

## ADDITION OF ARTIFICIAL LOADS TO LONG-EARED BATS *PLECOTUS AURITUS*: HANDICAPPING FLIGHT PERFORMANCE

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### Summary

A series of experiments is described in which two brown long-eared bats *Plecotus auritus* Linnaeus (Chiroptera: Vespertilionidae) were flown in a 1 m × 1 m × 4.5 m flight enclosure at a range of body masses ( $n=9$  experiments for a female bat, and  $n=11$  for a male bat). The highest three of these masses incorporated artificial loads. Stroboscopic stereophotogrammetry was used to make three-dimensional reconstructions ( $n=124$ ) of the bats' flight paths. Over the entire range of experiments, wing loading was increased by 44% for the female and 46% for the male bat. Effects arising from captivity were controlled for: experiments at certain wing loadings were repeated after a period in captivity and the response to load was found to be unaltered. Flight speed fell with total mass  $M$  or with wing loading, varying as  $M^{-0.49}$  in the female and  $M^{-0.42}$  in the male bat. Wingbeat frequency increased with total mass or wing loading, varying as  $M^{0.61}$  in the female and  $M^{0.44}$  in the male bat. Hence frequency, but not speed, changed with mass in the direction predicted by aerodynamic theory. These results were used in a mathematical model to predict wingbeat amplitude, flight power and cost of transport. The model was also used to estimate the optimal flight speeds  $V_{mr}$  and  $V_{mp}$ . The model predicted that amplitude increases with load. Measurements of wingbeat amplitude did not differ significantly from the predicted values. The observed flight speed was below the predicted minimum power speed  $V_{mp}$  (which increases with load), and diverged further from this with progressive loading. The increase in cost of flight calculated by the model over the range of wing loadings was approximately double that which it would have been had the bats adopted the optimal approach predicted by the model. The limitations inherent in the theoretical model, and the possible constraints acting on the animals, are discussed.

### Introduction

The wing loading of an individual bat can be extremely variable. Even over the winter when temperate species are largely inactive, wing loading will drop by around 30% from entering to leaving the hibernation site (see, for example, Beer

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and Richards, 1956; Krulin and Sealander, 1972; Beasley *et al.* 1984). Female bats cope with problems that are unknown to their avian counterparts: full-term pregnant females carry foetal and associated masses representing approximately 30 % of body mass (Myers, 1978; Kurta and Kunz, 1987) or higher, perhaps up to 43 % on average (Funakoshi and Uchida, 1981). After parturition, lactating females have body masses almost as high as when pregnant, and frequently or even habitually transport young in flight, thereby increasing wing loading by around one-third, or even doubling it compared to its values without young (see, for example, Brosset, 1962; Mumford and Zimmerman, 1962; Nelson, 1965; Davis, 1970; Morrison, 1980; Ansell, 1986; Habersetzer and Marimuthu, 1986). Male bats also experience load changes due to reproductive activities: Gerell and Lundberg (1985) noted a 13 % mass loss in male *Pipistrellus pipistrellus* defending breeding territories. Both sexes have to eat, and insectivorous bats have a nightly food intake of up to 20–30 % of body mass (Kunz, 1974); this figure rises to 52 % in the sanguivorous vampires (Wimsatt, 1969), and one food item has been measured as 40.5 % of body mass in fruit bats (Jones, 1972).

It is a straightforward exercise to predict on aerodynamic grounds how velocity, wingbeat frequency and power should scale with mass within and between individuals (Pennycuik, 1975, 1990; Norberg and Rayner, 1987; Rayner *et al.* 1989; Rayner, 1988, 1990; Hughes, 1990). Between individuals, larger animals have larger wings (if wings are the same shape, wing loading varies with the cube root of mass) and should fly faster [between species, speed is proportional to mass to the power 1/6, or to the square root of wing loading (weight/wing area)] and expend more energy (power is proportional to mass to the power 7/6). Within an individual the situation is somewhat different, since wing area will not vary with load or with natural changes in mass: in this case, mass and wing loading are directly proportional (and in this paper are used interchangeably). Speed should increase as mass or wing loading to the power 1/2, as should wingbeat frequency (which under conditions of dynamic similarity is proportional to speed; Alexander, 1982), and mechanical power should rise as mass to the power 3/2. *Interspecific* trends for the variation of performance with mass and/or wing loading have been previously investigated, e.g. Baagøe (1987), Norberg (1987), Norberg and Rayner (1987) and Rayner (1988, 1990), and the relationships observed in the field between speed and power with mass or wing loading have largely supported the predictions. Hitherto, there have been few attempts to formulate and test aerodynamic predictions concerning the *intraspecific* or intra-individual responses to load or to changes in total mass. Clearly an animal will be limited as to the maximum load with which it can fly, and this limit could be imposed by aerodynamic factors on the wings, by the physiological capacity of the respiratory system or the flight muscles, or by the mechanical strength of the wings and pectoral girdle. Moreover, as mass increases and the animal approaches this limit, it is reasonable to expect systematic changes in flight performance (e.g. flight speed, wingbeat frequency). As outlined above, individual bats often encounter increased wing loadings, and it may be predicted that they would be designed to

