

FLIGHT PHYSIOLOGY OF FLYING FOXES, *PTEROPUS POLIOCEPHALUS*

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SUMMARY

Oxygen consumption was measured during flight in two flying foxes (*Pteropus poliocephalus*) at airspeeds of $4\text{--}8.6\text{ ms}^{-1}$. There was good agreement with the measured power input of the only previously measured large bat, and with an allometric equation predicting power input for flying vertebrates. Measurements of respiratory exchange ratios, pulmonary water loss, respiratory frequencies, heart rates and body temperatures of both bats flying at intermediate airspeeds were compared with equivalent measurements on other bats or birds in flight. Despite a high non-evaporative thermal conductance in flight, the *P. poliocephalus* became severely hyperthermic at ambient temperatures (T_a) above 25°C . The failure to dissipate heat as successfully as flying birds at high T_a is apparently the result of an inability to increase pulmonary ventilation rates, and thus increase rates of evaporative heat loss.

The effect of airspeed on endurance was measured systematically on one bat. Endurance was not limited by energy reserves at all airspeeds, and flight times were significantly greater at the airspeed of minimum power input (V_{mp}). The endurance of both bats was so reduced at the higher airspeeds that they would not achieve maximum flight range in still air at the velocity where cost of locomotion is lowest. Contrary to a common assumption, flight range would be maximized at the V_{mp} .

INTRODUCTION

The last fifteen years have seen an enormous increase in our knowledge about the physiology of vertebrate flight, chiefly through the method of training animals to fly in wind tunnels for steady state measurement of selected parameters. Most of this work has been with birds; physiological data on bats in steady flight are limited to metabolic or ventilation measurements on four *Phyllostomus hastatus* (mean mass 0.093 kg) and two *Pteropus alecto* (as *P. gouldii*, synonymy according to Tate, 1942) with a mean mass of 0.825 kg that were flown in wind tunnels of the same design used in most of the bird studies (Thomas, 1975, 1981; Thomas & Lust, 1979).

The present study reports metabolic rates and associated parameters in flight for grey-headed flying foxes, *Pteropus poliocephalus* (suborder Megachiroptera). These data include the first measurements of respiratory water loss, heart rates, and body

Key words: Bat flight, metabolism, heart rate, temperature regulation, evaporative water loss, endurance.

temperatures of bats in sustained flight. The effect of velocity on the endurance of a flying animal is also examined for the first time, with interesting implications for estimates of flight speeds and metabolic costs of this form of locomotion. Finally, the data are of further interest because they were obtained in a wind tunnel of different design from that used in previous work.

MATERIALS AND METHODS

Animals used

Bats were collected in the vicinity of Brisbane, Australia. All data are from animals in good health; some survived more than six years of laboratory captivity. They were fed bananas, occasionally supplemented by vitamins and powdered milk; additional details of maintenance of fruit bats are summarized elsewhere (Carpenter, 1978).

Eight animals were trained to fly in the tunnel, five of which learned to fly with masks long enough to make some metabolic measurements, but the data in this report are primarily from the two bats for which metabolic rates were measured over all possible horizontal airspeeds. Bat no. 6 was a male with mean body mass of 0.770 kg, and which through unknown accident was missing an estimated 9 cm from the tip of the left wing at the time of capture. Bat no. 8 was a female with a mean mass of 0.647 kg. A few data are also included from bat no. 7, a female with a mean mass of 0.629 kg during the measurements summarized here. Because they were so variable, the bats' mean body masses are usually listed at the times that particular physiological measurements were made.

Wind tunnel

The tunnel was a non-return type, fixed in horizontal position, with the intake and exhaust outside the small building that housed the test section and instruments (Fig. 1). This had the disadvantage of making air flow susceptible to turbulence from breezes (see below), but permitted data collection over a wide range of temperatures and humidities, depending on time of day and season. The leading edges of the intake were curved fibreglass with a 0.3 m radius. The opening of the intake was the same size and shape as the cross section of the test section, and was fitted with a honeycomb of 1.9 cm diameter hexagonal cells made of 0.015 cm thick aluminium to aid in smoothing air flow.

Air was moved through the tunnel by a 1.5 m centrifugal fan and 10 horse power electric motor at the rear of the tunnel. The rate of air flow was controlled by adjusting louvres at the exhaust from the fan, and the maximum horizontal air speed (V) possible was 8.6 m s^{-1} . This design was much less expensive than a tunnel with bell-shaped contraction and driven with a propellor of variable pitch or speed.

Airspeed was read with a pitot tube placed in the centre of the tunnel in front of the test section, and connected to an inclined water manometer that could be read to a pressure of 0.13 mmH₂O (equivalent to approx. 0.15 m s^{-1}). Vertical and horizontal measurements across the tunnel with pitot tube and hotwire anemometer indicated that uniform velocity flow was achieved in the test section; velocities were 90 % of those in the centre within 0.075 m of the walls. Physiological measurements

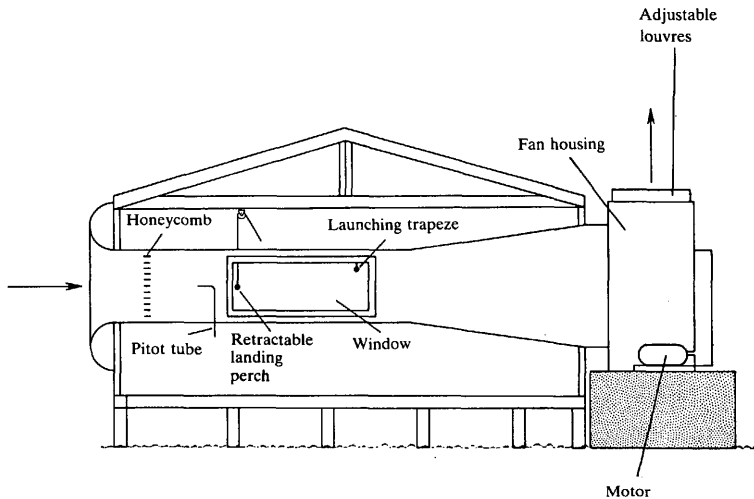


Fig. 1. Arrangement of wind tunnel in elevated building. Arrows indicate direction of air flow into intake and out of louvres on fan; length of arrows equals 1 m. Bats were confined by grids (not shown) to 2.4-m test section behind pitot tube.

were made when turbulence due to breezes produced variation of no more than ± 0.25 mm from the desired reading on the manometer (approx. 0.3 m s^{-1}). Temperatures of the airstream (T_a) were measured with a thermometer mounted through the tunnel wall, or with a thermocouple and potentiometer.

The test section was 2.4 m long, 1.5 m wide and 0.9 m high, with 0.15 m wide fillets running from the corners of the intake along the junctions of the sides with the top and floor. The floor and ends of the test section were fitted with an electrified grid made of 0.3-cm brass rods on 5-cm centres. Large Plexiglas windows in the ceiling and doors of the test section permitted observation and photography of animals in flight.

