FLIGHT PHYSIOLOGY OF INTERMEDIATE-SIZED FRUIT BATS (PTEROPODIDAE)

BY ROGER E. CARPENTER

Department of Biology, San Diego State University, San Diego, California 92182, U.S.A.

SUMMARY

Up to eight physiological parameters were measured on members of four species of fruit bats with a size range of 0·188–0·650 kg as they flew in a wind tunnel. Regression lines were calculated for the relationships between body masses of bats and their power inputs (P_i), heart and respiratory rates. These were compared to similar relationships for flying birds.

Respiratory evaporation dissipated only 10 % of the heat produced. At ambient temperatures (T_a) above 15 °C, heat loss was facilitated by vasodilation of feet and wing membranes, but this mechanism became less effective at high T_a when thermal differential between wings and air was reduced. Bats are apparently unable to increase greatly their respiratory evaporation, and overheated at T_a of 25–30 °C. At low T_a, the flight ability of two bats was reduced, suggesting that reduced coordination or even freezing of wings might be a general problem for bats flying at T_a close to 0 °C.

The endurance of three bats was so much greater near the middle of their speed ranges that the maximum flight distances ought to be achieved at these velocities, even though the cost of transport would be lower at higher speeds. Endurance at an airspeed was proportional to the relative power input ($P_i/P_{i,min}$) raised to the power of −7·45; flying at a speed that raised $P_i/P_{i,min}$ by 10 % reduced endurance by half.

INTRODUCTION

Wind tunnels have been used to make physiological measurements on at least six species of flying birds, but this approach has been used less extensively on bats. Physiological measurements are available from only three species of bats of two disparate sizes: *Phyllostomus hastatus,* body mass approximately 0·100 kg (Thomas, 1975; Thomas, Lust & Van Riper, 1984) and two species of flying foxes, of 0·650–0·870 kg body mass (Thomas, 1975, 1981; Carpenter, 1975, 1985).

As part of a study on the energetics of some West African fruit bats, I measured respiratory gas exchange, heart beat and respiratory frequencies, body temperatures and endurance from representatives of three species that are intermediate in size between the previously studied animals. In addition, I include some previously unreported data from several flying foxes (*Pteropus poliocephalus*) from Brisbane,

Australia. This report doubles the number of species and specimens of bats for which there are some physiological data while flying in wind tunnels. The sizes of animals involved, along with data from previous studies, permit preliminary descriptions of the allometric scaling relationships between the body masses of bats and several physiological parameters during steady flight.

MATERIALS AND METHODS

Animals used

Data were obtained from four animals that were captured in the vicinity of Makokou, Gabon, and shipped by air to San Diego (Table 1). I have also included at appropriate places previously unreported measurements on three Australian *Pteropus poliocephalus* (Table 1) that were made at the same time as those in a previous study (Carpenter, 1985).

Wind tunnel and training

The tunnel was the same one used previously (Carpenter, 1985), except that the fan was now powered by a 14·9 kW motor that allowed increased horizontal airspeeds (V).

Bats were trained as before, with a mild electric shock as a negative reinforcement for landing on the floor or ends of the test section, and the presentation of a landing perch as a reward for successful flights. It was essential that bats be flown daily for many weeks to develop the stamina necessary for physiological measurements. The *P. poliocephalus* (*Pp*) had generally learned to fly for brief periods with only 2–3 days of training, but all of the African bats were more difficult to train. The two *Eidolon helvum* (*Eh*) learned to fly without masks in 4–8 days, but only no. 3 eventually learned to fly with a mask. *Rousettus aegyptiacus* (*Ra* 3) was never successfully flown with a mask for respiratory measurements. The strong sexual dimorphism of *Hypsignathus monstrosus* (*Hm*) (Allen, Lang & Chapin, 1917; Bradbury, 1977) made the flight energetics of both sexes of special interest. But it took 2 weeks to train

Table 1. *Text symbols, sexes and body masses of bats used in this study*

Text symbol	Species	Sex	Mean body mass (kg)	Origin
Eh 3	straw-coloured fruit bat, *Eidolon helvum* (Kerr). no. 3	M	0·315	Gabon
Eh 4	*E. helvum*. no. 4	F	0·260	”
Hm 11	hammer-headed bat, *Hypsignathus monstrosus* H. Allen. no. 11	F	0·258	”
Ra 3	rousette bat, *Rousettus aegyptiacus* (Geoffrey). no. 3	M	0·188	”
Pp 1	grey-headed flying fox, *Pteropus poliocephalus* Temminck. no. 1	M	0·465	Australia
Pp 5	*P. poliocephalus*. no. 5	M	0·756	”
Pp 7	*P. poliocephalus*. no. 7	F	0·629	”

two females to fly for as long as 10 s, and a male never learned to fly in 6 months of training.

Respiratory gas exchange

At the start of each day's flight activities, including training flights or measurements of physiology or endurance, each of the African bats was given a 'warm-up' flight, usually of 120–150 s, at a moderate airspeed. Gas exchange was measured in *Eh* 3 and *Hm* 11, which were trained to fly with masks using the methods described earlier for this tunnel (Carpenter, 1985). In summary, a diaphragm pump drew air in through the rear of a mask worn by a bat in flight, and sent it through a rotameter that measured total rates of air flow, usually $14 \cdot 9 \, l \, min^{-1}$.

This air stream was divided into two parallel circuits, and the remainder bled off. Circuit no. 1 carried air at the rate of $0 \cdot 25 \, l \, min^{-1}$ through a desiccant (Drierite) and to an oxygen analyser (model E-2, Beckman Instrument Co.) which measured fractional O_2 content ($F_{E_{O_2}}$) to the nearest 10^{-5} over the sensitivity range ($0 \cdot 20$–$0 \cdot 21$) that could be used for all measurements in this study. Readings from the analyser and comments on a bat's behaviour were voice-recorded on tape recorder for later transcription and evaluation.

Parallel circuit no. 2 carried air at a rate of $0 \cdot 8 \, l \, min^{-1}$ through preweighed tubes of Drierite and then a CO_2 absorbent (Ascarite). Respiratory evaporative water loss (EWL) and rates of CO_2 production ($\dot{V}_{CO_2}$) were determined by measuring, to the nearest $0 \cdot 1$ mg, the weight gain of the tubes after subtraction of background readings made in the same way with the empty mask in the tunnel. Drierite was usually introduced into this circuit at 70 s after the start of flight, and the Ascarite added in series at 170 s. Determinations of response times of the system indicated that these times were sufficient to allow accurate readings of changes in steady-state gas concentrations. The rotameters were calibrated at the pressures used by introducing pure N_2 into the mask or other parts of the system with a rotameter accurate to within $0 \cdot 5 \%$ and measuring the reduction in $F_{E_{O_2}}$ with the analyser. Carbon dioxide introduced into the mask by syringe at rates several times the flight $\dot{V}_{CO_2}$ was recovered to within 1 % of the amount introduced. All gas volumes were corrected to STPD.

For the first ten metabolic measurements of *Eh* 3 and *Hm* 11, Ascarite was in the circuit for 170–770 s and 800–1500 s after the start of flight, in order to determine whether the respiratory exchange ratio (R) changed during flight duration. Rates of O_2 consumption ($\dot{V}_{O_2}$) and $\dot{V}_{CO_2}$ were determined according to equation 2 of Tucker (1968). For subsequent metabolic runs with both bats, two flights of shorter duration were made within 1 h of each other; for most of these, $\dot{V}_{CO_2}$ was measured between 170 and 770 s in each flight. Two mean values for R were calculated: from the first halves of flights 1–10 and the first of each subsequent day's shorter flights, and from the second halves of flights 1–10 and each day's second flight. In the few flights where $\dot{V}_{CO_2}$ was not measured, the appropriate mean values for R (lines 5 and 6, Table 2) were used in Tucker's equation 3 to calculate V_{O_2}.

Drag of the mask was also measured in a closed return tunnel as before (Carpenter, 1985), using a frozen, wingless *H. monstrosus* for measurements of drag of the body both with and without a mask. The differences at each airspeed were considered to be drag of the mask (D_m, in Newtons), which varied with V (m s^{-1}) according to the formula:

$$D_m = 7 \cdot 9 \times 10^{-4} V + 5 \cdot 2 \times 10^{-4} V^2. \tag{1}$$

The power input necessary to overcome mask drag ($P_{i,m}$) at each speed was calculated by the formula:

$$P_{i,m} = D_m V/E_p, \tag{2}$$

where E_p is the partial efficiency. This was assumed to have a value of $0 \cdot 25$ on the basis of values measured for other flying vertebrates (Tucker, 1972; Bernstein, Thomas & Schmidt-Nielsen, 1973; Thomas, 1975). Corrections of $3 \cdot 8$ to $5 \cdot 0\%$ were made for the D_m of the two *P. poliocephalus*, using D_m values previously measured for masks of that size (Carpenter, 1985).

Rectal and foot temperatures

For many flights on the African bats I measured body temperatures (T_b) over a wide range of ambient temperature (T_a). These were usually measured on runs when masks and other recording apparatus were not used. I was unable to secure rectal thermocouples for the duration of a flight. Therefore, body temperatures were measured by seizing an animal as soon as it landed, and inserting a shielded 38-gauge copper-constantan thermocouple at least 5 cm into the colon. Temperatures were indicated to the nearest $0 \cdot 1\,°C$, within 15 s of landing, on a multichannel digital readout instrument (Bailey Instrument Co., model BAT-8).

In some runs, thermocouples taped on the feet recorded foot temperatures (T_f) during the length of the flight as an index of circulatory changes through the wings or other naked membranes. These thermocouples were connected to a multichannel recording potentiometer (Leeds & Northrup, Speedomax W) that could be read to the nearest $0 \cdot 2\,°C$. T_a was recorded with a second thermocouple in the airstream. All thermocouples and instruments were calibrated by a mercury thermometer with accuracy traceable to the National Bureau of Standards.

Heart, respiratory and wing measurements

I measured heart rates (f_H) by attaching thin shielded recording leads from an oscillograph to the bats' skin at various sites. When the ECG signal was masked by the EMGs from flight muscles, counts were easily made within the first 8 s of a bat's landing. Continuous records during and after flight on some of the bats indicated that the decline in f_H over the first 8 s after landing averaged 92% of the in-flight rates ($N = 15$; $r = 83$–100%; S.E.M. $= 1 \cdot 5\%$).