adopt an aerodynamically or physiologically efficient response to the varying loads they experience.

Norberg and Rayner (1987) pointed out that small bats would have relatively more power in reserve than larger bats, and would therefore be better adapted to carry added weights. In addition, mass-carrying ability would be linked with wing loading. The authors cited bats of the genus *Plecotus* as an example of animals with relatively large wings with low wing loading (adapted for feeding by gleaning and for flying slowly in close cover). This is substantiated by the results of Davis and Cockrum (1964), who glued small balsa-wood boxes, into which loads of lead shot and clay were placed, onto the backs of several bat species. 'Maximum take-off weight', measured as a percentage of body mass, was greatest in the species *Plecotus townsendi*. We might then predict that the brown long-eared bat *Plecotus auritus* (Vespertilionidae) should be adept at coping with load; this animal, which is the second most common species in the UK, forms the basis of the present study.

### Materials and methods

One female and one male brown long-eared bat *Plecotus auritus* were found during the hibernation period in a demolished dry-stone wall. Wing area and wing span were measured according to Norberg and Rayner (1987) and are included in Table 1. The bats were exercised daily and fed mealworms *Tenebrio molitor* (which had been maintained on cabbage and bran and had mineral supplement added).

For experiments, the animals were flown within a black cotton flight enclosure of dimensions 1 m × 1 m × 4.5 m. A bat was introduced into the enclosure, and usually flew either immediately, or after a period spent grooming. Once flying, the long-eared bats would land rarely, but typically made continuous flights along the length of the enclosure, turning in flight at either end. The ends were not completely closed off. The enclosure had two circular apertures halfway along one side, into which the lenses of two cameras were fitted. The cameras were held by a machine-tooled mount supported on a tripod such that their lenses were exactly 250 mm apart. The use of two cameras in this way (with their optical axes parallel, lenses coplanar and a known distance apart) to obtain stereo photographs for the reconstruction of three-dimensional images has been described fully on several occasions (see for instance Wolf, 1983; Spedding *et al.* 1984; Rayner *et al.* 1986). A cube of known dimensions acts as a control for the reconstructed images. The cameras (a Nikon FE2 and Nikon FM) were triggered simultaneously by hand *via* motordrives by using a shutter release with a 2 m long cable. This meant that photographs could be taken from either end of the flight enclosure. Flights travelling to the left or right were considered equivalent, since the flight tunnel was symmetrical about the centre of the camera tripod and since only flights originating at an extreme end of the tunnel were photographed. Shutter speed was 0.5 s at maximum aperture, and the cameras were loaded with Ilford XP1 film. A Dawe 230C Strobosun stroboscope running at 50 Hz was placed in front of the

cameras, supported level with an aperture in the floor of the enclosure beneath the flight path of the animals, pointing upwards and slightly forwards, and with a shield to prevent back-lighting.

Images were traced (rather than printed) from under a Leitz Focomat V35 enlarger: stereo pairs were digitised on a Summagraphics Bit-Pad One digitising tablet linked to a BBC Master microcomputer, using the tragus as the digitising point. Data files were analysed on an Opus V personal computer according to methods described by Rayner and Aldridge (1985).

Wingbeat frequency was measured directly from the tracings by counting the number of images between identical phases of the wingbeat cycle. (The images were sufficiently overlapped to preclude any unseen wingbeats.) Since wingbeat frequency could be measured from photographs without a stereo pair, the total number of frequencies measured ( $n=151$ ) was greater than the number of films digitised for flight speed ( $n=124$ ). The stereo cameras were positioned laterally to the animals' flight paths, and a medial (head-on) view was not available. Wingbeat amplitude could therefore only be measured from photographs of wingbeat cycles which included the wingtip both at the top of the upstroke and bottom of the downstroke. On close inspection, most images showed wings not fully extended, and analysis of such wingbeat cycles would have seriously underestimated amplitude. Hence only 12 accurate measurements of wingbeat amplitude were obtained.