Training

A switch started a warning buzzer and electronic timer that, after a 2-s delay, charged both the grid and a wired trapeze in the rear of the test section. Bats were placed on the rear trapeze and trained to launch themselves against the wind at the sound of the buzzer. When the bat had flown for a desired period, a second perch was dropped from the ceiling in the front of the test section, allowing the animal to land. Well-trained bats usually launched themselves on cue from the buzzer, flew the desired interval and landed without experiencing any shock. (High speed motion pictures of bats no. 6 and no. 8 flying in this tunnel are available as *Mechanics of Flight in Flying Foxes*, from U.C.L.A. Instructional Media Library, Los Angeles, CA 90024, U.S.A.)

Endurance was increased by flying a bat for longer times, or by requiring a second short flight several minutes after an initial flight. Once a certain training regime was begun, the flight time of both individual flights and the total flight time each day could be increased by about 10 % per day. Bats would rarely fly much more than 110 % of the previous day's total time, and if pushed beyond this, they often appeared sore the following day or two, with greatly reduced endurance.

Respiratory gas exchange

Unlike most bats, megachiropterans are primarily dependent on vision, and the use of masks for measurement of respiratory gas exchange does not interfere with orientation by echolocation. Over successive days bats were trained to fly with a collar, short clear acetate mask, full mask with open front, closed mask with holes for respiration, and finally a complete mask attached to a flexible vinyl tube. The mask and length of tubing normally supported above the floor in flight had a mass of 16 g. The tubing was connected to a diaphragm pump that drew air through the rear of the mask and drove it through a large rotameter, usually at a rate of 14.9 l min^{-1} . A major portion of the air was then bled off, and the remaining fraction was divided into two parallel circuits.

Circuit no. 1 was used to measure O_2 consumption. Air passed at a rate of 0.25 l min^{-1} through a tube of fresh desiccant (Drierite) and to a paramagnetic oxygen analyser that measured fractional O_2 content in the air from the mask (FEO_2). During most runs, these measurements were made with a Beckman model E-2 analyser, on which FEO_2 within the range of 0.20 to 0.21 could be read to the nearest 10^{-5} . Some readings were made with a Beckman model F-3, which gave a 0.25-m deflection on a stripchart recorder for a change in FEO_2 from 0.20 to 0.21. Flow rates through the mask were high enough so that FEO_2 was almost always above 0.20, except at velocities ($4\text{--}5 \text{ m s}^{-1}$) where metabolic rates were maximum. The lowest value for FEO_2 in any run was 0.193; at FEO_2 values below 0.20 the sensitivity of both analysers was one-fifth of that in the range from 0.20–0.21.

Calibrations of instrumentation were made in the following ways. Analysers were calibrated immediately prior to metabolic runs by producing a desired air pressure of dry air (and thus PO_2) on the sensing cell. To assure that none of the expired gas escaped from the rear of the mask, the flow rate through the mask was reduced in several increments during some flights. The calculated rate of oxygen consumption ($\dot{V}\text{O}_2$) did not change until flow was reduced to below 9.7 l min^{-1} . During metabolic runs, observations of a bat's behaviour and simultaneous readings from the E-2 analyser and electric timer were voice-recorded on tape, usually at 10- or 20-s intervals; these data were later transcribed to notes and computer cards for processing.

Rotameters were calibrated at the pressures used by introducing pure N_2 into parts of the plumbing system through a calibrated rotameter and measuring the reduction in FEO_2 with the analyser. Flights at minimal speeds were often of short duration. To ensure that the response times of the air flow system and analysers were sufficient to detect a brief steady state value for FEO_2 , N_2 was introduced through a hose into the mask at a rate that was carefully adjusted to produce a reading on the analyser equal to the FEO_2 values obtained when bats were flying at these airspeeds. The lag time of the system was determined by recording the response times when

the N₂ hose was abruptly removed from the mask or replaced in the mask when the analyser was indicating the normal reading for background air. The lag time for first response was 20 s, and steady readings were reached in 60 s, which was sufficient to record FEO_2 values for all flights reported here.

Parallel circuit no. 2 was used to measure water vapour and CO₂ in mask air. At a selected time a preweighed tube of Drierite was connected to this circuit set at a flow of 0.5 l min⁻¹. After a period sufficient for air to pass through this tube (usually 50 s), a tube of CO₂ absorbent (Ascarite) was added after the Drierite. Both tubes were disconnected simultaneously after Ascarite had been in the circuit for the desired interval, usually 900 s, or as soon as a flight was terminated prematurely. Tubes were resealed and reweighed to the nearest 0.1 mg.

To obtain background readings for atmospheric water vapour and CO₂, the above process was repeated immediately after the day's first run, with an empty mask in place in the operating tunnel. The differences in weight gain of absorbent tubes between actual runs and background readings were used to calculate respiratory evaporative water loss (EWL) and rates of CO₂ production (\dot{V}_{CO_2}); weight gains of the Drierite used for background readings were used, with T_a data, to calculate atmospheric humidity. CO₂ introduced into the mask by syringe at rates several times the flight \dot{V}_{CO_2} was recovered to within 1 % of the introduced amount.

All metabolic runs were made when animals were postabsorptive. The \dot{V}_{O_2} value for a run was calculated from the mean of all FEO_2 values during steady flight, or for particular periods when EWL or \dot{V}_{CO_2} were being measured. The mean \dot{V}_{CO_2} of 20 early flights with bats nos 6–8 was used in Tucker's (1968) equation (2) to calculate \dot{V}_{CO_2} and mean respiratory exchange ratio (R). The mean R value was then used in his equation (3) to calculate all subsequent \dot{V}_{O_2} values except in those flights when additional measurements were made of \dot{V}_{CO_2} .

It was later noticed in a few runs that values for R made late in a flight were lower than those made soon after a flight had begun. Therefore, I measured \dot{V}_{O_2} and \dot{V}_{CO_2} of bat no. 8 in 11 runs at 170–770 s and 900–1500 s after each flight began. When the mean value for R was less in the second set of intervals (Table 1), five additional flights were made in which R was determined in each of four successive 300-s intervals.

All gas volumes were corrected to STPD. Metabolic rate is expressed as power input (P_i) according to the conversion factors determined by values for R (see Results).

Correction for drag of the mask

To correct metabolic readings for the effects of horizontal drag of the mask and tubing, the body of a bat with wings removed was frozen in normal flight posture and mounted in a closed return wind tunnel on a six-component strain gauge (Kenney Engineering Systems, Pasadena, CA, U.S.A.) connected to a Hewlett Packard data acquisition system. The drag of the body, both with and without the mask and tubing, was measured ten times at each of four airspeeds from 4.5 to 18 m s⁻¹. Differences in drag of the bat with and without the mask were considered to be the drag of the mask (D_m , in Newtons), which varied with V (m s⁻¹) according to the formula:

$$D_m = 2.41 \times 10^{-3} V + 8.6 \times 10^{-4} V^2. \quad (1)$$

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

$$P_{i,m} = D_m V / \text{Eff}_p, \quad (2)$$

where Eff_p is the partial efficiency. This was not measured in this study, but was assumed to have a value of 0.25, based on values of 0.19 to 0.30 in flying birds (Tucker, 1972), and 0.24–0.27 for one *P. alecto* (Thomas, 1975). The value for $P_{i,m}$ at each V was subtracted from the corresponding values for total metabolic rate in order to determine the P_i of each bat unencumbered by drag of the mask and tubing. No correction was made for the weight of the mask.