Respiratory frequencies (f_R) were initially determined at moderate airspeeds by using the oscillograph to record temperature changes of a thermocouple mounted in front of the animal's nose in the mask. During some flights, simultaneous records

were also made of wingbeat frequencies (fw) by recording EMGs from leads attached to skin over the pectoral muscles. Subsequent counts of fw only were made by filming bats flying at assorted airspeeds with a 1 rev. s^{-1} timer in the field of view.

Wingspans of *Eh* 3 and *Ra* 3 were measured by gluing a 15-cm ruler on their backs and photographing them from above while in flight at their apparent speeds of lowest power input. Negatives were projected to full size, using the ruler as a scale, and span was measured directly.

There now seem to be enough data to describe the relationships between several physiological parameters and body masses of bats. However, there were unequal numbers of individuals representing the species for which data are available, and in some cases (e.g. *P. poliocephalus*), there was nearly a two-fold variation in size among individuals of a species. Rather than using an average value for each species, I have made the assumption that the primary factor affecting physiological parameters is body mass, and have used each individual as a separate data point in calculating least squares regression lines of log-transformed data on physiological rates and body masses.

Endurance

The effect of airspeed on endurance was measured for *Eh* 3, *Hm* 11 and *Ra* 3. Each bat was flown twice each day without mask or other encumbrance until it showed reliable symptoms of fatigue (see next section). One flight was at the speed already known from $\dot{V}_{O_2}$ data to be the velocity of minimum power input (V_{mp}), or, for *Ra* 3, the speed ($V = 5$ m s^{-1}) at which posture and behaviour suggested the least effort to fly. The other flight was made at a chosen test speed (V_t), with at least 4 h rest between flights. V_t or V_{mp} were used for the first flight of the day on alternate days, and all measurements were completed at one V_t value before proceeding to the next V_t value. The duration of each flight was timed, and endurance was expressed as the ratio of the endurance at a test speed (E_t) to the endurance on the same date at the V_{mp} (E_{mp}).

RESULTS

Behaviour

Each bat flew in a somewhat distinctive manner, with occasional changes of position within the test section. However, these movements had no apparent effect on physiological measurements. Flight behaviour of *Eh* 3 and *Hm* 11 was apparently not influenced by the masks, except that *Eh* 3 would fly briefly at $V = 5$ m s^{-1} and 9 m s^{-1} only without the mask.

At high speeds, bats flew more consistently at the rear of the test section; at the slowest speeds they flew at the front, and oscillated from side-wall to side-wall. Airspeed had an obvious effect on the angle of flapping plane and inclination of the body, as described for *P. poliocephalus* (Carpenter, 1985). Thus, it was again easy to

use behaviour to determine with fair accuracy the airspeed at which power input was minimum.

Each animal showed reliable symptoms of fatigue shortly before being unable to continue in a flight, after which it landed or crashed. All bats began flying again immediately if they received a shock, but would soon stop again if the front perch was not lowered for normal landing.

The four African bats showed symptoms of overheating at high T_a values (Figs 3, 4). Bats opened their mouths either intermittently or continuously, and curled their tongues upward in the manner employed by *P. poliocephalus*. In *Eh* 3 the testes descended at T_b above 39·7°C and this bat often licked its scrotum after being replaced in its cage when overheated. However, after landing, additional cooling behaviour seen in the Australian bats, such as licking of the wrists or fanning the wings, was never observed.

Respiratory exchange ratio (R)

The mean R values for all flights of *Eh* 3 and *Hm* 11 were 0·78 and 0·79, respectively. Thus, the energy equivalent used in converting $\dot{V}_{O_2}$ to power input (P_i) and correcting for drag of the mask was 5·58 W when $\dot{V}_{O_2}$ was 1·01 h^{-1}. For both bats, the R values in first halves of flights 1–10 and first flights on subsequent days were significantly higher than values from second halves of runs 1–10 and second flights in a day (paired sample t-test, $P < 0.005$; Table 2).

Oxygen consumption and power input

The start of flight caused an abrupt increase in $\dot{V}_{O_2}$ from preflight rates; this pattern was reversed when a bat landed. *Eh* 3 would fly with a mask only at $V = 6-8 \, \text{m s}^{-1}$. Its V_{mp} was 7 m s^{-1}, but P_i differed only slightly at the other two speeds (Table 3; Fig. 1). For *Hm* 11, the V_{mp} was 5 m s^{-1}; P_i increased by 11 % at $V = 4 \, \text{m s}^{-1}$, but increased only slightly at three higher speeds (Table 3; Fig. 1). At $V = 8 \, \text{m s}^{-1}$, $\dot{V}_{O_2}$ was actually higher than at any speed except 4 m s^{-1}, but corrections for D_m resulted in a lower P_i value at $V = 8 \, \text{m s}^{-1}$ than at 7 m s^{-1} (Table 3).

It was not possible to determine systematically the effect of V on $\dot{V}_{O_2}$ of *Pp* 1 or *Pp* 7, but flight posture, good endurance and absence of prolonged heavy breathing after flight suggested that $\dot{V}_{O_2}$ was measured at speeds close to the V_{mp} (Table 3).

Evaporative water loss

Pulmonary EWL of *Eh* 3 and *Hm* 11 was measured during all flights in which $\dot{V}_{O_2}$ was measured, regardless of airspeed. To compensate for variations in pulmonary ventilation at different values of $\dot{V}_{O_2}$, the EWL value for each flight was expressed relative to $\dot{V}_{O_2}$. These measurements were all made at T_a of 18–25·6°C; there was no significant correlation of EWL with T_a. However, there were significant ($P < 0.001$) negative correlations of EWL with ambient vapour pressure (VP) (Fig. 2). Bats did not open their mouths in the stereotyped cooling response while wearing masks and there are no data on the rates of evaporation during this behaviour.

Mean EWL from *Pp* 1 was $0.604 \, g \, H_2O \, l^{-1} \, O_2$ ($N = 3$, S.E.M. $= 0.05$), or $6.92 \, g$ $H_2O \, kg^{-1} \, h^{-1}$ ($N = 3$, S.E.M. $= 0.58$) at a mean VP of 5.3 Torr (S.E.M. $= 0.07$). For *Pp* 7, EWL was $0.375 \, g \, H_2O \, l^{-1} \, O_2$ ($N = 4$, S.E.M. $= 0.07$), or $3.75 \, g \, H_2O \, kg^{-1} \, h^{-1}$ ($N = 4$, S.E.M. $= 0.06$) at a mean VP of 13.2 Torr (S.E.M. $= 0.6$).

Table 2. *Respiratory quotient (R) of* Eidolon helvum *no. 3 and* Hypsignathus monstrosus *no. 11*

Flight duration (s)	*E. helvum* no. 3	*H. monstrosus* no. 11
Runs 1–10, 170–770 s	0.820 (10, 0.013)	0.760 (10, 0.009)
Runs 1–10, 800–1500 s	0.737 (10, 0.009)	0.742 (10, 0.013)
First flight of day, 170–770 s	0.848 (6, 0.011)	0.835 (16, 0.012)
Second flight of day, 170–770 s	0.729 (6, 0.010)	0.796 (15, 0.006)
Mean value for first intervals and first flights	0.831 (16, 0.009)	0.806 (26, 0.011)
Mean value for second intervals and second flights	0.734 (16, 0.007)	0.774 (25, 0.008)
Overall mean	0.782 (32, 0.010)	0.790 (51, 0.007)

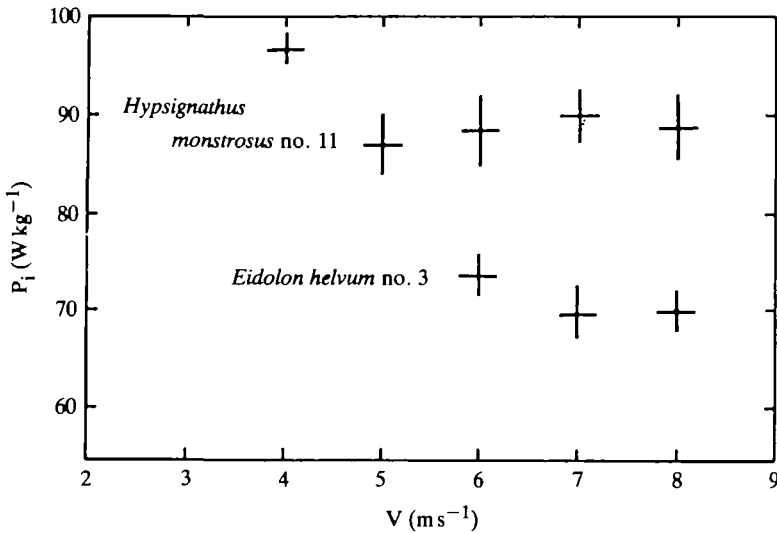Numbers in parentheses are number of flights, followed by S.E.M.

Fig. 1. Effect of velocity on power input of *Eh* 3 (three lower symbols) and *Hm* 11 (upper symbols). Symbols are mean ± 2 S.E.M.

Body temperatures

Body temperatures of three African bats after flights of 200 s or longer are shown in Figs 3 and 4. *Eh* 4 would rarely fly this long; therefore, data are reported for all flights of this bat lasting 120 s or longer. For all four bats the correlation of T_b with T_a was significantly different from zero ($P < 0.001$).

Low T_a had a dramatic effect on *Ra* 3 and *Hm* 11. During three flights at T_a between 2.7 and 5.3 °C, *Ra* 3 landed repeatedly in flights lasting less than 170 s, despite being able to fly for 600–640 s later on each morning, when T_a had increased to about 11–15 °C.

Hm 11 was especially affected by low T_a. On very cold mornings, this bat started each flight normally but soon appeared to lose wing coordination. Shortly afterwards, it crashed against the side or floor of the tunnel, even though the wings were pumping vigorously. In each instance, the bat was able to fly normally and for its characteristic duration (800–1000 s) at warmer T_a later in the morning. Review of data and comments in the notebooks used to record training flights showed a striking pattern of drastically reduced endurance at $T_a < 11$ °C (Fig. 5). Body temperatures measured immediately after these abbreviated flights were often as high or higher than those recorded at the ends of flights at T_a of 12–20 °C (Fig. 4). T_a as low as 3.5 °C had no apparent effect on *Eh* 3, and *Eh* 4 was not flown at T_a below 13.5 °C.