Wingbeat frequency and flight speed measured in each experiment and the morphological measurements of the bats were used to predict mechanical performance in flight. The model used (developed by Rayner, 1986, 1987) is based on the observed structure of the vortex wake in fast-flying bats (e.g. Rayner *et al.* 1986; Rayner, 1987) and uses the force balance on the animal to predict mechanical power output from speed, kinematics and morphology (including load); for our purposes the most significant predictions are the optimum flight speeds, minimum power speed  $V_{mp}$  and maximum range speed  $V_{mr}$  (Pennycuick, 1969), and the wingbeat amplitude corresponding to steady flight for the observed speed and wingbeat frequency.

Changes in flight patterns are plotted against wing loading rather than body mass, since changes in body mass take effect on the flight of an animal *via* changes in wing loading. Although wing area is usually constant, this is not always the case (in growing bats etc.) and so we chose to adopt the above convention. Linear and log-linear correlations were computed. Because the range of loading was relatively small, log-linear models did not significantly improve the fit, and so, to display the true amount of scatter in the results, linear plots are shown in all figures. Despite this, log-linear results with mass (proportional to wing loading) are discussed in the text for ease of comparison to theoretical predictions, which are usually derived in power-law form.

The bats were observed in flight at a range of wing loadings. Since the bats were hibernating when captured, they had relatively low body masses. The amount of food that the bats received could be controlled precisely, because the bats were fed

Table 1. Morphological data for the two bats, and the minimum and maximum masses of the bats during experiments

	Female	Male
Wing span (m)	0.264	0.26
Wing area (m <sup>2</sup> )	0.0119	0.0114
Minimum mass (kg)	0.08	0.076
Maximum mass (kg)	0.115	0.12
0.008 kg incorporated	Top two masses	Highest mass only

individually by hand during exercise periods in the mornings. Experiments were performed in the afternoons. Mass was increased gradually by feeding. The uppermost wing loadings were achieved by attaching small non-toxic fishing weights (0.8 g) between the shoulder blades by using Superglue 3. This was only necessary for the highest mass for the male bat (one weight) and for the two highest masses for the female bat (two weights at the upper, and one for the lower mass). After the experiments at the highest wing loadings had been performed, the bats' food supply was gradually decreased so that the experiments could be repeated for some of the lower wing loadings. The total changes in wing loading compared to the lowest loadings in the experiments were 44 % for the female and 46 % for the male bat. The maximum and minimum masses for each bat in an experiment are shown in Table 1.

The bats were released in a stone mine outside Bristol following completion of the experiments.

## Results

### *Flight speed*

Speed was negatively correlated with wing loading in both bats. Results are expressed as means  $\pm$  standard deviation throughout. For the female bat, speed fell from  $3.06 \pm 0.30 \text{ m s}^{-1}$  at a wing loading  $N = 6.70 \text{ N m}^{-2}$  to  $2.40 \pm 0.20 \text{ m s}^{-1}$  at  $9.64 \text{ N m}^{-2}$ , and for the male bat from  $3.00 \pm 0.16 \text{ m s}^{-1}$  at  $7.19 \text{ N m}^{-2}$  to  $2.30 \pm 0.16 \text{ m s}^{-1}$  at  $N = 10.53 \text{ N m}^{-2}$  (Fig. 1). The relationships were significant (female bat,  $r = -0.70$ ,  $P < 0.05$ ; male bat  $r = -0.68$ ,  $P < 0.05$ ). Log-linear regression of the flight speed data against body mass  $M$  (kg) revealed that speed fell as  $M^{-0.49}$  for the female bat and as  $M^{-0.42}$  for the male bat.

Accelerations across the section of the tunnel contained within the camera field of view were small. For all of the flights analysed, the mean change in speed from the first to last image of the bat (across a period of around one-eighth to one-quarter of a second) was an increase of  $0.10 \pm 0.63 \text{ m s}^{-1}$  ( $n = 124$ ). (The bats showed a deceleration across the frame almost as often as an acceleration.) This can be compared to the typical flight speeds within the tunnel, which are given in the above paragraph. Acceleration showed no relationship to wing loading ( $r = -0.02$ , NS).

