encountered by bats on a nightly basis (Jones, 1972), but bats might reach their limit for slow climbing flight well before they lose the ability to fly at all, as in forward flight the oncoming air flow assists in the generation of the required lift forces. In support of this, we note that the forward flight velocity did increase with loading (Fig. 2E), and this might suggest that as the load increases, the bat is attempting to generate a greater contribution to lift from forward flight.

Another factor that might contribute to the lack of increased power with load is the meager motivation of animals in our study for rapid climbing flight. Although the bats repeatedly flew out of the vertical enclosure, these tests were conducted under relatively calm, non-threatening conditions. The animals were not exposed to a sudden stimulus that might initiate an escape maneuver (e.g. Jackson, 2009). In addition, each individual repeated the experiments multiple times

and thus was, at least to some extent, accustomed to the procedure. These all contributed to a learned experimental environment that might not have elicited an extreme escape response. At higher levels of motivation, such as might be generated by the presence of a perceived threat, these bats would likely increase their power output to achieve even greater vertical flight velocities than those observed here. Thus, although ascending flight trials in the laboratory provide an excellent opportunity to probe the abilities and limitations of the locomotor system in a controlled fashion, we suspect that the performance we observed represents only a small portion of the natural flight repertoire of animals in nature.

Because the total induced power did not change across treatments but the power required to hover ( $P_H$ ) increased, it is not surprising that climbing performance diminished with increased loading (Fig. 2). Climbing power varied among trials, but was not increased by bats in response to loading. The small and constant fraction that the kinetic power contributes suggests that, for such climbing conditions, and during these mid-ascent measurements, acceleration is not a significant component of the power budget.

A stated assumption in our analysis is that the profile, parasitic and inertial power expenditures are approximately constant over all flights and loading conditions, and can thus be ignored. As noted earlier, changes in flight kinematics across all conditions were modest. For this reason we feel confident that, within the limits of our measurements, these secondary power requirements can be assumed to be unchanged and that the premise of our analysis remains sound.

### How do bats modulate aerodynamic power?

Although we did not observe a change in  $P_T$  with increased loads among bats in our study, its variability among trials is still useful for investigating the kinematic correlates of power production. To increase their aerodynamic power, bats (and other flying animals) have multiple kinematic resources available. These include increasing the wing extension or amplitude, thereby increasing the actuator disk area, or increasing the wingbeat frequency, for example.

Bats in this study modulated power output by means of multiple changes in kinematics, most significantly frequency and amplitude. However, although we did observe the expected increase in wingbeat frequency, trends towards increased wing extension, and decreased (more horizontal) SPA with increases in  $P_T$ , it is somewhat surprising that amplitude decreased with increasing power production. This might have occurred because the higher wingbeat frequencies prevented bats from simultaneously achieving large wing stroke amplitudes. Increases in amplitude with loading have been reported in studies examining loaded hovering and horizontal flight in birds (Chai and Millard, 1997; Videler et al., 1988), and make logical sense based on vortex wake theory (Rayner, 1979). Although increasing both frequency and amplitude would produce greater power, we hypothesize that the mechanical limitations of the musculoskeletal system might have precluded bats from using both mechanisms simultaneously.

Bats are known to increase wingbeat frequency and SPA with decreases in flight speed, presumably to make up for the decreased lift that accompanies the relatively slower flow of air across the wings (Norberg, 1976). Our results demonstrate that when *C. brachyotis* perform climbing flight, they modulate their kinematics in a slightly different manner to increase power.

Significant variation among animals in their kinematic responses to loading has been encountered many times among studies of vertebrates. One study of the effects of added loads on horizontal bat flight found that the frequency but not the amplitude

of the wingbeat changed significantly with increasing mass (Hughes and Rayner, 1991). Similarly, one study of pigeons found that amplitude but not frequency changed with increases in the climbing flight power output (Dial and Biewener, 1993), and another found that neither frequency nor amplitude changed significantly with increased climbing angle (Berg and Biewener, 2008). These differences in kinematic response among species and among experimental conditions might reflect limits in the efficacy of certain kinematic responses under specific conditions. For example, it is possible that the proportionality of power output to wingbeat frequency at times of maximum exertion may differ based on the morphology of the animal and the nature of the task (Hughes and Rayner, 1991). Alternatively, the explanation for these kinematic differences might be rooted in some other non-biomechanical difference among individuals. Regardless, it would appear that for the bats in this study, increasing the wingbeat frequency was sufficient to increase lift production, even despite a decrease in wing stroke amplitude with increased power production. We hypothesize that the extreme nature of nearly vertical flight might require that the animal reduce its flapping amplitude as it increases its frequency.