Foot temperatures

Temperatures of the feet (T_f) were usually high at the time of thermocouple attachment (Fig. 6). Prior to, or at the start of, flight, T_f usually dropped to low levels. At $T_a < 15$ °C, T_f declined (Fig. 6C,D,G) until there was almost no difference between T_f and T_a (Fig. 7). At warmer T_a, T_f usually increased after the start of

Table 3. *Mass-specific oxygen consumption ($\dot{V}_{O_2}$), corrected power input (P_i) and cost of transport of four bats*

Bat	Airspeed (m s^{-1})	$\dot{V}_{O_2}$ (l O$_2$ kg^{-1} h^{-1})	Corrected P$_i$ (W kg^{-1})	Cost of transport*
Eidolon helvum no. 3	6	13.52 (10, 0.20)	73.8 (10, 1.1)	1.25
	7	12.98 (10, 0.26)	69.8 (10, 1.5)	1.02
	8	13.23 (11, 0.19)	69.9 (11, 1.1)	0.89
Hypsignathus monstrosus no. 4	4	17.45 (10, 0.14)	96.7 (10, 0.8)	2.46
	5	15.84 (10, 0.28)	87.1 (10, 1.5)	1.77
	6	16.26 (9, 0.32)	88.6 (9, 1.8)	1.54
	7	16.75 (14, 0.24)	90.1 (14, 1.3)	1.31
	8	16.93 (8, 0.28)	88.9 (8, 1.7)	1.13
Pteropus poliocephalus no. 1	5.8	10.38 (7, 0.09)	55.5 (7, 0.46)	0.97
Pteropus poliocephalus no. 7	7.0–7.4	10.34 (4, 0.29)	55.1 (4, 1.65)	0.78
	8.3	11.44 (3, 0.37)	61.3 (3, 2.1)	0.75

Numbers in parentheses are numbers of flights and S.E.M.
*The metabolic cost of moving the animal's weight (in Newtons) a given distance ($= P_i$/weight V).
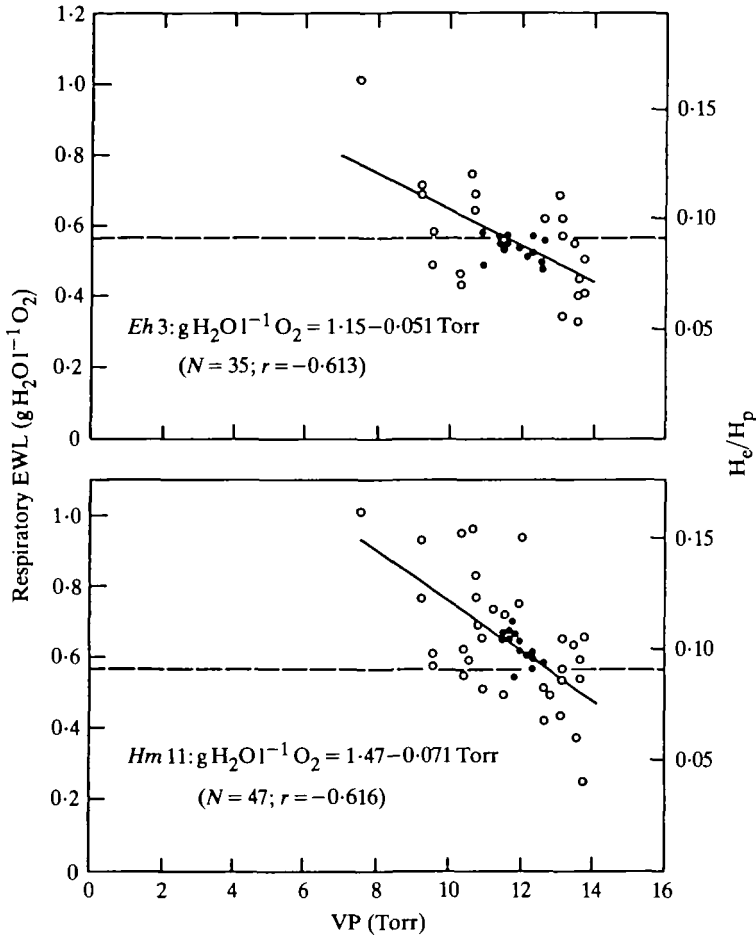
Fig. 2. Relationships for *Eh* 3 and *Hm* 11 between ambient vapour pressure (VP) and respiratory water loss (EWL, left ordinate) and the ratio of evaporative heat loss to heat production (H_e/H_p, right ordinate). Shaded circles indicate grouped values selected for calculating mass-specific water loss in Fig. 9. Equations describe least squares regression lines. Horizontal dashed lines indicate on left ordinate the rate of metabolic water production (MWP) per litre O_2 consumed.

flight to a nearly constant high level (Fig. 6B,E), but sometimes cycled (Fig. 6F). T_f typically declined promptly after a bat landed. However, when a bat was clearly overheated, T_f remained at high levels after landing (Fig. 6A). The highest T_f values were at the warmest T_a, but the greatest (T_f-T_a) differences occurred around $T_a = 20°C$ (Fig. 7).

Heart, respiratory and wingbeat frequencies

Heart rates increased abruptly with the start of flight, and dropped quickly to below pre-flight levels soon after landing (see Table 4).

In both *Eh* 3 and *Hm* 11, the fw and fR were coupled 1:1 at or near the V_{mp} of these bats. For *Pp* 1, the respiratory frequencies measured with a mask thermocouple

matched almost exactly the visual counts of wingbeats over the same time intervals. Although measurements of fR were not feasible over a wide range of airspeeds for any of these bats, it was easy to use fW, measured from films, as an index of the probable relationship between V and fR (Table 5).

The fW values determined from films were close to their minimum values at the measured V_{mp} of *Eh* 3 and *Hm* 11; for all bats, these frequencies were maximal at the lowest flight speeds (Table 5).

The mean wingspan of *Eh* 3 at $7 \, \text{m s}^{-1}$ was $0.777 \, \text{m}$ ($N = 14$, S.E.M. $= 0.007$), and the wingspan of *Ra* 3 at $V = 5 \, \text{m s}^{-1}$ was $0.646 \, \text{m}$ ($N = 4$, S.E.M. $= 0.008$).

Endurance

Hm 11 died abruptly of unknown causes after endurance measurements were completed only for the test speed of $8 \, \text{m s}^{-1}$, for which mean endurance was significantly less (one-tailed paired sample *t*-test, $P < 0.001$) than that at $V_{mp} = 5 \, \text{m s}^{-1}$ (Table 6). The endurance of *Ra* 3 was significantly greater at $V_t = 5 \, \text{m s}^{-1}$ than at any other V_t except $6 \, \text{m s}^{-1}$ ($P < 0.01$). Although the mean value at this
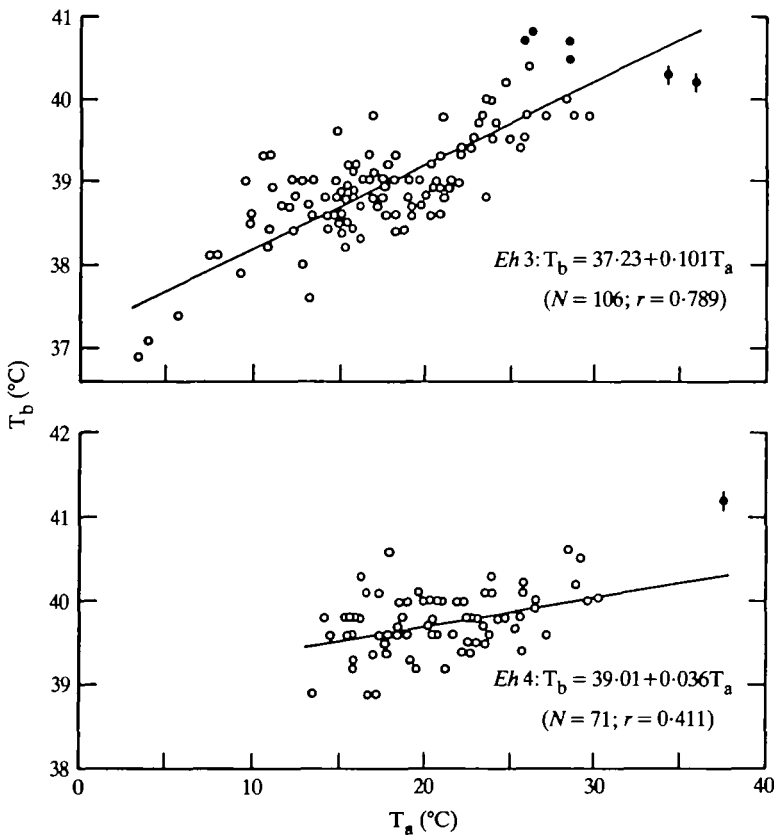

Fig. 3. Effect of T_a on flight T_b for flights over 200 s for *Eh* 3 and over 120 s for *Eh* 4. Shaded circles are flights in which bats showed cooling behaviour; vertical bars are flights terminated prematurely due to overheating. Equations describe regression lines.

velocity was less than at $5 \, \mathrm{m \, s^{-1}}$, the bat's endurance was significantly greater for the first flight of each day than for the second one of each pair, whichever airspeed was the first used ($P < 0.05$).

For *Eh* 3, endurance at $7 \, \mathrm{m \, s^{-1}}$ was significantly greater than at 5 or $9 \, \mathrm{m \, s^{-1}}$ ($P < 0.001$) or $6 \, \mathrm{m \, s^{-1}}$ ($P < 0.05$), but the difference between endurance at $8 \, \mathrm{m \, s^{-1}}$ and the V_{mp} was insignificant. Like the pattern for *Ra* 3 at 5 and $6 \, \mathrm{m \, s^{-1}}$, when endurance of *Eh* 3 was measured at $8 \, \mathrm{m \, s^{-1}}$, the duration of the day's first flight averaged 45 % greater ($P < 0.01$) than that in the second flight, whichever of the two airspeeds was the first used.