Body temperatures

In some flights, body temperatures (T_b) were measured by inserting a 30-gauge copper-constantan thermocouple at least 8 cm into the colon of a bat and securing the lead by tape to the fur and one ankle. The thermocouple was connected to a calibrated multichannel recording potentiometer that could be read to the nearest 0.2°C (Leeds & Northrup, Speedomax W). During these runs, additional thermocouples simultaneously measured tunnel T_a .

Cardiac and respiratory frequencies

Heart rate in flight (f_H) was recorded on an oscillograph (Physiograph, Narco Biosystems, Houston, Texas) by attaching leads to the skin of the throat and left flank with small brass safety pins. The EKG signal was usually masked by the strong signals from the contraction of the wing muscles, but subtle adjustments in the placement of the pins eventually yielded clear signals in flight.

Respiratory frequencies (f_R) were initially measured by placing a thermocouple in the entrance to the tube within the mask. The thermocouple was connected to the oscillograph to measure temperature changes caused by each expiration. Later measurements included use of both a thermocouple and wire leads through the skin of the shoulders or chest to record simultaneously the contractions of the wing muscles and the respiratory cycle. As soon as a bat landed f_R was easily determined by stop watch and visual counting of abdominal movements.

Wing movements

A few measurements were made of wing span in flight by photographing the bats from above while they flew with 15 cm plastic rulers glued to their backs. The negatives were then projected to full size, using the image of the ruler as a guide, and the wing spans measured directly. Wingbeat frequencies (f_W) were measured by visual counts with a stopwatch or by counting from high speed motion pictures in which there was a one-revolution-per-second timer in the field of view with the bat.

Anatomy

Small blood samples were withdrawn from wing veins with heparinized syringes, and a portion centrifuged in haematocrit tubes. Some blood samples were then

transferred to paediatric EDTA tubes and chilled for one of the following analyses. Haemoglobin concentration was determined by a modified stable cyanmethaemoglobin method. O₂-carrying capacity was measured by equilibrating blood with 100% O₂ for 5 min at 37°C in a microtonometer, and reading O₂ content with a Lex-O₂ Con blood gas analyser (Lexington Inst. Co., Cambridge).

On the day of its last flight, bat no. 6 was killed by injection of pentobarbitol, weighed, sealed in plastic bags and frozen. At a later date it was thawed; weight loss was only 5 g (0.6%), and wing membranes were still freely pliable. Without identifying individual muscles, all pectoral and wing musculature was removed by scalpel and weighed, as was the remaining skeletal musculature. The heart was weighed after clearing the chambers of blood.

Endurance

During the course of these measurements it became clear that bats could not fly at maximum and minimum airspeeds for as long as they could at intermediate velocities. I therefore systematically measured the effect of *V* on endurance in bat no. 8. For these measurements the bat was flown without mask or other encumbrance until it showed reliable symptoms of fatigue (see Results), or was actually unable to fly further, at which time it was allowed to land. The electrified grid discouraged landings unless animals were genuinely fatigued.

Such measurements of endurance might actually influence a bat's endurance in subsequent flights, either by gradually improving its stamina or by causing fatigue. Therefore bat no. 8 was flown twice per day, once at a test velocity (*V_t*) and once at its previously determined velocity of minimum power input (*V_{mp}*), with a rest of at least 4 h between the two flights. The duration of each flight was timed, and the bat's endurance was expressed as the ratio of the endurance at the test speed (*E_t*) to its endurance the same day at the *V_{mp}* of 6 m s⁻¹ (*E_{mp}*). In the 8–14 pairs of flights to determine endurance at each *V_t*, there were equal number of days, usually alternated, when the *V_t* or *V_{mp}* was the speed of the day's first flight. This was in order to compensate for possible effects of daily fatigue on the duration of the day's second flight. Usually all test flights were completed for one *V_t* before measurements were begun at another.

RESULTS

Behaviour

Bats flew equally well at all times of day or night. It was almost essential that they be flown every day; flying only on alternate days usually resulted in a gradual reduction of endurance over a period of time. Bats not flown for a week usually suffered reduction of endurance of at least 10% of previous flight times, and animals kept for several months without flying became incapable of flight or even of full extension of their wings.

The grid in the test section often short circuited in damp or rainy weather, and when bats discovered that no shock resulted, they would often fly for less than a few minutes before settling to the floor, even though capable of flights of 30 min or more. Training for longer flights at intermediate speeds (6–7 m s⁻¹) appeared to be

limited only by the patience of the trainer; four bats flew for at least 50 min, and at one time bat no. 6 would fly continuously for 3 h.

Unless fatigued, most flying bats maintained a steady position in flight, although there were small individual preferences in the positions chosen. Bat no. 6 flew with its left wing grazing one window, as did bats no. 5 and no. 7 on occasion. This behaviour was associated with the door on the left side through which they were normally removed after flights; all of the bats also moved to the corresponding ends of both perches in anticipation of the opportunity to climb onto the hand of the operator for removal. There were other slight individual differences in flight pattern, so that it was possible for an experienced observer to recognize at a glance which one was flying. Bat no. 6 flew steadily in what appeared to be a normal manner, but it was unable to fly over as wide a range of airspeeds as no. 8 (Table 2, Fig. 3).

Bat no. 8 usually accelerated toward the front of the test section, then glided, or flew more slowly, so as to drift to the rear of the section, whereupon it repeated the cycle. Despite the apparent variation of effort and airspeed in these cycles, lasting 10–20 s each, there was no corresponding variation in $\dot{V}_{E_{O_2}}$, which remained quite constant during a flight. At low V the wing beat was more frequent (Table 2), and its plane obviously less vertical (angle not measured), reflecting the strong positive angles of attack of the bat's body. The feet were strongly depressed, pulling the trailing edge of the proximal portions of the wings into a high camber. Bats flew in the front of the test section, near the front grid, appearing to succeed in such slow flight only with great difficulty.

At increasing airspeeds, the body became less inclined, and the plane of the wing beat became more vertical, until, at $V = 8.6 \text{ m s}^{-1}$, the body was completely flat, with feet extended straight behind the body, and the wings beating in a vertical plane. At this V , animals remained in the rear of the test section, usually with feet protruded into the rear of the grid, and clearly had difficulty in maintaining flight speed. These variations in inclination of the body and pattern of wing movement made it easy to determine visually when a bat was flying at a speed at which \dot{V}_{O_2} levels would be close to the minimum.