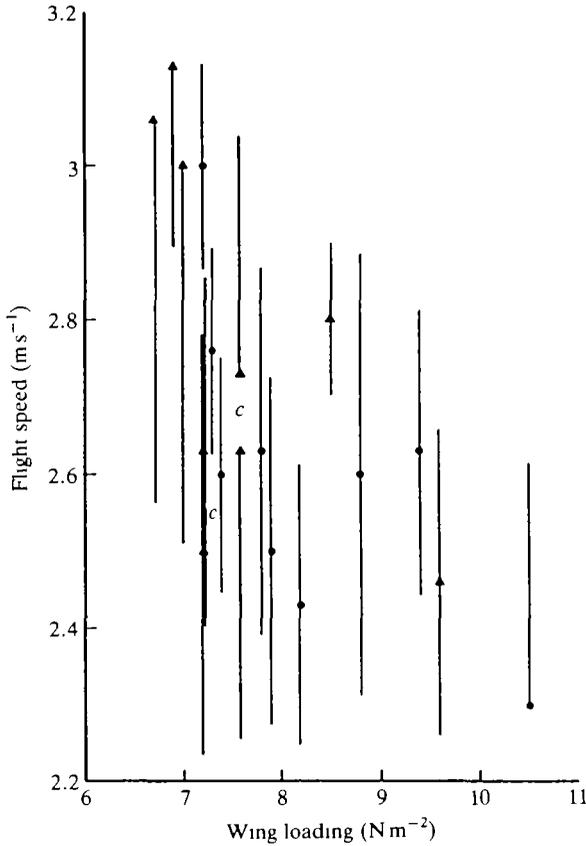


Fig. 1. Linear changes in flight speed ( $V$ ) with wing loading ( $N$ ) for the female ( $\blacktriangle$ ) and male ( $\bullet$ ) long-eared bats. Each point on the graph represents the mean speed from at least six reconstructed flightpaths,  $\pm$  one standard deviation. Where, for clarity, an error bar is shown on only one side of a point, this bar represents two standard deviations. The flights of the female shown at  $c$  are repeated wing loadings, and show similar speeds. Female: speed  $V=3.98-15.91N$  ( $r=-0.70$ ,  $P<0.05$ ) or  $V\propto N^{-0.49}$ . Male:  $V=3.61-12.16N$  ( $r=-0.68$ ,  $P<0.05$ ) or  $V\propto N^{-0.42}$ .

The response to load was unaffected by the time spent in captivity. The female bat was flown twice at two wing-loading values, with the experiments separated both by some time in captivity and by the experiments at maximum mass. There was no difference in flight speed (shown at  $c$  in Fig. 1: at  $7.2\text{ N m}^{-2}$  wing loading,  $t=0.31$ , d.f.=12, NS; at  $7.6\text{ N m}^{-2}$ ,  $t=0.87$ , d.f.=12, NS).

#### Wingbeat frequency

Both bats increased wingbeat frequency  $f$  with total mass or wing loading (Fig. 2;  $f=M^{0.61}$ ,  $r=0.86$ ,  $P<0.01$ , 95% confidence limits=0.31–0.90 for the female;  $f=M^{0.44}$ ,  $r=0.85$ ,  $P<0.01$ , 95% confidence limits=0.25–0.64 for the male). The female bat increased wingbeat frequency from  $9.53\pm 0.32\text{ Hz}$  to  $11.64\pm 0.64\text{ Hz}$  over the same range of wing loadings as for flight speed, while