DISCUSSION

Respiratory exchange ratio

The pattern in which R declines during the course of a flight, or is lower in a second flight on a given day, has been reported in all metabolic measurements in bats
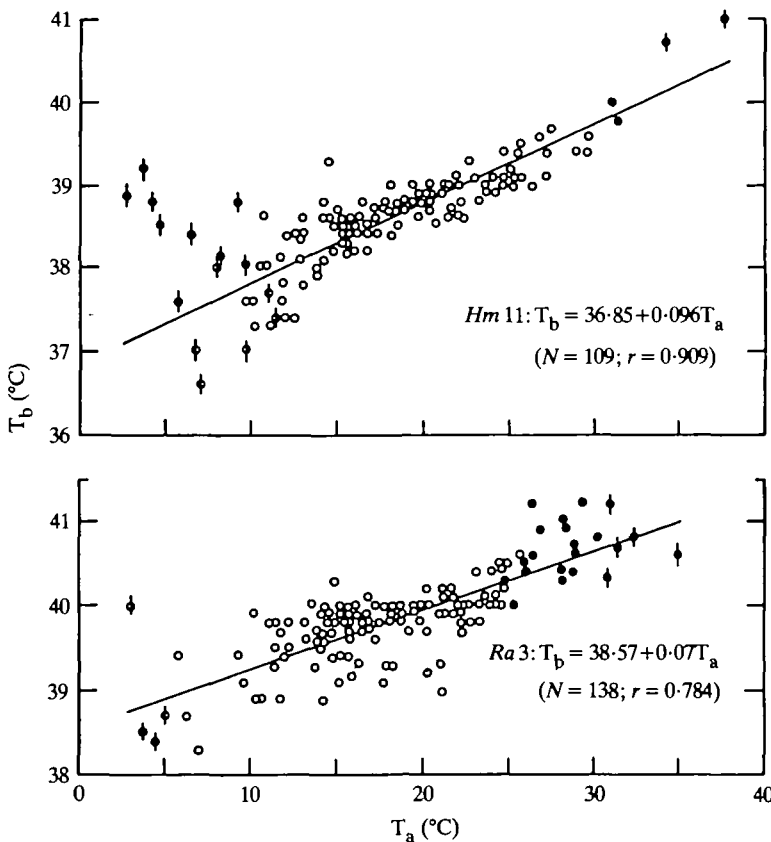

Fig. 4. Effect of T_a on flight T_b for flights over 200 s for *Hm* 11 and *Ra* 3. Shaded circles are flights in which bats showed cooling behaviour; vertical bars are flights terminated in less than 200 s due to overheating or chilling, and not used in calculations of regression lines.
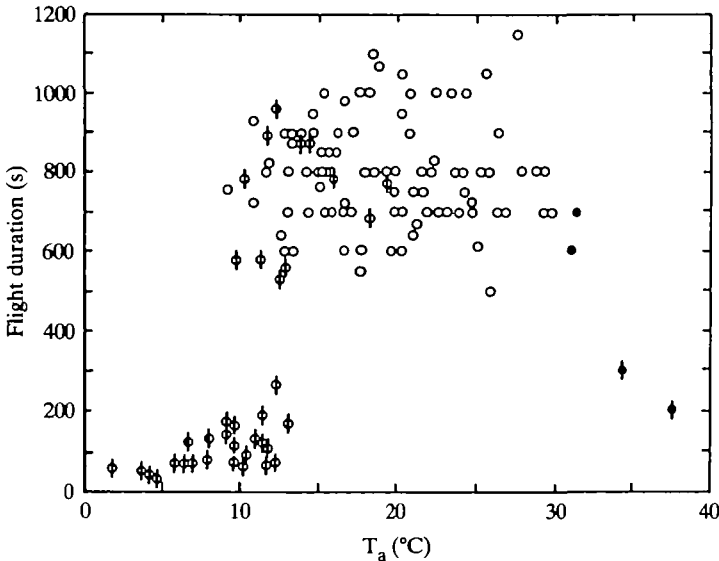
Fig. 5. Effect of T_a on flight duration of *Hm* 11 without a mask, when accustomed to flying 800–1000 s. Shaded circles are flights in which the bat showed cooling behaviour; vertical bars are flights terminated prematurely, usually associated with cold or overheating.

(Thomas, 1975; Carpenter, 1985), and for at least one species of bird (Hudson & Bernstein, 1983). The minimum R values for *Eh* 3 and *Hm* 11 are the lowest reported thus far for any bat, and indicate that fat accounts for as much as 77–92 % of the energy required for flight. However, it is not clear that steady R values have been reached in any previous measurements on bats. If flights are sufficiently long, R might decline to the minimum value of 0·70–0·72 measured in birds (Tucker, 1972; Torre-Bueno & Larochelle, 1978), which would indicate that fat is the exclusive energy source.

Oxygen consumption and power input

There are no $\dot{V}_{O_2}$ data from other bats similar in size to *Eh* 3 and *Hm* 11. However, Thomas (1975) presented a scaling formula fitted to the minimum mass-specific power input values ($P_{i,min}$) of the five flying birds and bats that had been measured to date (Table 7). The $P_{i,min}$ of *Eh* 3 was only 2 % greater than the value predicted from body mass, but the data for *Hm* 11 were 22 % above the expected value. Even greater variation is known among birds of equal size; the $P_{i,min}$ of fish crows was 48 % greater than that of a laughing gull of the same mass (Bernstein *et al.* 1973). This may have resulted from the lower aspect ratio and higher fw of the crow. The fw of *Hm* 11 and *Eh* 3 were similar at their V_{mp} (Table 5), but *Hm* 11 died before wing measurements could be made in flight.

The number of individual fliers for which $\dot{V}_{O_2}$ has been measured in wind tunnels has now tripled since Thomas's (1975) formula was published. New regression lines (Fig. 8) fitted to data for bats only and from all eleven animals for which $P_{i,min}$ values

are known are very similar to his original line (Table 7). The inclusion of P_i values from *Pp* 1, *Pp* 7 and from pigeons flying at $10 \, \mathrm{m \, s^{-1}}$, which may not have been their V_{mp} (Butler, West & Jones, 1977), affects the regression only slightly (equation 4, Table 7).

Evaporative water loss

The inverse relationship between evaporative water loss and vapour pressure (Fig. 2) conforms to the pattern reported in two *P. poliocephalus* in flights over a wider range of vapour pressure (Carpenter, 1985). The wide scatter in these data is presumably the result of non-respiratory water loss such as nasal secretion or salivation, although data were omitted from flights when these were apparent in the mask. The EWL of *Eh* 3 and *Hm* 11 was about the same per litre of consumed O_2, but the greater $\dot{V}_{O_2}$ of *Hm* 11 resulted in a higher mass-specific EWL (Fig. 9, points 8, 9).
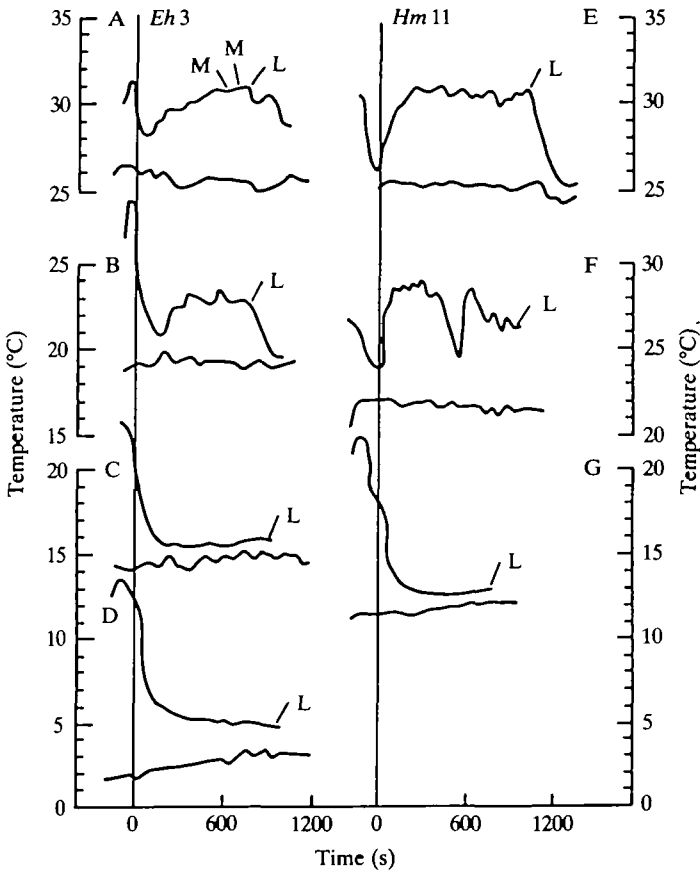

Fig. 6. Typical flight records of T_f (upper traces) and T_a (lower traces) for *Eh* 3 (left column) and *Hm* 11 (right column). Thin vertical lines indicate starts of flights; L indicates times of landing. Temperature scales are for adjacent records. Record A was made during a flight when *Eh* 3 was overheated, as indicated by stereotyped mouth opening at times indicated by M.
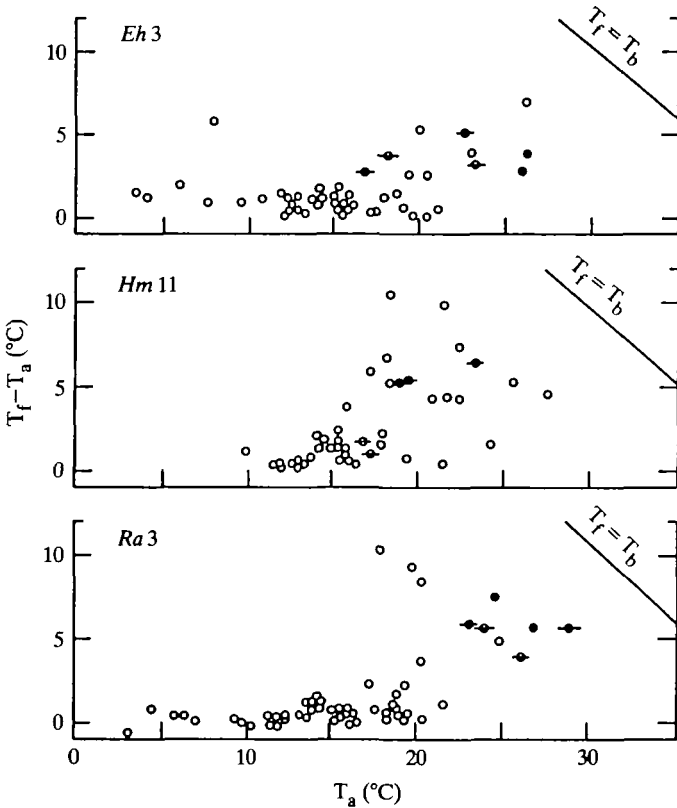
Fig. 7. Differences between T_f and T_a as a function of T_a. Shaded circles are flights during which bats showed cooling behaviour; horizontal bars indicate that T_f was not stable. Diagonal lines indicate the theoretical maximum values for (T_f-T_a), if foot temperatures had equalled T_b (read from regression lines in Figs 3 and 4).