When fatigued at moderate to high velocities, bats flew closer to the floor and farther to the rear of the test section. Wing beats seemed more laboured, and the animals appeared to have difficulty in maintaining orientation, especially in correcting yaw. This behaviour was quite distinct from behaviour when overheated (see section on body temperature). If not given the perch for landing, hind claws usually became entangled in the rear grid, or bats simply landed on the floor, often within a minute of the appearance of these symptoms. Bat no. 8 often applied her sternum tentatively to the floor grid, obviously testing whether a shock was possible.

Presence of a mask and tubing had no observable effect on flight behaviour with the possible exception of some small reduction in the endurance at minimum and maximum airspeeds, and an inhibition of the cooling behaviour when overheated. Bat no. 6 would fly at $V = 8.6 \text{ m s}^{-1}$, and no. 8 flew for a few seconds at $V = 3 \text{ m s}^{-1}$, only when without masks.

The bats were often flown for exercise at times when turbulence was as great as $\pm 50\%$ of the desired airspeed. This seemed to have no effect at all on flight

Table 1. *Change in respiratory exchange ratio (R) during time of flight*

Interval of measurement (s)	Bats used	Mean duration of measurement (s)	R (N, s.e.m.)
Various, between 250 and 1330	nos 6, 7, 8	840	0.796 (20, 0.113)
170-770	no. 8	600	0.841 (11, 0.006)
900-1500	no. 8	600	0.778 (11, 0.015)
150-450	no. 8	300	0.865 (5, 0.015)
450-750	no. 8	300	0.836 (5, 0.015)
750-1050	no. 8	300	0.776 (5, 0.008)
1050-1350	no. 8	300	0.771 (5, 0.011)

patterns, except at the maximum and minimum velocities of which the bats were capable, when it reduced endurance.

Respiratory exchange ratio

The mean value for R measured at assorted times during flights by bats nos 6-8 was 0.796 (Table 1). This indicates that the energy equivalent for oxygen consumption was 20 kJ (4.8 kcal) per l O₂ consumed, or a power input (P_i) of 5.58 W when \dot{V}_{O_2} was 1.0 l O₂ h⁻¹. The mean value of R for no. 8 was significantly higher (paired sample *t*-test, $P < 0.005$) between 170 and 770 s after the start of flights than between 900 and 1500 s. R values from 300-s intervals suggest that the decline in R may not have stabilized by as late as 1050 s after the start of flight (Table 1).

Oxygen consumption

At no time was non-flight \dot{V}_{O_2} in the tunnel as low as metabolic levels of 2.95 W kg⁻¹ (0.53 l O₂ kg⁻¹ h⁻¹) of this species at rest in thermal neutrality (Bartholomew, Leitner & Nelson, 1964). The start of flight dramatically increased \dot{V}_{O_2} to much higher levels that varied little throughout a flight (Fig. 2). Upon landing there was a second abrupt shift to values below the pre-flight levels.

The shape of the curve representing shifts between flying and non-flying \dot{V}_{O_2} was determined both by the rate of change in \dot{V}_{O_2} and by the response time of the plumbing and the analyser. It was complicated by the fact that bats often crawled to a preferred position on the perch, or scratched at the mask with a foot for a brief period after landing. Nevertheless, in eight flights with bats nos 6-8, the area between the curve representing the N₂-determined response time and the line showing the transition from flight to resting levels indicated an average O₂ debt of 0.085 l O₂ (s.e.m. = 0.021).

The V of minimum power input (V_{mp}) were 7 and 6 m s⁻¹ for bats no. 6 and no. 8, respectively; \dot{V}_{O_2} increased gradually at higher airspeeds (Fig. 3). At V below V_{mp} , P_i increased greatly (Fig. 3, Table 2). At velocities of 4 or 5 m s⁻¹, flights were short and followed by up to 2 min of heavy breathing with closed mouth. Because bats often quit before the perch was lowered, and then climbed about on the floor, attempts to measure the O₂ debt incurred at these speeds were unsuccessful.

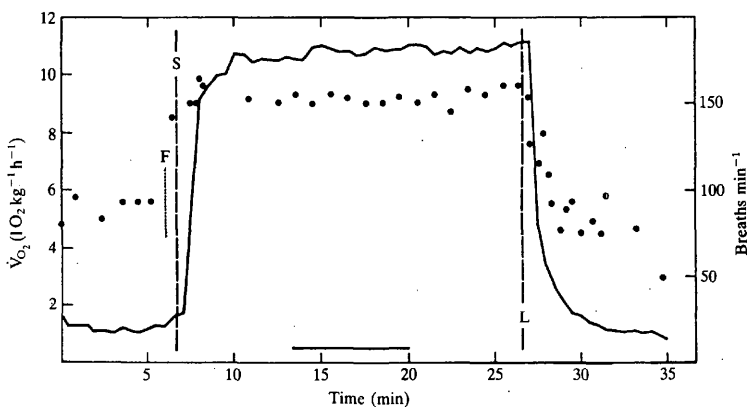


Fig. 2. Typical record of $\dot{V}O_2$ (continuous line) and respiratory frequencies (individual points) before, during and after flight, uncorrected for instrument response time or drag of mask: run no. 66, bat no. 6, 0.848 kg, 20 min duration at $V = 7 \text{ m s}^{-1}$. Short horizontal line indicates standard metabolic rate of this species (Bartholomew, Leitner & Nelson, 1964); vertical lines indicate times of start of fan (F) and start (S) and end (L) of flight. Respiratory frequencies based on visual counts of wingbeats in flight and from abdominal movements when bat was on perches.

Evaporative water loss

In order to compensate for the variation in $\dot{V}O_2$ and pulmonary ventilation at various air speeds, EWL data were graphed as $\text{g H}_2\text{O l}^{-1} \text{O}_2$ consumed. Over the relatively narrow range of T_a in this study, there was no significant correlation between T_a and EWL from both bats (Fig. 4; $N = 109$, $r = -0.137$). Bats never opened their mouths in the stereotyped cooling response while wearing a mask (see below), so no data are available on the effectiveness of this response in adding to evaporative cooling.

There were significant ($P < 0.01$) negative correlations of EWL and vapour pressure (V.P.) (Fig. 5). Data were not used from runs when licking was obvious or frequent, or when there was liquid deposited on the inside of the mask. Nevertheless, some non-respiratory contribution may have occurred without notice, increasing the variability of the measurements. Purely respiratory evaporation is probably reflected most accurately by closely grouped data points of low value at a particular V.P. Such selected data are indicated by closed circles in Fig. 5, and are the ones used in the calculation of mass specific values in Table 3.

Body temperature

The mean T_b of bats hanging on perches in the wind tunnel was $37.4\text{--}38.5^\circ\text{C}$, and there was some elevation of T_b at the start of flight. T_b values at the time of landing were significantly ($P < 0.01$) correlated with T_a for bat no. 6, but the correlation was insignificant for bat no. 8 (Fig. 6).