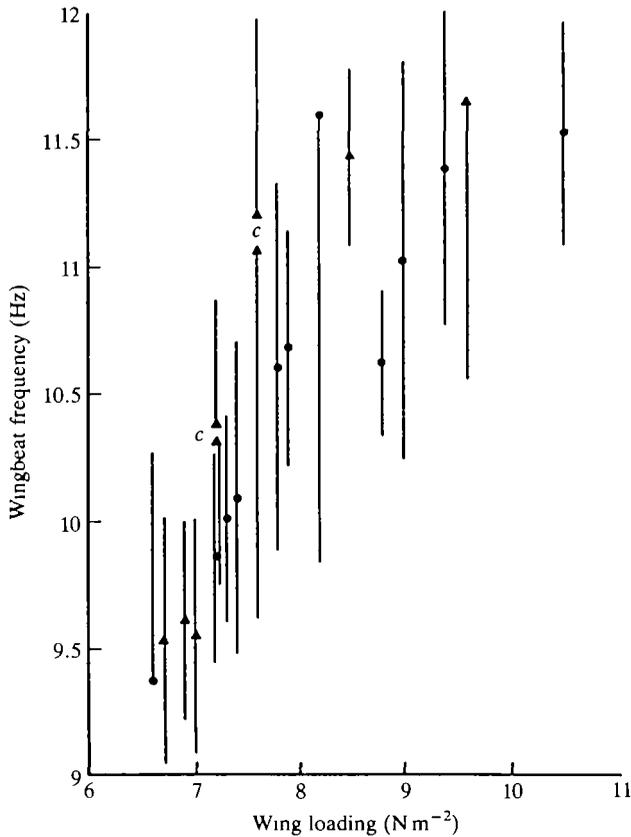


Fig. 2. Wingbeat frequency ( $f$ ) of female ( $\blacktriangle$ ) and male ( $\bullet$ ) bats with wing loading ( $N$ ).  $c$  indicates the control results (see text). Linear relationship for female: frequency  $f=4.62+0.78N$  ( $r=0.86$ ,  $P<0.01$ ) or  $f\propto N^{0.61}$ . Male:  $f=6.15+0.54N$  ( $r=0.85$ ,  $P<0.01$ ) or  $f\propto N^{0.44}$

frequency in the male bat ranged from  $9.37\pm 0.65$  Hz at  $6.67$   $\text{N m}^{-2}$  to  $11.52\pm 0.62$  Hz at  $10.53$   $\text{N m}^{-2}$ . The relationship between frequency and total mass (Fig. 2) appeared to be slightly curvilinear at higher loadings (see Discussion). Again, repeated experiments with the female gave the control results indicated at  $c$  in Fig. 2 (no difference in wingbeat frequency at  $7.2$   $\text{N m}^{-2}$ ,  $t=0.37$ , d.f.=12, NS, or at  $7.6$   $\text{N m}^{-2}$ ,  $t=0.39$ , d.f.=12, NS).

### Theoretical predictions

#### Wingbeat amplitude

The equilibrium wingbeat amplitude predicted by the theoretical model at each experimental loading (with the speed, wingbeat frequency and morphological parameters of the animal matching those measured) increased with wing loading (Fig. 3A;  $r=0.83$ ,  $P<0.001$  female bat;  $r=0.94$ ,  $P<0.001$  male bat). Although the slope of the measured wingbeat amplitudes plotted against wing loading was also