To compare mass-specific values with other species, I used the closely grouped data within a small range of VP (Fig. 2). Available data from other species in flight (Fig. 9) were obtained over a wide range of ambient VP, both by total weight loss during short flights, or by collection of only respiratory water loss through masks. Despite the nearly two-fold variation in EWL among bats within a narrow size range, the least squares regression line fitted to these data (equation 5, Table 7) may have crude predictive value in estimating water budgets of bats.

The metabolic demands of flight result not only in high rates of water loss, but in a proportional production of metabolic water. Since the overall average value of R was about 0·78 for both *Eh* 3 and *Hm* 11 (Table 2), the mean rate of metabolic water production (MWP) would be $0.57\,g\,l^{-1}\,O_2$ consumed. The horizontal dashed lines in Fig. 2 indicate this ratio; the mean respiratory EWL of the two animals would apparently exceed MWP at any vapour pressure below 12–14 Torr. However, even in the 'dry' season in the rain forests of Gabon, the atmospheric humidity is frequently high enough to result in heavy ground fog, and a high water intake is provided by the bats' soft fruit diet.

The EWL data in Fig. 2 can also be used to calculate the fraction of heat lost by pulmonary evaporation. I have again assumed that heat production is 75 % of metabolic rate, as in other fliers (Tucker, 1972; Bernstein, 1976; Thomas, 1975), and that evaporation of $1 g H_2O$ dissipates $2.44 kJ$ ($0.58 kcal$). Thus, when EWL is $1 g H_2O$ $l^{-1} O_2$, the ratio of evaporative heat loss to metabolic heat production (H_e/H_p) is 0.161 (Fig. 2). These data show that about 10 % of the heat produced was lost by respiratory evaporation, a fraction similar to that measured for *P. poliocephalus* (Carpenter, 1985) and *P. hastatus* (14 %; Thomas & Suthers, 1972).

In flying birds, cutaneous water loss may account for 10 % of heat production (Hudson & Bernstein, 1981), but there have been no attempts to measure this in flying bats. In the few measurements on non-respiratory water loss in caged bats, the

Table 4. *Heart rates (beats min^{-1}) and respiratory rates (breaths min^{-1}) in six flying bats*

	Heart rate		Respiratory rate	
	at airspeed		at airspeed	
Bat	(m s^{-1})	(beats min^{-1})	(m s^{-1})	(breaths min^{-1})
Eidolon helvum no. 3 0·315 kg	6·5	576 (6, 5)*	7·0	295 (26, 2)
Eidolon helvum no. 4 0·260 kg	5·5–6·0	601 (3, 15)*	5·5	316 (6, 2)†
Hypsignathus monstrosus no. 11 0·258 kg	5·5	620 (5, 4)	5·5	293 (8, 2)
Rousettus aegyptiacus no. 3 0·188 kg	5·0	728 (4, 2)*	—	—
Pteropus poliocephalus no. 1 0·459 kg	—	—	6·0	181 (14, 1)
Pteropus poliocephalus no. 5 0·756 kg	6·5–7·5	476 (18, 2)	6·5–7·5	163 (23, 2)†

Numbers in parentheses are numbers of counts followed by S.E.M.
* Post-flight measurements described in text.
† Based on EMGs of wing beats.

Table 5. *Wingbeat frequencies from films of four flying bats*

Speed (m s^{-1})	*Eidolon helvum* no. 3 0·315 kg	*Eidolon helvum* no. 4 0·260 kg	*Hypsignathus monstrosus* no. 11 0·258 kg	*Rousettus aegyptiacus* no. 3 0·188 kg
4	340 (1)	343 (3, 6)	318 (3, 3)	410 (3, 0)
5	320 (1)	302 (4, 6)	305 (4, 6)*	367 (3, 6)*
6	326 (3, 15)	295 (6, 6)	301 (4, 10)	370 (2, 0)
7	291 (5, 7)*	275 (2, 7)	302 (3, 10)	345 (2, 7)
8	300 (3, 0)	267 (3, 6)	310 (3, 10)	340 (2, 0)

Numbers in parentheses are number of counts, followed by S.D.
* Indicates speed of minimum P_i, as determined by $\dot{V}_{O_2}$ or maximum endurance.

R. E. CARPENTER

Table 6. *Effect of velocity on endurance, maximum distance possible and metabolic capacity of three bats*

Bat	Velocity $(m\,s^{-1})$	Relative endurance (E_t/E_{mp})	Relative endurance (E_t/E_{mp}) required for equivalent distance $(= V_{mp}/V_t)$	Maximum distance (km) possible $(= E_t \times V_t)$[*]	Metabolic capacity (kJ) $(= P_t \times E_t)$[*]
Eh 3	5	0·014 (6, 0·00)	1·4	0·25	no P_t data
	6	0·782 (12, 0·16)	1·16	16·89	65·5
	7	1·0†	1·0	25·20	79·2
	8	0·846 (12, 0·12)	0·875	24·4	67·1
	9	0·051 (10, 0·00)	0·78	1·66	no P_t data
Hm 11	5	1·00†	1·00	18·00	80·9
	8	0·20 (10, 0·04)	0·625	5·76	16·51
Ra 3	3	0·134 (10, 0·02)	1·65	1·45	no P_i data
	4	0·487 (10, 0·06)	1·25	7·01	no P_i data
	5	1·00†	1·00	18·00	no P_t data
	6	0·848 (12, 0·10)	0·83	18·32	no P_t data
	7	0·483 (10, 0·12)	0·71	12·17	no P_t data
	8	0·061 (6, 0·03)	0·625	1·76	no P_i data

Numbers in parentheses are number of measurements, followed by S.E.M.
[*] Calculated on assumption that $E_{mp} = 3600$ s.
† Absolute endurance at these velocities was variable, but was always treated as the reference value in calculating E_t/E_{mp}; hence there is no statistic calculated.
For abbreviations see Table 7.

experimental conditions and assumptions do not permit application of those data to consideration of thermoregulation during flight (Chew & White, 1960; Laburn & Mitchell, 1975). However, the sweat glands of bats are generally considered to be of little significance in thermoregulation (Quay, 1970), and the typical responses to heat stress are panting, wing fanning and licking the wings, without observable sweating (Bartholomew, Leitner & Nelson, 1964; Carpenter & Graham, 1967; Laburn & Mitchell, 1975). Thus, the respiratory system is probably the only significant avenue for evaporative heat loss in flight.

Temperature regulation

The positive correlation between T_a and T_b of the African bats has been reported for other flying bats (O'Farrell & Bradley, 1977; Carpenter, 1985). As with the flying foxes, there was a fairly distinct upper T_a above which sustained flight could not occur. This was higher for *Eh* 4 than for *Eh* 3, but the former typically flew for shorter periods before measurement of T_b, which may not have stabilized. However, in longer flights *Hm* 11 tolerated a T_a about 5 °C warmer than did the flying foxes or the other bats in this study. Thus, it is of interest to compare their maximum rates of non-evaporative thermal conductance in flight (C_f), which is described by the formula:

$$C_f = (H_l - H_e)/(T_b - T_a), \tag{12}$$

where the total heat loss (H_l) is the fraction (here, 0·75) of exercising metabolic rate not represented as work and H_e is the rate of heat loss by evaporation. In calculating values for these three bats, values for T_b were read from regression lines in Figs 3 and 4, at the highest T_a that never provoked cooling behaviour in flight. A $P_{i,min}$ value of

Table 7. *Coefficients for the allometric equation* $y = aM^b$, *relating physiological variables in flight to body mass (M) in kilograms*

Variable and units	a	b	N	r^2	Equation no.
Bats and birds: $P_{i,min}$ (W kg^{-1}; Thomas, 1975)	52·6	−0·223	5	—	3
Bats only: known $P_{i,min}$ (W kg^{-1})	50·03	−0·296	6	0·902*	4
Bats and birds: known $P_{i,min}$ (W kg^{-1})	50·6	−0·260	11	0·809*	5
Bats and birds: known $P_{i,min}$ (W kg^{-1}) from equation 5 and P_i from Pp 1, Pp 7 and pigeons (see text)	50·1	−0·264	14	0·810*	6
Bats: evaporative water loss (g H$_2$O kg^{-1} h^{-1})	4·23	−0·602	13	0·853*	7
Bats: heart beats min^{-1}	453·6	−0·224	9	0·974*	8
Birds: heart beats min^{-1}	533·8	−0·145	21	0·899*	9
Bats: breaths min^{-1}	170·5	−0·301	16	0·884*	10
Birds: breaths min^{-1}	159·9	−0·148	18	0·441*	11

* r significantly different from zero, $P < 0·01$.
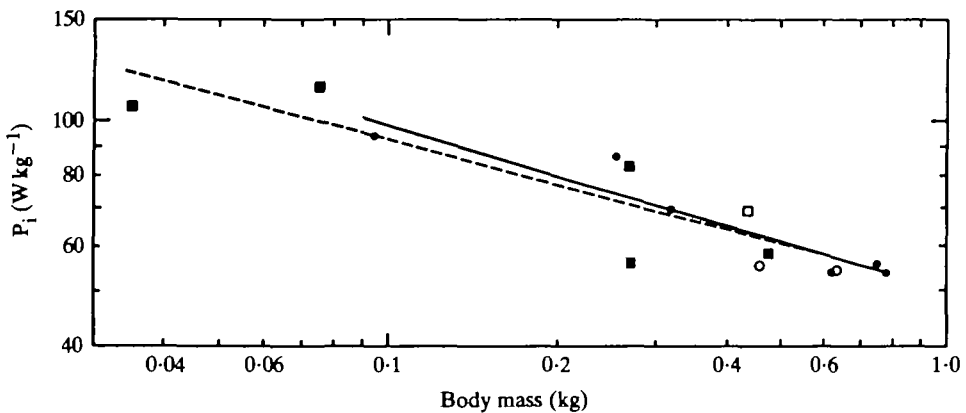For abbreviations see Table 1.