Table 2. Effect of airspeed on \dot{V}_{O_2} , corrected P_i , wingbeat frequency and wing span

Airspeed (m s ⁻¹)	Mean body mass (kg)	\dot{V}_{O_2} (l O ₂ kg ⁻¹ h ⁻¹ , uncorrected for drag of mask)	Corrected P_i (W kg ⁻¹)	f_w (beats min ⁻¹) f = count from film v = visual count	Wing span (m)
3at no. 6	(mean = 0.770)				
5	0.800	12.350 (8, 0.058)	68.09 (8, 0.32)	268 (f, 3)	1.11 (1)
6	0.746	10.81 (10, 0.134)	58.87 (10, 0.74)	215 (v, 10)	1.11 (3)
7	0.750	10.179 (10, 0.182)	54.58 (10, 1.02)	154 (v, 20) (at 7.4 m s ⁻¹)	1.04 (3)
8	0.783	10.964 (12, 0.075)	57.94 (12, 0.429)	161 (v, 32)	1.11 (4)
8.6	—	—	—	170 (f, 3)	—
3at no. 8	(mean = 0.647)				
3	—	—	—	290 (f, 2)	—
4	0.669	13.894 (6, 0.127)	77.0 (6, 0.71)	262 (f, 3) (at 4.5 m s ⁻¹)	1.24 (2)
5	0.648	11.145 (11, 0.104)	61.17 (11, 0.58)	202 (v, 2)	1.14 (3)
6	0.617	10.018 (10, 0.155)	53.84 (10, 0.88)	153 (v, 11)	1.12 (5)
7	0.627	10.923 (10, 0.141)	58.33 (10, 0.79)	144 (v, 15)	1.09 (2)
8	0.662	11.559 (11, 0.065)	60.93 (11, 0.36)	145 (v, 36)	1.09 (2)
8.6	0.660	11.692 (11, 0.111)	60.80 (11, 0.60)	168 (v, 12) 170 (f, 3)	— —

Numbers in parentheses are number of flights and s.e.m.

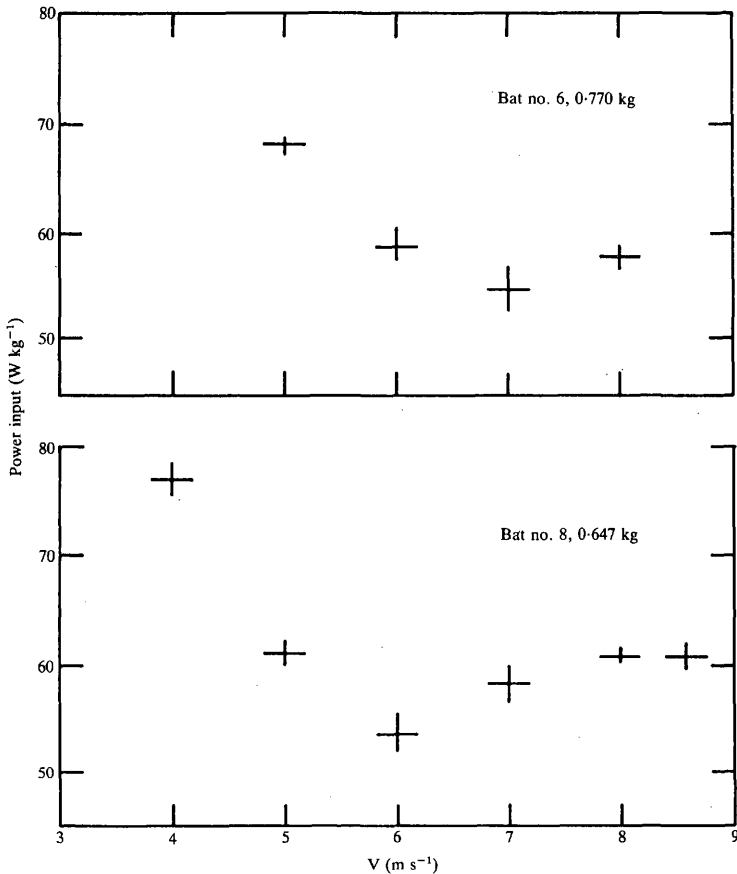


Fig. 3. Effect of airspeed (V) on mass specific power input (W kg^{-1}) of bats no. 6 and no. 8, corrected for drag of the mask and tubing. Symbols are means ± 2 s.e.m.

Bats showed symptoms of overheating when flown at T_a above about 24°C . At these temperatures, T_b reached $39\text{--}40^\circ\text{C}$, and bats showed a stereotyped thermoregulatory behaviour when flying without masks. Initial symptoms were frequent opening of the mouth, which was invariably closed at lower temperatures. If the flight continued, a bat usually opened its mouth continuously and curled its tongue upward. Some licking of the muzzle and discharge of fluid from the nostrils was common. If not permitted to land the animal often appeared to lose flight control, and either deliberately landed on the floor or crashed. If allowed to land when

Table 3. Respiratory evaporative water loss from flying bats

Species and body mass (kg)	Speed (m s ⁻¹)	Mean V.P. (Torr)	EWL	
			(g H ₂ O kg ⁻¹ h ⁻¹)	(g H ₂ O l ⁻¹ O ₂)
<i>teropus poliocephalus</i>				
Bat no. 6, 0.774 kg*	6.7	3.3	5.95 (8, 0.24)	0.550 (8, 0.022)
	8	13.2	3.49 (8, 0.27)	0.363 (8, 0.028)
Bat no. 8, 0.660 kg*	7	3.4	6.69 (12, 0.16)	0.619 (12, 0.007)
	6	11.0	5.94 (11, 0.16)	0.501 (11, 0.013)
<i>Myotis hastatus</i>				
Bat F, 0.101 kg†	5.8 (circular path)	6.7-16.9	23.8 (7, s.d. = 2.69)	0.86
Bat R, 0.87 kg†	3.6 (circular path)	6.7-16.9	23.6 (7, s.d. = 9.38)	0.956

* Mean body masses during these runs.

† Thomas & Suthers, 1972.

Numbers in parentheses are numbers of flights and s.e.m.

overheated, the bats always panted with open mouth and curled tongue, licked both wrists, and fanned their wings. Thus, at $T_a > 24^\circ\text{C}$, flights of more than a few minutes' duration were not possible.

Respiratory rates and wingbeat frequencies

Early measurements with thermocouples in the masks suggested strongly that respiratory frequencies (f_R) were the same as visual counts of wingbeat frequencies (f_W). This was confirmed with simultaneous EMG and thermocouple measurements on both bats no. 6 and no. 8 at $V = 6$ and 8 m s^{-1} , although it was not possible to determine whether inspiration coincided with downstroke or upstroke of the wings. Therefore, f_R increased immediately with the start of flight, and subsided quickly after landing (Fig. 2), unless the bat had flown at the low airspeeds requiring extreme metabolic expenditures. At the lower and the higher airspeeds animals would not fly with leads, masks and thermocouple necessary to determine if respiration and wingbeat were invariably coupled. Data on f_W and wing span are summarized in Table 2.