#### Inference on other vertical fliers from *C. brachyotis* data

Like all bats, *C. brachyotis* experience load carrying as a normal part of their natural history. Like many frugivores, they carry fruits or fruit fragments of considerable size during flight (Tan et al., 1997), and females of the species are subject to the same demands of load carrying during pregnancy as are all other female bats. We do not expect that this species possesses any special ability to generate unusual amounts of lift based on its wing form, and have observed no other specializations in its musculoskeletal structure to lead us to believe that it is particularly distinctive. Our results should therefore be applicable to other bats, though interspecific differences linked to ecological and morphological interspecific variation must undoubtedly exist.

The body mass of *C. brachyotis* (ca. 35 g) is small for bats in its family, the Pteropodidae, but is larger than the masses of most bat species (Jones and MacLarnon, 2004). Wing area in *C. brachyotis* is typical for a bat of its body mass (Norberg and Rayner, 1987). Because wing loading scales positively under isometry, flying with added loads should become easier as the size of a bat decreases. Thus, climbing performance with added loads should be even greater for bats smaller than *C. brachyotis*. Indeed, Marden's (Marden, 1987) study included three species, and the maximum lift production per unit body weight was inversely proportional to body mass across those species (*Micronycteris megalotis*: 6 g, 1.8 body weights of force; *Artibeus watsoni*: 16.5 g, 1.7 body weights; *A. jamaicensis*: 43 g, 1.6 body weights). Of course, three species is not sufficient to deduce the significance of that trend, but more comparative work might elucidate ecologically relevant patterns. Our prediction at present, then, is that the responses to loading that we observed in *C. brachyotis* could well be characteristic of bats in general and, on the basis of the size of the animals, may underestimate the performance potential of many bat species.

Although the kinematics and mechanics of climbing flight has received far less attention to date than those of many other flight behaviors, the ability to accelerate vertically, in both unloaded and loaded states, is clearly of great relevance to flying animals in nature. In addition to other roles, these flights can play a crucial role in attempts to escape predators (Van der Veen and Linstrom, 2000; Burns and Ydenberg, 2002; Fernandez-Juricic et al., 2006). Although some studies of escape flights in birds have suggested that such

flights, which share many of the characteristics of the flights we describe here, show varying degrees of performance dependence on both body mass and wing architecture (Witter et al., 1994; Lockwood et al., 1998; Swaddle and Lockwood, 1998; Fernandez-Juricic et al., 2006), there is clearly much still to learn. Vertical flight performance of bats, birds and insects will likely prove to share some common features, but each of the major flying taxa is likely to display many distinctive traits related to their unique evolutionary histories. Understanding the interspecific patterns of variation in accelerating and/or ascending flights within each of these groups, particularly in relation to body size and morphological variation, will contribute not only new insights into the behavioral responses of flying animals to threats of predation, but also greater understanding of broader issues in flight biology.

#### Future study

Given the significant loading bats experience in their natural environments, it is not surprising that bats are able to perform these relatively simple escape maneuvers. Bats in our study responded to increased loads with approximately constant induced power production, resulting in a decline in their climbing performance due to the increased mass loading. These results, however, do not directly address to what extent a wider range of flight tasks, e.g. maneuvering, are affected by body loading. In studies of wild bats in natural environments, researchers have found that increasing mass leads to selection of less cluttered foraging environments (Aldridge and Brigham, 1988; Kalcounis and Brigham, 1995), which may imply reductions in flight maneuverability, and this, in turn, could result at least partly from deficiencies in power production under increased load. Our results demonstrate that bats flying vertically in a laboratory setting use a flight strategy that accommodates increased loading. In the future, it will be important to examine how level flight, maneuverability and other aspects of normal locomotion in these animals are affected by increased loads.

#### ACKNOWLEDGEMENTS

We thank Allyson Walsh and the Lube Bat Conservancy for access to experimental animals and Allyce Sullivan for assistance with experiments. We thank Angela Berg and the referees for helpful comments on earlier versions of this manuscript. Frank Bonaccorso provided helpful discussion on the topic of load carrying in frugivorous bats. This study was supported by a Brown University Karen T. Romer Undergraduate Teaching and Research Award (L.C.M.), and by the United States Air Force Office of Scientific Research and the National Science Foundation.