Fig. 8. Relationship between body mass and minimum power input in flight ($P_{i,min}$) for bats (circles) and birds (squares). Unshaded symbols indicate P_i values that may not have been minimum for several fliers, and which were not used in calculations of least squares regression lines. Solid line is fitted to $P_{i,min}$ data for bats only; dashed line is fitted to data for bats and birds. Coefficients for lines are given in Table 7. Bat data are from Thomas (1975) and Carpenter (1985 and this study). Bird data are from Tucker (1968, 1972), Bernstein, Thomas & Schmidt-Nielsen (1973), Torre-Bueno & Larochelle (1978), Butler, West & Jones (1977) and Hudson & Bernstein (1983).

$78 \cdot 7 \, \mathrm{W \, kg^{-1}}$ was calculated for $Ra\,3$ from equation 3 of Table 7, and its H_e was also assumed to be 10% of H_l.

The resulting C_f values of $3 \cdot 2$, $6 \cdot 1$ and $3 \cdot 5 \, \mathrm{W \, kg^{-1} \, °C^{-1}}$ for $Eh\,3$, $Hm\,11$ and $Ra\,3$, respectively, are greater than the value of $2 \cdot 5 \, \mathrm{W \, kg^{-1} \, °C^{-1}}$ calculated for *P. poliocephalus* (Carpenter, 1985), reflecting the greater mass-specific metabolic rates of these smaller species at about the same T_a. The high C_f of $Hm\,11$ is associated with its ability to fly at a higher T_a than any of the other bats, despite losing an equal fraction of its heat production by pulmonary evaporation (Fig. 2).

Foot temperatures

Van Cleave (1975) showed that changes in patterns of blood flow could be detected in flying *P. poliocephalus* by changes in skin temperature, and that the patterns of change were the same on wing surfaces and the feet (although the magnitudes of temperature changes differed). Thus, the measurements of T_f for these African species indicate the conditions under which blood flow to the feet, and presumably the wings as well, increased or decreased in response to heat loads imposed by flight.

At $T_a < 15\,°C$, the small $(T_f - T_a)$ differences (Fig. 7) show that blood flow to naked surfaces was minimal, which results in heat conservation at low T_a. At $T_a > 15\,°C$, blood flow to the feet was high; if the bat showed behavioural signs of
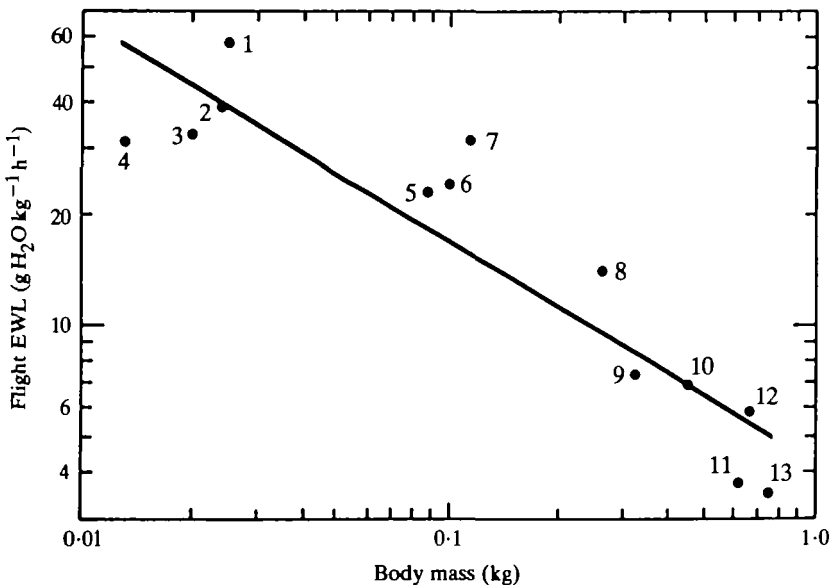

Fig. 9. Relationship between body mass and mass-specific evaporative water loss (EWL) in flying bats. Point no. 1 from Carpenter (1968), nos 2–4, Carpenter (1969), nos 12, 13, Carpenter (1985), nos 5, 6, Thomas & Suthers (1972), no. 7, Kulzer (1979). Point no. 8, *Hm* 11; no. 9, *Eh* 3; no. 10, *Pp* 1; and no. 11, *Pp* 7 of present study. Coefficients for line are given in Table 7.

hyperthermia, blood flow remained high after landing, presumably until T_b declined to some (unmeasured) set point (Fig. 6A).

There are obvious theoretical limitations to the usefulness of this mechanism. The rate of heat loss from wings and feet should be proportional to the magnitude of the (T_f-T_a) differences and the rate at which blood flow can carry heat to these surfaces. However, as T_a increases, the maximum (T_f-T_a) difference must become smaller, even though T_b increases slightly. The maximum differences possible are shown in Fig. 7 by diagonal lines representing (T_f-T_a) when $T_f = T_b$, with T_b derived from the regression lines in Figs 3 and 4. The differences in (T_f-T_a) never reached this limit, although at higher T_a, the (T_f-T_a) values of *Hm* 11 seemed to parallel the decline in theoretical maxima.

The second limitation of this mechanism is the amount of blood that can be sent to wings and feet, since blood used for cooling is presumably less available for O_2 transport to the muscles. Ever increasing amounts of blood would be required to dissipate heat as T_f approaches T_a. Thus, as useful as this system might be at moderate temperatures, its effectiveness actually diminishes as increasing T_a reduces the (T_f-T_a) differential. Elevated pulmonary ventilation and evaporative cooling, which birds employ at high T_a (Torre-Bueno, 1978*a*; Hudson & Bernstein, 1981), is free of both of these limitations. However, the 1:1 coupling of fw and fR in all bats studied thus far (Suthers, Thomas & Suthers, 1972; Thomas, 1981; Carpenter, 1985) apparently precludes major increases in pulmonary ventilation necessary to achieve this effect. The rates of evaporative heat loss caused by opening the mouth in flight have not been measured, but all bats have usually been unable to continue flights at T_a that caused this behaviour.

The limited thermoregulatory capabilities of flying bats appears to be one factor associated with flight activity primarily during cooler nocturnal temperatures in the tropical and subtropical habitats where they are most abundant (Carpenter, 1985). However, all measurements on metabolic rate, body temperature and evaporative heat loss on bats in sustained flight have been made in wind tunnels. Under these circumstances, the opportunity for radiative heat losses to the night sky is absent, and the apparent limitations to flight of bats at high T_a may be artificially exaggerated by this situation.

The dramatic effect of low T_a on *Hm* 11 and *Ra* 3 suggests that wing structure imposes another climatic limitation on bats. Convective heat losses to cold air may be so great that wing muscles are chilled to a degree prohibiting the precise coordination necessary for flight. Indeed, in isolated forearm muscles from several species of temperate zone bats, the durations of contractions at temperatures below 8°C were 8–10 times those at 32°C (Nelson, Hirshfield, Schreiweis & O'Farrell, 1977). Even if non-tropical species are less sensitive to cold, there must be an absolute minimum T_a at which bats can fly, set by the freezing point of tissues in the wings.

The wings might be warmed through vasodilation, but at T_a near 0°C the resulting rate of heat loss from the body must be enormous. Even at warm T_a, the smallest differences between T_b and T_f in the African bats were 8–10°C, which indicates how rapidly heat was lost from the (relatively) thick feet when T_a was as high as 27°C.

The reports of small bats in flight at T_a as low as $-5\,°C$ (O'Farrell & Bradley, 1977)¶ suggest a need for very careful environmental measurement or further physiological study, especially in light of the data on lengthened contraction times in the same species. Hibernation or autumn migration to warmer climates may be as important in enabling temperate zone bats to avoid the difficulties of flight at low temperatures as they are to alleviating the energy imbalances when food is scarce. Birds are presumably relatively immune to the control problems in flight owing to the insulation on their wings, and the absence of muscles in the wing surface.

Heart rate

Data are now available for f_H during, or immediately after, flight for nine bats over a range of body masses from about 0·020 to 0·80 kg (Thomas & Suthers, 1972; Carpenter, 1985; Table 4). Separate least squares regression lines were fitted to log-transformed data on f_H and body masses of bats and birds; the resulting slopes (equations 8, 9, Table 7) were both significantly different from zero ($P < 0·01$), and were also different from each other (analysis of covariance; Zar, 1974). However, values along the two lines were identical at a body mass of about 0·11 kg, and did not differ by more than 15 % at any body mass within the size range of the bats (Fig. 10).

Respiratory and wingbeat cycles

In this study f_W and f_R have been measured in several ways. In some cases, such as $Eh\,3$ at $V = 7\,m\,s^{-1}$, there was good agreement between values obtained with a thermocouple in a mask (Table 4) and counts from films of bats flying without any encumbrance (Table 5). However, in other instances, the f_W values from mask thermocouples were up to 20 % greater than values determined by film or EMG records. The difference may reflect the added work to overcome drag of the mask and tubing; if so, photography should produce more accurate data.

Despite some inconsistency in data when f_W and f_R were measured separately, a 1:1 coupling of f_W and f_R has now been recorded in bats of five species across a size range of approximately 0·10 to 0·87 kg. In bats measured at the extremes of this size range, *P. hastatus* and *P. alecto* (as *P. gouldii*, synonymy according to Tate, 1942), the coupling occurs across all airspeeds at which the animals would fly (Suthers *et al.* 1972; Thomas, 1981). Thus, it seems justifiable to assume that f_W data are indirect measures of their f_R values.