Heart rates

Heart rates of bats no. 6 and no. 8 were measured only at their respective V_{mp} values. The f_H changed abruptly with the start of flight and landing in the pattern of \dot{V}_{O_2} and f_R . The mean f_H of bat no. 6 was $476\text{ beats min}^{-1}$ for the three flights represented in Fig. 7, and mean f_H of bat no. 8 was $489\text{ beats min}^{-1}$ during three

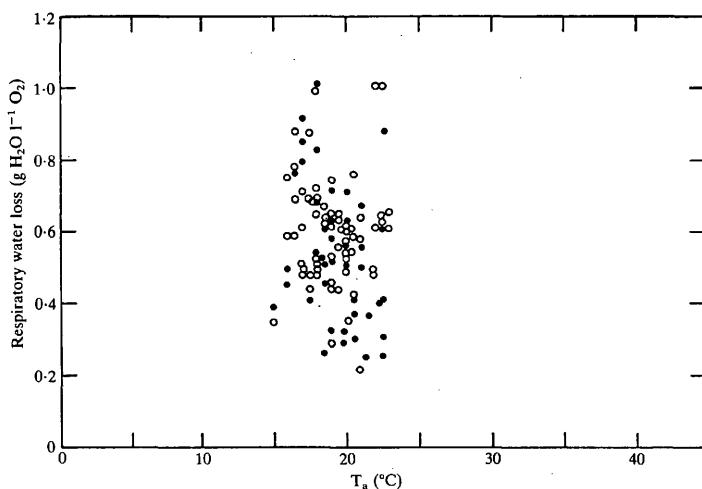


Fig. 4. Relationship between ambient temperature (T_a) and respiratory water loss from measurements $>300\text{ s}$ duration. Shaded circles, bat no. 6; open circles, bat no. 8. There was no significant correlation between T_a and water loss over this range.

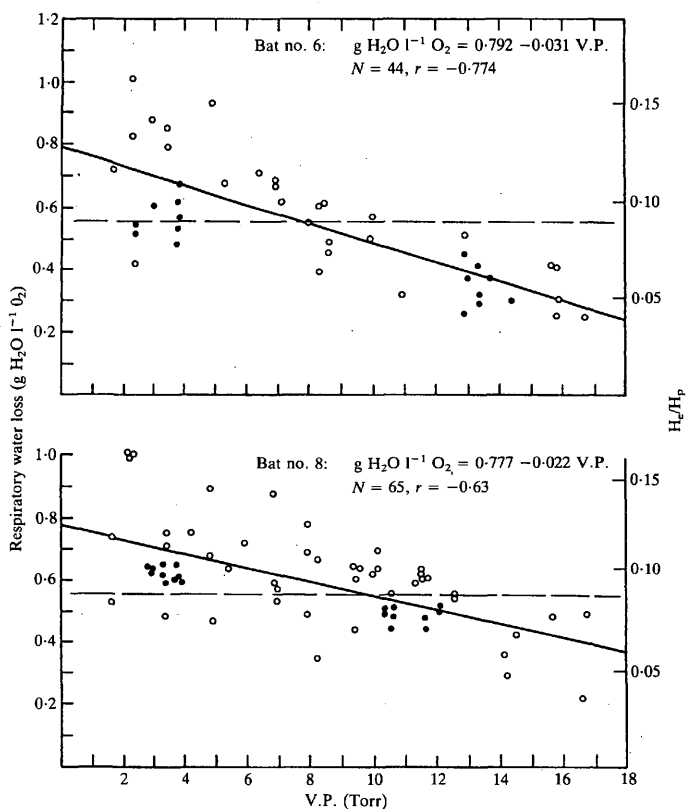


Fig. 5. Relationships between ambient vapour pressure (V.P.) and respiratory water loss (left ordinate) and the ratio of evaporative heat loss to heat production (H_e/H_p ; right ordinate). All measurements >300 s duration. Shaded circles indicate grouped data for calculating mass specific water loss in Table 3. Formulae describe least squares regression lines, which were significantly different from zero for both bat no. 6 and no. 8.

flights. Post-flight rates of bats no. 6 and no. 8 averaged $343 \text{ beats min}^{-1}$ and $291 \text{ beats min}^{-1}$, respectively, for the brief periods they would remain on the landing perch without scratching at the recording leads.

Endurance

At $V = 6-7 \text{ m s}^{-1}$, these bats could easily be trained to fly for an hour; therefore, values for endurance of bat no. 8 are expressed both as the ratio $E_t:E_{mp}$ and as actual time, by setting the value for E_{mp} to 3600 s (Table 4; Fig. 8A). The effect of

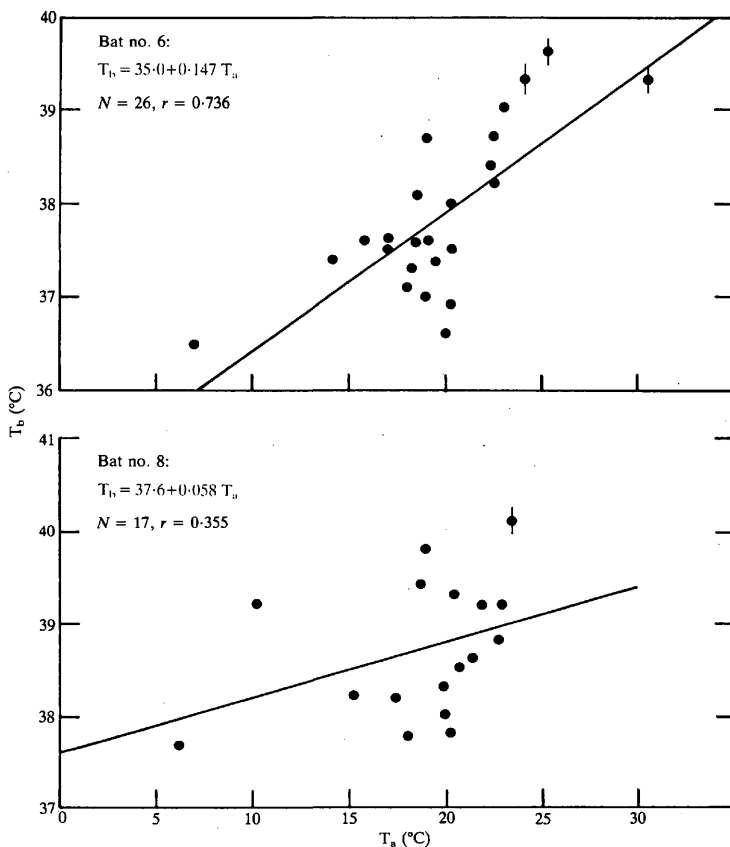


Fig. 6. Relationship between ambient temperature (T_a) and body temperature (T_b) at ends of flights of 173–12 500 s duration ($\bar{X} = 4800$ s) for bat no. 6, and 670–5700 s ($\bar{X} = 2670$ s) for bat no. 8. Vertical bars indicate flights in which bats showed symptoms of overheating.

air speed was even greater on endurance than on \dot{V}_{O_2} . At the V_{mp} of 6 m s^{-1} , the endurance was significantly greater than at any other speed (one-tailed paired t -test, $P < 0.05$).