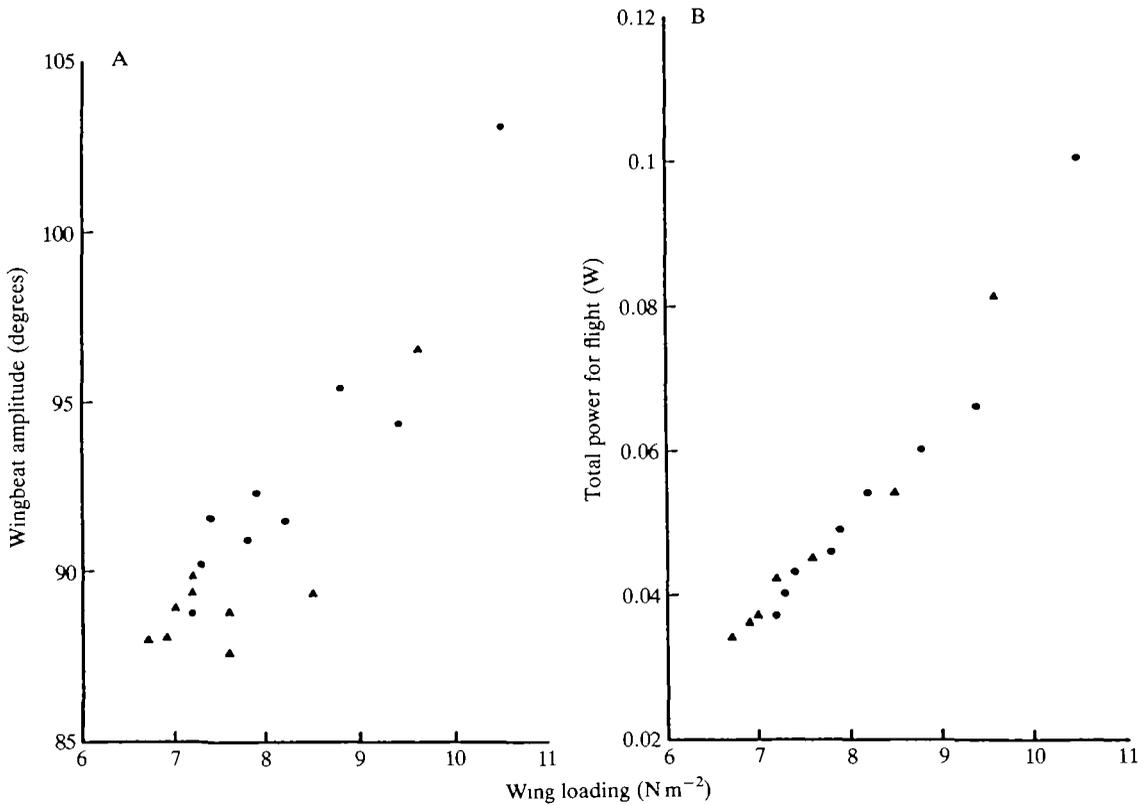


Fig. 3. Predictions of the theoretical model. (A) Equilibrium wingbeat amplitude estimated by the model, for each experiment. (B) Calculated mechanical power requirements for flight at the speeds and frequencies observed in experiments. Female is denoted by triangles, male by circles.

positive (measured amplitude =  $37.6 + 5.63N$ ) the correlation was not quite significant ( $r = 0.435$ , NS), but this could be because the 12 wing cycles analysed represented only eight different experimental loadings. The measured stroke amplitudes could, nevertheless, be used to test the model predictions. A paired  $t$ -test showed no significant difference between measured wingbeat amplitudes and those predicted in each case by the model ( $t = 0.526$ , d.f. = 11, NS). The measured wingbeat amplitudes ranged from  $70.1^\circ$  to  $105.8^\circ$ .

#### Power requirements

The calculated total mechanical power requirements ( $p$ ) for the bats flying at the speeds and frequencies observed in experiments, assuming equilibrium wingbeat amplitude, increased over the range of loadings by a total of 138% for the female bat ( $p = M^{2.27}$ ,  $r = 0.98$ ,  $P < 0.001$ ) and by 170% for the male bat ( $p = M^{2.41}$ ,  $r = 0.98$ ,  $P < 0.001$ ). The changes in power requirements with load are shown in Fig. 3B.

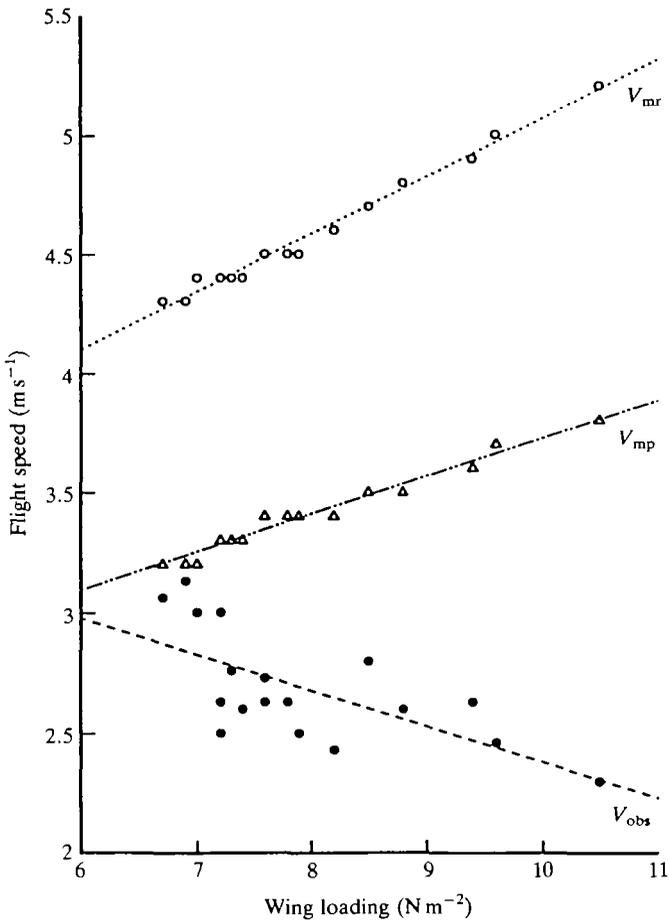


Fig. 4. Predicted and observed flight speeds. Minimum power speed ( $V_{mp}$ ,  $\Delta$ ) and maximum range speed ( $V_{mr}$ ,  $\circ$ ) predicted by the theoretical model for bats with the morphology and wing loading of the long-eared bats. Closed circles are the observed flight speeds  $V_{obs}$  from the experiments, for comparison. Records for the female and male are shown combined. The observed speeds are below both optimum speeds and diverge further from them as wing loading rises.