Fig. 11 plots the minimum f_W data for a variety of bats, indicating those individuals in which f_W and f_R are known to be coupled for at least one airspeed. The slope of the regression line for these data differs significantly from zero ($P < 0·01$), as well as from a regression line fitted to f_R data for flying birds (Fig. 11; equations 10, 11, Table 7). There is less agreement between these two data sets than for the f_H data, which might be expected in view of the greater differences in mammalian and avian respiratory systems. But understanding the significance of such similarities or differences depends on further work like that of Thomas (1981), and quantitative data on all aspects of the O_2 delivery system across the range of sizes of fliers.

Endurance

In view of the nice endurance data for *Ra* 3 and the wide power curve for *Hm* 11, it is regrettable that the complementary data are missing for each bat. However, some assumptions about their patterns may be made. It would be contrary to the pattern for other bats if the endurance of *Hm* 11 at V = 6 or 7 m s^{-1} had been significantly greater than that at V = 5 m s^{-1}. Further, the power curve of *Ra* 3 probably increased
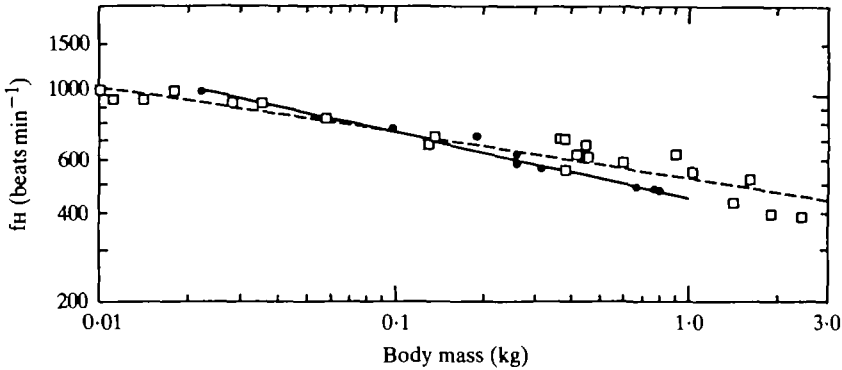

Fig. 10. Relationship between body mass and heart rates (fH) of bats (circles and solid regression line) and birds (squares and dashed line). Coefficients for lines are given in Table 7. Bat data are from Studier & Howell (1969), Thomas & Suthers (1972), Carpenter (1985 and this study). Bird data are from Berger, Hart & Roy (1970), Aulie (1971, 1972), Butler, West & Jones (1977), Gessaman (1978, 1980), Kanwisher, Williams, Teal & Lawson (1978) and Butler & Woakes (1980).
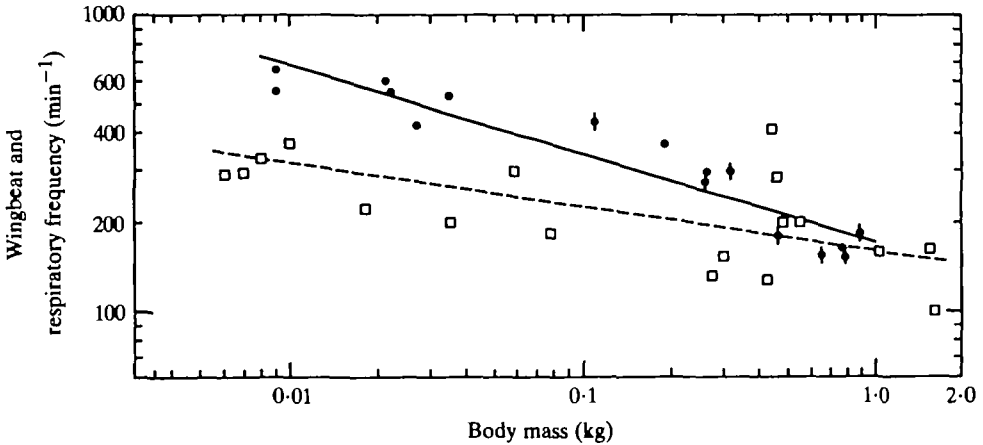

Fig. 11. Relationships between body mass and wingbeat frequencies (fw) of bats (circles) and respiratory frequencies (fR) in birds (squares). Vertical bars indicate bats in which fR and fw are known to be coupled at one or more airspeeds. Coefficients for regression lines are given in Table 7. Bat data are from Craft, Edmondson & Agee (1958), Richardson (1973), Norberg (1976a,b), Thomas (1981), Thomas, Lust & Van Riper (1984) and Carpenter (1985 and this study). Bird data are from Tucker (1968, 1972), Berger, Hart & Roy (1970), Fig. 8 of Berger, Roy & Hart (1970), Berger & Hart (1972), Bernstein (1976), Butler, West & Jones (1977), Berger (1978), Torre-Bueno (1978a,b), Butler & Woakes (1980) and Hudson & Bernstein (1981).

only gradually with increasing speeds above its speed of maximum endurance, which was probably its V_{mp}. If so, then its cost of transport would have been minimal at $V = 8\,m\,s^{-1}$.

The effect of velocity on the endurance of all three bats has the same energetic implications that it did for two $P.\ poliocephalus$ (Carpenter, 1985). The relative distances that might be possible at each V_t were calculated by assuming that bats could fly for 3600 s at V_{mp}, and multiplying the other relative endurances (in s) by the respective V_t values (Table 6). The endurances at V_{mp} so greatly exceeded those at the velocities of 'maximum range' that the maximum ranges in still air would actually have been achieved at slower but less economical speeds. It is interesting that the V_{mp} of Eh 3 was close to the middle of the range of flight speeds ($4\cdot5$–$8\cdot3\,m\,s^{-1}$) reported for this species in the wild (Kulzer, 1968). In such cases, the actual costs of transport (Table 3) in still air would probably be greater than the minimum values at maximum speeds; this cost would be especially high for Hm 11, which had a high power input at its relatively slow V_{mp}. If Ra 3 maximized its range by flying at $V = 6\,m\,s^{-1}$ (Table 6), and its $P_{i,\,min}$ were accurately predicted by equation 3 of Table 7, then its actual cost of transport would be about $1\cdot3$. As with $P.\ poliocephalus$ (Carpenter, 1985), the products of P_i and endurance at each speed (the 'metabolic capacity') were unequal across the range of speeds. This indicates that endurance was not limited at every velocity merely by fuel reserves as one would expect of an aeroplane.

The fact that endurance was maximal at V_{mp}, and diminished at the extreme airspeeds, suggests that there was a relationship between endurance and power input. For comparative purposes, each bat's endurance value at each V_t was plotted as the ratio E_t/E_{mp}, and its corresponding P_i was plotted as the ratio to the bat's $P_{i,\,min}$, since there were such great differences in body sizes and absolute P_i data among various species. The least squares regression line for a log–log transformation of these data has the following equation:

$$E_t/E_{mp} = 0\cdot837(P_i/P_{i,\,min})^{-7\cdot45}. \tag{13}$$

The slope is significantly different from zero ($N = 11$, $r = -0\cdot877$, $P < 0\cdot01$); the 95 % confidence limits for the slope are $-4\cdot46$ and $-10\cdot44$. A point indicating the relative endurance of Pp 6 at $V = 8\cdot6\,m\,s^{-1}$ and its relative P_i at $V = 8\,m\,s^{-1}$ is included in Fig. 12, but these values were not used in calculating the regression line.

If endurance is dependent on P_i, it should be fairly constant at those velocities causing small changes in P_i, as was the case with Eh 3 at $V = 7$ and $8\,m\,s^{-1}$. But the magnitude of the negative exponent in equation 13 is so great that only a 10 % increase in relative P_i would reduce endurance to about 50 % of that at V_{mp}. Even if the exponent were the more conservative 95 % confidence limit of $-4\cdot46$, endurance would be only 65 % of that at V_{mp} with a 10 % increase in P_i.

In athletes, endurance is inversely proportional to power input ($E \propto P^{-1}$; Wilkie, 1980). This seems intuitively correct, since it could be the result of an animal expending energy at some rate until the accessible fuel was exhausted. But the exponent in equation 4 results in a much greater decline in endurance with increased
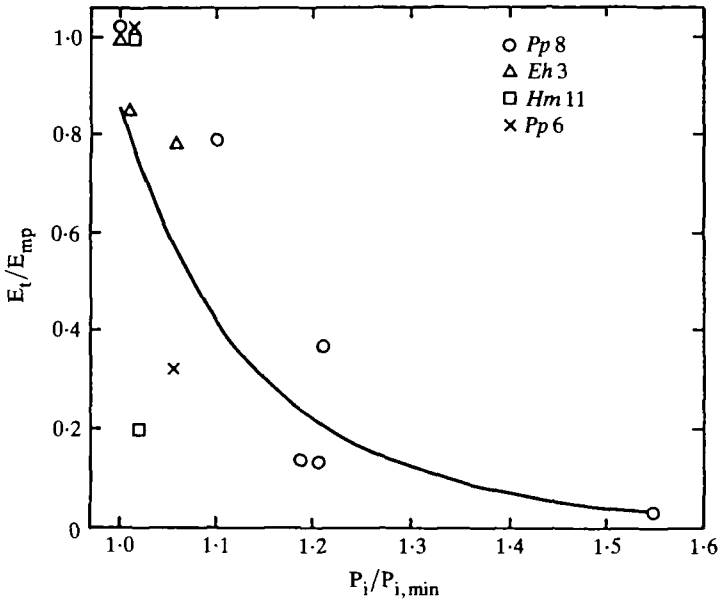
Fig. 12. Relationship between relative endurance (E_t/E_{mp}) and relative power input ($P_i/P_{i,min}$) of four bats. Data point for *Pteropus poliocephalus* no. 6 indicates endurance at $8.6\,m\,s^{-1}$ but $P_i/P_{i,min}$ at $8\,m\,s^{-1}$, which was not used in the calculation of the least squares regression line.

P_i than the expected inverse relationship. In effect, this expresses again the calculations of very unequal metabolic capacities (Table 6), for which roughly similar values would be expected at all airspeeds, if fuel were always the factor limiting endurance.