Bat no. 6 showed a portion of the same pattern during daily training without a mask for (unsuccessful) metabolic measurements at 8.6 m s^{-1} . This bat was flown first each day at 8.6 m s^{-1} and then at its measured V_{mp} of 7 m s^{-1} , with an average rest period of 4.4 h between flights. Average endurance at 8.6 m s^{-1} was only 32 %

($N = 13$, S.E.M. = 2.4%) of that at 7 m s^{-1} , despite the possibility that the animal was more fatigued during the second flight each day.

Anatomy

The mean haematocrit value of bats no. 6, no. 8 and five other bats was 52%. There were no haemoglobin determinations from bats no. 6 and no. 8; the mean value from four other bats was 16.9 g%. Oxygen carrying capacities from bats no. 6 and no. 8 were 29.7 and 28.9 vol%, respectively.

At the time of dissection, bat no. 6 had a body mass of 0.782 kg and the heart mass was 6.14 g. The total mass of muscles inserting on the scapulae, humeri, and attached to other bones within the wing was 155.2 g. Muscles of the pelvis and legs totalled 29.1 g; an additional 12.5 g was removed from the neck, at which point the skeleton was quite clean except for intercostal and jaw muscles. There were 51.8 g of subcutaneous fat in the back and neck, and 18.6 g of fat from the abdomen and around the heart.

DISCUSSION

Behaviour

The performance of bat no. 6 seemed to be unaffected by the missing wing tip at medium airspeeds, despite the importance of wing span on estimated power requirements in flight (Pennycuik, 1968; Tucker, 1973). This bat was also capable of flying up to three times the maximum periods attained by any of the others, but the reduced span may have caused the limited range of airspeeds at which this bat could fly (Table 2, Fig. 2).

Wing span and fw were maximum at the lowest V , and were minimum at a point slightly below the highest V , at or near each bat's V_{mp} (Table 2). Both patterns occur in the bat *Leptonycteris sanborni*, although the P_1 was not measured in that study (Richardson, 1973). Other bats (Norberg, 1976; Thomas & Lust, 1979; Thomas, 1981) and some birds (Pennycuik, 1968) show an inverse relationship between at least fw and V , but wing spans have not always been measured.

Bats were easily trained for flights much longer than the measurement periods reported in laboratory studies of non-flying mammals (e.g. Baudinette, Seymour & Orbach, 1978; Taylor *et al.* 1981), although well short of the flights of 10 and 8 h reported for gulls and starlings respectively (Tucker, 1969; Torre-Bueno, 1976). However, flying foxes may make nightly flights up to 48 km from roosts to feeding sites (Bartholomew *et al.* 1964), and Sterndale (1884) reported an individual *Pteropus* in flight more than 200 miles at sea. The distribution of members of this genus across most of the archipelagos of the western Pacific Ocean is also evidence of impressive flight endurance, even allowing for the probable role of storms in dispersal.

Respiratory exchange ratio

The average values for R measured at random times during flights and 900 s or later after the start of flight fall in the range of 0.70 to 0.80 reported for flying birds (Tucker, 1968, 1972; Torrebuena & Larochelle, 1978), and are lower than the

Table 4. Power input, endurance, maximum distance possible, and metabolic capacity of *Pteropus poliocephalus* no. 8, with a mean mass of 0.647 kg

V_t ($m\ s^{-1}$)	P_t (Watts)	Cost of transport (P_t/WV)	Endurance		Endurance* required for equivalent distance (s)	Maximum* distance possible (km)	Metabolic* capacity (kJ)
			Percentage of E_{mp}	Time (s) when $E_{mp} = 3600\ s$			
4	51.51 (6, 1.14)	2.03	3.08 (8, 0.25)	108	5400	0.43	5.55
5	39.64 (11, 0.42)	1.25	14.15 (8, 1.16)	511	4320	2.55	20.24
6	33.22 (10, 0.60)	0.87	100.0	3600	3600	21.6	119.70
7	36.57 (10, 0.69)	0.82	79.92 (14, 8.64)	2877	3085	20.14	105.33
8	40.33 (11, 0.23)	0.79	37.11 (12, 3.40)	1318	2700	10.54	53.13
8.6	40.13 (11, 0.43)	0.74	13.6 (10, 1.22)	491	2512	4.22	19.67

* Explained in text, calculated on assumption that $E_{mp} = 3600\ s$.
Numbers in parentheses are number of measurements followed by standard error of mean.
Absolute endurance at $V = 6\ m\ s^{-1}$ was variable but was always treated as the reference point in calculating endurance as E_t/E_{mp} , hence there is no statistic calculated.
The ratio P_t/WV is dimensionless when using units in text.

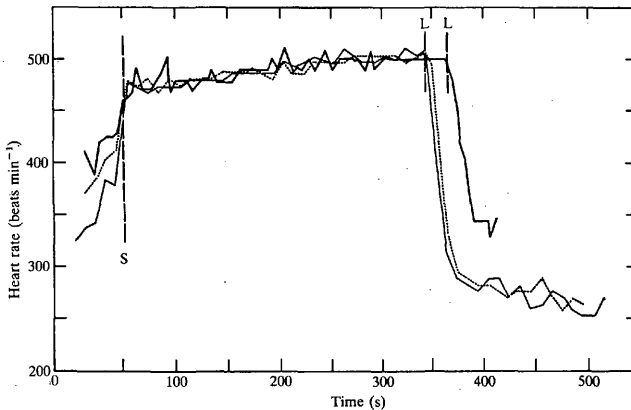


Fig. 7. Heart rates of bat no. 6 before, during and after three flights ≥ 300 s at $V_{mp} = 7 \text{ m s}^{-1}$. Vertical lines indicate the start (S) and landings (L).

minimal values of 0.82 reported for two bat species (Thomas, 1975). Thomas (1975) and Hudson & Bernstein (1983) reported consistent decreases in R for *P. hastatus* and ravens, respectively, from one flight to the next on the same day, a pattern similar to the decline at 300-s intervals for bat no. 8. For exercising humans, declining R values are the result of increases in the fraction of energy gained from fat during the course of exercise (Astrand & Rodahl, 1977), and washing out of CO_2 stores with increased ventilation and buffering of lactic acid (Consolazio, Johnson & Pecora, 1963).