#### Predicted optimum flight speeds

The model was used to predict the optimum flight speeds  $V_{mp}$  and  $V_{mr}$  for the two long-eared bats at each experimental loading. Fig. 4 shows these speeds, with the speeds observed in experiments also shown for comparison. Both maximum range and minimum power speed are predicted to rise with load (female:  $V_{mp}=M^{0.42}$ ,  $V_{mr}=M^{0.42}$ ; male:  $V_{mp}=M^{0.37}$ ,  $V_{mr}=M^{0.46}$ ). Since the speed used by the bats was, even at the lowest wing loadings, never above predicted minimum power speed, and since, moreover, it decreased with load, the flight speeds adopted in experiments diverged further from the predicted optimum speeds with progressive loading.

As wing loading increased, the predicted power for flight at  $V_{mp}$  also grew higher, by 73 % over the entire range of loadings for the female bat ( $p_{mp}=M^{1.51}$ ) and by 83 % for the male bat ( $p_{mp}=M^{1.58}$ ). These are substantially smaller increases than those that were calculated for the flight patterns observed in experiments, and are therefore probably substantially less than those actually incurred by the bats; as expected, the indices computed here agree closely with the traditional aerodynamic prediction of a scaling index of 1.5.

### Discussion

An increase in wing loading as large as that imposed on the bats in this study is bound to incur an increase in total flight power requirements. A large component of the mechanical work done in flight is associated with weight support, and with increasing loading this power component must increase. The model predicted that, over the range of loads, the female bat should have increased  $V_{mp}$  by 15.6 % and the male bat by 15.1 %. The same figures for  $V_{mr}$  were 16.3 % and 18.2 %. This response would have resulted in a predicted increase in flight power requirements of around only 70–80 % for a bat flying at minimum power speed. These results are consistent with the expected scaling of response to load with an increase in speed proportional to  $M^{0.5}$  and in power proportional to  $M^{1.5}$  (Pennycuik, 1969, 1975; Norberg and Rayner, 1987; Rayner *et al.* 1989; Rayner, 1990).

Clearly, the bats did not conform to the predictions of the model and, in fact, their flight speed fell. The actual power requirements calculated for the flight speeds and wingbeat frequencies used by the two bats increased by approximately twice the predicted amount (138 % for the female, 170 % for the male bat) over the series of wing loadings. Since minimizing power in flight must be attractive adaptively, and since experimental animals have no concept of theoretical models, we must conclude that the bats were producing the best possible performance under the circumstances of the experiment, and must therefore examine the possible limitations of the model.

In all cases the flight speed observed in experiments was below the predicted optimum speeds for that morphology, and the discrepancy between the observed speed and  $V_{mp}$  grew larger as wing loading increased. Frequency did increase, scaling in a manner close to that predicted. This, taken in conjunction with the calculated (and perhaps from the measured) rise in wingbeat amplitude, suggests that perhaps the bats were attempting to maintain speed (in the sense that they were flapping 'harder' to increase airflow over the wing) but that they were unable to overcome the handicap of increased load and drag. The model assumes that the aerodynamic conditions on the wing do not change with speed or load, i.e. that lift coefficient  $C_L$  is constant: power or cost of transport (power/distance) is therefore minimized at the same values of  $C_L$  regardless of load, and therefore to maintain  $C_L$  a loaded bat must fly faster. There is no *a priori* reason to assume that  $C_L$  is sufficiently limiting that it should form a major constraint. Indeed, in the long-eared bat with its large wings  $C_L$  is likely to be relatively small compared to  $C_L$  in

other bats, and the bat is likely to tolerate modest increases in  $C_L$  associated with load.

There are a number of other, potentially stricter, constraints acting on the bats which may preclude the maintenance of constant  $C_L$ . Of these, an important limit is likely to be the power margin, which is the relative excess power available (power available from muscles minus the cruising power as a fraction of the cruising power). The heavier bat has more than one possible response to load. The animal may be constrained to maintain power margin (by reducing frequency and/or speed) or it may, instead, be able to reduce its power margin, maintain optimal aerodynamic conditions (constant  $C_L$ , minimum power at maximum range speed) and increase speed with load. Whether power was limiting for the bats in this way is difficult to ascertain. The observed response of a reduction in speed but an increase in frequency is also consistent with the hypothesis that the captive animal opted to maintain some form of 'safety factor' constant, either in the mechanical sense of minimizing maximum stresses on the flight muscles, skeleton or wing surface, or in the sense of maintaining manoeuvrability (*sensu* Norberg and Rayner 1987) to cope with flight within the enclosure. Rayner *et al.* (1989) argued that constraints on the maximum wing root pitch (flapping) moment might constrain selection of speed and kinematics in loaded serotine bats *Eptesicus serotinus*. The response is also consistent with the proposition that, in conditions approaching maximum exertion, power output from the flight muscles is proportional to wingbeat frequency, and that the bat is unable to increase frequency (and hence power) sufficiently to maintain constant aerodynamic conditions (e.g.  $C_L$ ). A moderate increase in frequency with load may provide sufficient power output as long as flight speed is also reduced.