#### LIST OF SYMBOLS AND ABBREVIATIONS

$A$	wing stroke amplitude
$b$	wingspan
$f$	wingbeat frequency
$g$	the magnitude of acceleration due to gravity
$k$	induced velocity correction factor
$m$	body mass
$P_H$	induced hovering power
$P_{KE}$	kinetic power
$P_{PE}$	climbing power
$P_T$	total induced power
$R$	wing extension
$S$	disk area, defined as the area swept out by the wing motion
SPA	stroke plane angle
$T$	net thrust including gravity and body acceleration
$v_f$	induced velocity derived from actuator disk theory
$V$	net speed of the body
$V_{tip}$	velocity of the wingtip during downstroke
$V_x$	forward velocity of the body
$V_z$	vertical velocity of the body
$x_b, y_b, z_b$	body-referenced coordinate system

$x_g, y_g, z_g$	global coordinate system
$\theta$	body pitch
$\Pi$	climbing angle
$\rho$	density of air
$\phi$	angle between thrust vector and flight direction
$\psi$	yaw

## REFERENCES

- Aldridge, H. D. J. N. and Brigham, R. M.** (1988). Load carrying and maneuverability in an insectivorous bat: a test of the 5% "rule" of radio-telemetry. *J. Mamm.* **69**, 379-382.
- Altenbach, J. S.** (1979). Locomotor morphology of the vampire bat, *Desmodus rotundus*. *Am. Soc. Mammal. (J. Mammal.)* **6**, 1-137.
- Askew, G. N., Marsh, R. L. and Ellington, C. P.** (2001). The mechanical power output of the flight muscles of blue-breasted quail (*Coturnix chinensis*) during take-off. *J. Exp. Biol.* **204**, 3601-3619.
- Bailey, A. M.** (1937). A hoary bat family. *J. Mammal.* **18**, 514-515.
- Beer, J. R. and Richards, A. G.** (1956). Hibernation of the big brown bat. *J. Mammal.* **37**, 31-41.
- Berg, A. M. and Biewener, A. A.** (2008). Kinematics and power requirements of ascending and descending flight in the pigeon (*Columba livia*). *J. Exp. Biol.* **211**, 1120-1130.
- Betz, A.** (1937). Die Hubschraube in Bodennahe (The ground effect on lifting propellers). *Zeitschrift für angewandte Mathematik und Mechanik* **17**, 68-72.
- Burns, J. G. and Ydenberg, R. C.** (2002). The effects of wing loading and gender on the escape flights of least sandpipers (*Calidris minutilla*) and western sandpipers (*Calidris mauri*). *Behav. Evol. Sociobiol.* **52**, 128-136.
- Chai, P. and Millard, D.** (1997). Flight and size constraints: hovering performance of large hummingbirds under maximal loading. *J. Exp. Biol.* **200**, 2757-2763.
- Dial, K. P. and Biewener, A. A.** (1993). Pectoralis muscle force and power output during different modes of flight in pigeons (*Columba livia*). *J. Exp. Biol.* **176**, 31-54.
- Ellington, C. P.** (1984). The aerodynamics of hovering insect flight. I. The quasi-steady analysis. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* **305**, 1-15.
- Fernández-Juricic, E., Blumstein, D. T., Abrica, G., Manríquez, L., Adams, L. B., Adams, R., Daneshrad, M. and Rodríguez-Prieto, I.** (2006). Relationships of anti-predator escape and post-escape responses with body mass and morphology: a comparative avian study. *Evol. Ecol. Res.* **8**, 731-752.
- Hughes, P. M. and Rayner, J. M. V.** (1991). Addition of artificial loads to long-eared bats *Plecotus auritus*: handicapping flight performance. *J. Exp. Biol.* **161**, 285-298.
- Jackson, B. E.** (2009). The allometry of bird flight performance. PhD thesis, University of Montana, Missoula, MT, USA.
- Johnson, W.** (1980). *Helicopter Theory*. New York, NY: Dover Press.
- Jones, C.** (1972). Comparative ecology of three pteropodid bats in Rio Muni, West Africa. *J. Zool., Lond.* **167**, 353-370.
- Jones, K. E. and MacLarnon, A. M.** (2004). Affording larger brains: testing hypotheses of mammalian brain evolution on bats. *Am. Nat.* **164**, E20-E31.
- Kalcounis, M. C. and Brigham, R. M.** (1995). Intraspecific variation in wing loading affects habitat use by little brown bats (*Myotis lucifugus*). *Can. J. Zool.* **73**, 89-95.
- Kunz, T. H.** (1974). Feeding ecology of a temperate insectivorous bat (*Myotis velifer*). *Ecology* **55**, 693-711.
- Kurta, A. and Kunz, T. H.** (1987). Size of bats at birth and maternal investment during pregnancy. *Symp. Zool. Soc. Lond.* **57**, 79-106.
- Lockwood, R., Swaddle, J. P. and Rayner, J. M. V.** (1998). Avian wingtip shape reconsidered: wingtip shape indices and morphological adaptations to migration. *J. Avian Biol.* **29**, 273-292.