The actual limitations are unknown. A previous suggestion (Carpenter, 1985) that O_2 delivery was insufficient at extreme velocities seems justified at the lowest airspeeds, which caused animals to be clearly out of breath after very brief flights. At velocities closer to the centre of the power curve, endurance may be limited by fatigue of specific muscle groups required for control at atypical velocities. There seems no *a priori* reason that all muscles should become incapable of normal function after the same interval, especially at flight speeds requiring unusual contributions to the wingbeat.

The fact that the V_{mr} is apparently the same as the V_{mp} in representatives of four bat species raises more strongly the question of whether such patterns exist in migratory birds. Even without metabolic data, wind tunnel measurements of endurance could identify the V_{mr}, presumably with more definitive results than have been obtained by measurement of birds' freely chosen airspeeds in nature (Tucker & Schmidt-Koenig, 1971; Schnell & Hellack, 1979).

REFERENCES

ALLEN, J. A., LANG, H. & CHAPIN, J. P. (1917). The American Museum Congo Expedition collection of bats. *Bull. Am. Mus. nat. Hist.* **37**, 405–563,

AULIE, A. (1971). Co-ordination between the activity of the heart and the flight muscles during flight in small birds. *Comp. Biochem. Physiol.* **38A**, 91–97.

AULIE, A. (1972). Co-ordination between the activity of the heart and the pectoral muscles during flight in the pigeon. *Comp. Biochem. Physiol.* **41A**, 43–48.

BARTHOLOMEW, G. A., LEITNER, P. & NELSON, J. E. (1964). Body temperature, oxygen consumption and heart rate in three species of Australian flying foxes. *Physiol. Zoöl.* **37**, 179–198.

BERGER, M. (1978). Ventilation in the hummingbirds *Colibri coruscans* during altitude hovering. In *Respiratory Function in Birds, Adult and Embryonic* (ed. J. Piiper), pp. 85–88. Berlin: Springer-Verlag.

BERGER, M. & HART, J. S. (1972). Die Atmung beim Kolibri *Amazilia fimbriata* während des Schwirrfluges bei verschiedenen Umgebungstemperaturen. *J. comp. Physiol.* **81**, 363–380.

BERGER, M., HART, J. S. & ROY, O. Z. (1970). Respiration, oxygen consumption and heart rate in some birds during rest and flight. *Z. vergl. Physiol.* **66**, 201–214.

BERGER, M., ROY, O. Z. & HART, J. S. (1970). The co-ordination between respiration and wing beats in birds. *Z. vergl. Physiol.* **66**, 190–200.

BERNSTEIN, M. H. (1976). Ventilation and respiratory evaporation in the flying crow, *Corvus ossifragus. Respir. Physiol.* **26**, 371–382.

BERNSTEIN, M. H., THOMAS, S. P. & SCHMIDT-NIELSEN, K. (1973). Power input during flight of the fish crow, *Corvus ossifragus. J. exp. Biol.* **58**, 401–410.

BRADBURY, J. W. (1977). Lek mating behavior in the hammer-headed bat. *Z. Tierpsychol.* **45**, 225–255.

BUTLER, P. J., WEST, N. H. & JONES, D. R. (1977). Respiratory and cardiovascular responses of the pigeon to sustained, level flight in a wind-tunnel. *J. exp. Biol.* **71**, 7–26.

BUTLER, P. J. & WOAKES, A. J. (1980). Heart rate, respiratory frequency and wing beat frequency of free flying barnacle geese *Branta leucopsis. J. exp. Biol.* **85**, 213–226.

CARPENTER, R. E. (1968). Salt and water metabolism in the marine fish-eating bat, *Pizonyx vivesi. Comp. Biochem. Physiol.* **24**, 951–964.

CARPENTER, R. E. (1969). Structure and function of the kidney and the water balance of desert bats. *Physiol. Zoöl.* **42**, 288–302.

CARPENTER, R. E. (1975). Flight metabolism of flying foxes. In *Swimming and Flying in Nature*, Vol. 2, (eds T. Y.-T. Wu, C. J. Brokaw & C. Brennen), pp. 883–890. New York: Plenum Press.

CARPENTER, R. E. (1985). Flight physiology of flying foxes. *J. exp. Biol.* **114**, 619–647.

CARPENTER, R. E. & GRAHAM, J. B. (1967). Physiological responses to temperature in the long-nosed bat, *Leptonycteris sanborni. Comp. Biochem. Physiol.* **22**, 709–722.

CHEW, R. M. & WHITE, H. E. (1960). Evaporative water losses of the pallid bat. *J. Mammal.* **41**, 452–458.

CRAFT, T. J., EDMONDSON, M. I. & AGEE, R. (1958). A comparative study of the mechanics of flying and swimming in some common bats. *Ohio J. Sci.* **58**, 245–249.

GESSAMAN, J. A. (1978). Body temperature and heart rate of the snowy owl. *Condor* **80**, 243–245.

GESSAMAN, J. A. (1980). An evaluation of heart rate as an indirect measure of daily energy metabolism of the American kestrel. *Comp. Biochem. Physiol.* **65A**, 273–289.

HUDSON, D. M. & BERNSTEIN, M. H. (1981). Temperature regulation and heat balance in flying white-necked ravens, *Corvus cryptoleucus. J. exp. Biol.* **90**, 267–281.

HUDSON, D. M. & BERNSTEIN, M. H. (1983). Gas exchange and energy cost of flight in the white-necked raven, *Corvus cryptoleucus. J. exp. Biol.* **103**, 121–130.

KANWISHER, J. W., WILLIAMS, T. C., TEAL, J. M. & LAWSON, K. D., JR. (1978). Radiotelemetry of heart rates from free ranging gulls. *Auk* **95**, 288–293.

KULZER, E. (1968). Der Flug des afrikanischen Flughundes *Eidolon helvum. Natur und Museum* **48**, 181–194.

KULZER, E. (1979). Physiological ecology and geographical range in the fruit-eating cave bat genus *Rousettus* Gray 1821. A review. *Bonner zool. Beitr.* **30**, 233–275.

LABURN, H. P. & MITCHELL, D. (1975). Evaporative cooling as a thermoregulatory mechanism in the fruit bat, *Rousettus aegyptiacus. Physiol. Zoöl.* **48**, 195–202.

NELSON, Z. C., HIRSHFIELD, J. R., SCHREIWEIS, D. O. & O'FARRELL, M. J. (1977). Flight muscle contraction in relation to ambient temperature in some species of desert bats. *Comp. Biochem. Physiol.* **56**A, 31–36.

NORBERG, U. M. (1976*a*). Some advanced flight manoeuvres of bats. *J. exp. Biol.* **64**, 489–495.

NORBERG, U. M. (1976*b*). Aerodynamics, kinematics, and energetics of horizontal flapping flight in the long-eared bat *Plecotus auritus. J. exp. Biol.* **65**, 179–212.

O'FARRELL, M. J. & BRADLEY, W. G. (1977). Comparative thermal relationships of flight for some bats in the southwestern United States. *Comp. Biochem. Physiol.* **58**A, 223–227.

QUAY, W. B. (1970). Integument and derivatives. In *Biology of Bats,* Vol. 2, (ed. W. A. Wimsatt), pp. 1–56. New York, London: Academic Press.

RICHARDSON, B. A. (1973). Photographic analysis of flight in a wind tunnel by the western long-nosed bat, *Leptonycteris sanborni*. Thesis, San Diego State University, San Diego. 118 pp.

SCHNELL, G. D. & HELLACK, J. J. (1979). Bird flight speeds in nature: optimized or a compromise? *Am. Nat.* **113**, 53–66.

STUDIER, E. H. & HOWELL, D. J. (1969). Heart rate of female big brown bats in flight. *J. Mammal.* **50**, 842–845.

SUTHERS, R. A., THOMAS, S. P. & SUTHERS, B. J. (1972). Respiration, wing-beat and ultrasonic pulse emission in an echo-locating bat. *J. exp. Biol.* **56**, 37–48.

TATE, G. H. H. (1942). Results of the Archbold Expedition. No. 48. Pteropodidae (Chiroptera) of the Archbold Expedition. *Bull. Am. Mus. nat. Hist.* **80**, 331–347.

THOMAS, S. P. (1975). Metabolism during flight in two species of bats, *Phyllostomus hastatus* and *Pteropus gouldii. J. exp. Biol.* **63**, 273–293.

THOMAS, S. P. (1981). Ventilation and oxygen extraction in the bat *Pteropus gouldii* during rest and steady flight. *J. exp. Biol.* **94**, 231–250.

THOMAS, S. P., LUST, M. R. & VAN RIPER, H. J. (1984). Ventilation and oxygen extraction in the bat *Phyllostomus hastatus* during rest and steady flight. *Physiol. Zoöl.* **57**, 237–250.

THOMAS, S. P. & SUTHERS, R. A. (1972). The physiology and energetics of bat flight. *J. exp. Biol.* **57**, 317–335.

TORRE-BUENO, J. R. (1978*a*). Evaporative cooling and water balance during flight in birds. *J. exp. Biol.* **75**, 231–236.

TORRE-BUENO, J. R. (1978*b*). Respiration during flight in birds. In *Respiratory Function in Birds, Adult and Embryonic,* (ed. J. Piiper), pp. 89–94. Berlin: Springer-Verlag.

TORRE-BUENO, J. R. & LAROCHELLE, J. (1978). The metabolic cost of flight in unrestrained birds. *J. exp. Biol.* **75**, 223–229.

TUCKER, V. A. (1968). Respiratory exchange and evaporative water loss in the flying budgerigar. *J. exp. Biol.* **48**, 67–87.

TUCKER, V. A. (1972). Metabolism during flight in the laughing gull. *Am. J. Physiol.* **222**, 237–245.

TUCKER, V. A. & SCHMIDT-KOENIG, K. (1971). Flight speeds of birds in relation to energetics and wind directions. *Auk* **88**, 97–107.

VAN CLEAVE, G. (1975). Heat budgets of flying bats. M.S. thesis, San Diego State University.

WILKIE, D. R. (1980). Equations describing power input by humans as a function of duration of exercise. In *Exercise Bioenergetics and Gas Exchange,* (eds P. Cerretelli & B. J. Whipp), pp. 75–80. Amsterdam: Elsevier/North-Holland Biomedical Press.

ZAR, J. H. (1974). *Biostatistical Analysis.* Englewood Cliffs, N.J.: Prentice-Hall.