The bats may have responded to flying within the confines of a flight enclosure by using artificially low speeds. However, *Plecotus* is a highly manoeuvrable animal with low wing loading, adapted for gleaning from foliage in close cover, often in very slow flight or hovering. The same flight enclosure (width approximately four times the size of the bats' wingspan, and the entire length of it used in flight) was large enough to allow *Pipistrellus pipistrellus* to increase flight speed upon occasion (Hughes, 1990): this species is smaller than *P. auritus*, but probably less manoeuvrable (Aldridge, 1985). It is in any case difficult to envisage how the *trend* in results with increasing load could arise as an enclosure artefact. It was not due to a change in power used for acceleration, since acceleration did not change with wing loading.

The effects on flight speed of the addition of fishing weights (uppermost wing loadings) were not discernibly different from those of the fed masses, but there were some differences evident for kinematic parameters. Wingbeat frequency, wingbeat amplitude and total power all show a slight change in their relationship with wing loading at the very highest masses, which presumably exceed those normally encountered naturally (Figs 2, 3A,B). The plot of frequency reaches a plateau, and conversely amplitude and power appear disproportionately high at the top loadings. The fishing weights were not associated with such a large increase

in wingbeat frequency as the trend at lower (fed) masses would suggest by extrapolation, possibly because of a limit to muscle stress, and the values calculated by the model for amplitude and power are consequently enhanced at these upper loadings, presumably to compensate for this lower frequency.

There have been few previous experimental assessments of the effects of load on animal flight. Davis and Cockrum (1964) gave some indication of the high percentages of body mass (up to 73.3 %) that bats can lift: the amount sustainable once in flight would be higher, but unfortunately there was no investigation of the effects of load once airborne. Marden (1987) found that the ratio of flight muscle mass to unladen body mass could best explain the ability of loaded birds and bats to take off and negotiate an upwards escape route under load. In both these cases, however, the animals were operating for short flights and performing an escape response, and the results cannot be considered of great relevance to naturally occurring situations.

The first investigation of the more subtle effects of load on level flight was made by Videler *et al.* (1988*a,b*), who described the effects on flight speed and on flapping flight kinematics of adding lead weights to the feet of trained kestrels *Falco tinnunculus* flown in a long corridor. Like the bats in the present study, these birds were unstressed and were performing reasonably steady flight. Similar to our bats, the kestrels decreased flight speed and increased wingbeat frequency in response to increased loading; wingbeat amplitude also increased with wing loading. The relationship of speed with loading was similar to that reported here, although the observed (unloaded) speed was initially close to predicted  $V_{mr}$  and finally, when loaded, was just less than predicted  $V_{mp}$ .

Why should kestrels (which need to transport food items in flight) and the bats in this study respond by decreasing flight speed? In both cases the animals were well exercised. Importantly, this study has shown that the responses of the bats were influenced solely by load, and were not an artefact of captivity, such as muscle atrophy or habituation to surroundings. (Bats kept in captivity quickly deteriorate in flight ability if they are not regularly flown.) It could be suggested that the kestrels may have experienced a reduced power margin because they were necessarily kept slightly underweight (in a roughly 150–200 g bird, 20–30 g lower than when captured), and muscle mass may have been depleted; this low mass is normal in captive falcons to make them keen to fly, and these birds were exercised regularly. However, the bats in the present study were at or above typical wild body masses for this species, in most cases well-fed (except in the later stages of the experiments when body masses were being progressively reduced). In any case, the range of loadings formed a significant regression both when the bats were overweight and when they were slightly underweight. This makes their inability to achieve the increase in flight speed predicted by aerodynamic theory even more puzzling, particularly considering the increased wing loadings that bats are likely to encounter in the wild. It may be that the long-eared bats had little opportunity to accelerate much above  $V_{mp}$  in the enclosure. We know little of the response of wild bats to load [but see Hughes (1990) for preliminary observations of flight

behaviour of noctule and greater horseshoe bats during the breeding season]. Evidently the captive long-eared bats responded to strict physiological or mechanical constraints on load-carrying.

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