- Marden, J. H.** (1987). Maximum lift production during takeoff in flying animals. *J. Exp. Biol.* **130**, 235-258.
- Norberg, U. M.** (1976). Aerodynamics, kinematics and energetics of horizontal flapping flight in the long-eared bat *Plecotus auritus*. *J. Exp. Biol.* **65**, 179-212.
- Norberg, U. M.** (1990). *Vertebrate Flight*. New York, NY: Springer, Berlin Heidelberg.
- Norberg, U. M. and Rayner, J. M. V.** (1987). Ecological morphology and flight in bats (Mammalia, Chiroptera) – wing adaptations, flight performance, foraging strategy and echolocation. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* **316**, 337-419.
- Norberg, U. M., Kunz, T. H., Steffensen, J. F., Winter, Y. and 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.
- Nudds, R. L. and Bryant, D. M.** (2002). Consequences of load carrying by birds during short flights are found to be behavioral and not energetic. *Am. J. Physiol. Regul. Integr. Comp. Physiol.* **283**, R249-R256.
- Pennycook, C. J.** (1975). Mechanics of flight. In *Avian Biology* (ed. D. S. Farner and J. R. King), vol. 5, pp. 1-75. London: Academic Press.
- Pennycook, C. J., Fuller, M. R. and McAllister, L.** (1989). Climbing performance of Harris' hawks (*Parabuteo unicinctus*) with added load: implications for muscle mechanics and for radiotracking. *J. Exp. Biol.* **142**, 17-29.
- Rayner, J. M. V.** (1979). A new approach to animal flight mechanics. *J. Exp. Biol.* **80**, 17-54.
- Riskin, D. K., Willis, D. J., Iriarte-Díaz, J., Hedrick, T. L., Kostandov, M., Chen, J., Laidlaw, D. H., Breuer, K. S. and Swartz, S. M.** (2008). Quantifying the complexity of bat wing kinematics. *J. Theor. Biol.* **254**, 604-615.
- Riskin, D. K., Bahlman, J. W., Hubel, T. Y., Ratcliffe, J. M., Kunz, T. H. and Swartz, S. M.** (2009). Bats go head-under-heels: the biomechanics of landing on a ceiling. *J. Exp. Biol.* **212**, 944-953.
- Riskin, D. K., Iriarte-Díaz, J., Middleton, K. M., Swartz, S. M. and Breuer, K. S.** (2010). The effect of body size on the wing movements of pteropodid bats, with insights into thrust and lift production. *J. Exp. Biol.* **213**, 4110-4122.
- Schutt, W. A., Jr, Altenbach, J. S., Chang, Y. H., Cullinane, D. M., Hermanson, J. W., Muradali, F. and Bertram, J. E. A.** (1997). The dynamics of flight-initiating jumps in the common vampire bat *Desmodus rotundus*. *J. Exp. Biol.* **200**, 3003-3012.
- Siemers, B. M. and Ivanova, T.** (2004). Ground gleaning in horseshoe bats: comparative evidence from *Rhinolophus blasii*, *R. euryale* and *R. mehelyi*. *Behav. Ecol. Sociobiol.* **56**, 464-471.
- Speakman, J. R. and Racey, P. A.** (1987). The energy costs of pregnancy and lactation in heterothermic bats. *Symp. Zool. Soc. Lond.* **57**, 107-125.
- Swaddle, J. P. and Lockwood, R.** (1998). Morphological adaptations to predation risk in passerines. *J. Avian Biol.* **29**, 172-176.
- Tan, K. H., Zubaid, A. and Kunz, T. H.** (1997). Tent construction and social organization in *Cynopterus brachyotis* (Muller) (Chiroptera: Pteropodidae) in peninsular Malaysia. *J. Nat. Hist.* **31**, 1605-1621.
- Usherwood, J. R. and Ellington, C. P.** (2002). The aerodynamics of revolving wings. II. Propeller force coefficients from mayfly to quail. *J. Exp. Biol.* **205**, 1565-1576.
- Van der Veen, I. T. and Lindstrom, K. M.** (2000). Escape flights of yellowhammers and greenfinches: more than just physics. *Anim. Behav.* **59**, 593-601.
- Videler, J. J., Vossebelt, G., Gnodde, M. and Groenewegen, A.** (1988). Indoor flight experiments with trained kestrels. II. The effects of added weight on flapping flight kinematics. *J. Exp. Biol.* **134**, 185-199.
- Vonhof, M. J., Whitehead, H. and Fenton, M. B.** (2004). Analysis of Spix's disc-winged bat association patterns and roosting home ranges reveal a novel social structure among bats. *Anim. Behav.* **68**, 507-521.
- Wakeling, J. M. and Ellington, C. P.** (1997). Dragonfly flight. 3. Lift and power requirements. *J. Exp. Biol.* **200**, 583-600.
- Witter, M. S., Cuthill, I. C. and Bonser, R. H. C.** (1994). Experimental investigation of mass-dependent predation risk in the European starling, *Sturnus vulgaris*. *Anim. Behav.* **28**, 201-222.