Metabolic rate

The lowest mass-specific power inputs (Table 2) of bats no. 6 and no. 8 were 2% and 8%, respectively, below the minimum values predicted by Thomas' (1975) scaling equation for both birds and bats, and within 2% of his measurement of 53.4 W kg^{-1} for the *P. alecto* at $V = 8 \text{ m s}^{-1}$. This is remarkable agreement considering the differences in tunnels and species. It is a further suggestion that bat no. 6 suffered no serious impairment from its missing wing tip at moderate airspeeds. With increasing velocities, both bats showed a gradual increase in P , kg^{-1} (Fig. 2, Table 2), similar to that of the *P. alecto*, although they never attained such high velocities as did the latter (9.9 m s^{-1}). However, no. 6 and no. 8 flew at lower airspeeds than the minimum for *P. alecto*, which resulted in metabolic levels as high or higher than the maximum of 69.6 W kg^{-1} achieved by that bat.

Thomas & Suthers (1972) have pointed out that even the minimal \dot{V}_{O_2} of flying bats far exceeds the maximum rates ($\dot{V}_{\text{O}_{2,\text{max}}}$) of terrestrial mammals of similar size. This fact is put into better perspective by the recent determination (Taylor *et al.* 1981) that the $\dot{V}_{\text{O}_{2,\text{max}}}$ of running mammals is about ten times their standard rate

($\dot{V}_{O_2, \text{std}}$), and scales allometrically over a wide range of body masses (M_b , in kg) according to the (rearranged) equation,

$$\dot{V}_{O_2, \text{max}} = 6.98 M_b^{0.79}, \quad (3)$$

where $\dot{V}_{O_2, \text{max}}$ is in $\text{l O}_2 \text{ h}^{-1}$. The uncorrected $\dot{V}_{O_2, \text{max}}$ of *P. poliocephalus* (Table 2) are 23–26 times the $\dot{V}_{O_2, \text{std}}$ (Bartholomew *et al.* 1964), and 1.7 times the $\dot{V}_{O_2, \text{max}}$ predicted by equation (3). Even the minimal \dot{V}_{O_2} values of all five flying bats measured to date are 1.46–1.6 times the $\dot{V}_{O_2, \text{max}}$ predicted by equation (3).

The 1–2 min of heavy breathing after flights at low V suggested that O_2 debts were greater than those measured at $V = 6\text{--}8 \text{ m s}^{-1}$. At the latter V , the O_2 debt was 50 % greater than that of *P. hastatus* in tethered flight (Thomas & Suthers, 1972), but half that of budgerigars flying in turbulent air (Tucker, 1966). It is quite likely that the O_2 debt was acquired at the end of the flight. When the perch was dropped, it was necessary for the bats to accelerate against the air stream in order to make the landing. At the minimum levels of \dot{V}_{O_2} measured in flight, it should have taken only 30 s to repay the debt. This agrees with typical observations of the brief period of heavy breathing after landing (Fig. 2), but it sometimes took up to 4 min for \dot{V}_{O_2} to reach stable minimum values, reflecting the animals' movements on the perch.

Anatomy

The simple dissections permit some interesting calculations when coupled with metabolic data. Muscles involved in wing movement made up about 21 % of the body mass of bat no. 6, or about twice the fraction reported for only ventral thoracic muscles of assorted microchiropterans (Hartman, 1963). In flight, the uncorrected \dot{V}_{O_2} of bat no. 6 was as high as $12.35 \text{ l O}_2 \text{ kg}^{-1} \text{ h}^{-1}$ (Table 2), but was only about $11 \text{ l O}_2 \text{ kg}^{-1} \text{ h}^{-1}$ after landing (Fig. 2). With a mass of 0.780 kg , the difference in total O_2 consumption was 8.85 l h^{-1} . If only the heart and muscles involved with wing movement were responsible for this increase in \dot{V}_{O_2} , as has been assumed for birds (Tucker, 1966), the 0.161 kg of tissue increased its consumption by $551 \text{ l O}_2 \text{ h}^{-1} \text{ kg}^{-1}$ muscle. But the muscles of the neck support the head in flight, and posterior limb and trunk muscles are in sustained contraction to position the legs for the necessary shape of the trailing edge of the wings. If the increase in \dot{V}_{O_2} was the result of all 0.203 kg of dissected muscle and heart, the mean increase in \dot{V}_{O_2} was about $441 \text{ l O}_2 \text{ h}^{-1} \text{ kg}^{-1}$ muscle. It is difficult to make comparisons with the muscle mass-specific power of other species, for there appear to be no measurements on animals of equivalent size. Values for flying budgerigars ($162 \text{ l O}_2 \text{ h}^{-1} \text{ kg}^{-1}$; Tucker, 1966) or for human athletes ($181 \text{ l O}_2 \text{ h}^{-1} \text{ kg}^{-1}$; Keul, Doll & Keppeler, 1972) must be strongly influenced by scaling effects.

R values after 750 s of flight indicate primary dependence on fat as the energy source, as reported for birds (Tucker, 1972; Torre-Bueno & Larochelle, 1978; Hudson & Bernstein, 1983). Fat yields approximately 39.8 kJ g^{-1} (9.5 kcal g^{-1}). Assuming that all of the 52 g fat dissected from no. 6 was readily available in flight, the maximum endurance of this bat would have been about 13.5 h at the minimum P_i of 42.6 W (Table 2). This P_i occurred at $V_{\text{mp}} = 7 \text{ m s}^{-1}$, and therefore the expected range at this V would be 340 km. The maximum flight of this bat in the

tunnel was a 'distance' of 84 km during a 3-h flight (Carpenter, 1975). But it took many days of daily training to develop such endurance even though the fat content of the bat was presumably at about this level at all times. The great disparity between actual endurance and that predicted by these rough calculations is one suggestion that endurance is not limited simply by fat reserves.

Evaporative water loss

The mass specific rates of respiratory water loss from flying *P. poliocephalus* (Table 3) are about four to seven times the values of $1\text{--}2\text{ g H}_2\text{O kg}^{-1}\text{ h}^{-1}$ for this species at rest (R. E. Carpenter, unpublished data), but much less than the EWL of smaller bats in flight. Respiratory EWL from *P. hastatus* in tethered flight was $23.7\text{ g H}_2\text{O kg}^{-1}\text{ h}^{-1}$ (Thomas & Suthers, 1972), although when expressed in relationship to \dot{V}_{O_2} , the rate (approx. $0.9\text{ g H}_2\text{O l}^{-1}\text{ O}_2$) was within the range of values for bats no. 6 and no. 8 (Fig. 5). Pulmocutaneous EWL was estimated by changes in body mass to be $31\text{--}57\text{ g H}_2\text{O kg}^{-1}\text{ h}^{-1}$ for desert bats between 0.013 and 0.025 kg mass (Carpenter, 1968, 1969), and $31\text{ g H}_2\text{O kg}^{-1}\text{ h}^{-1}$ for 0.113-kg fruit bats, *Rousettus aegyptiacus* (Kulzer, 1979). Differences in methods may have contributed to this variation, but there still should be a negative relationship between mass specific EWL and body mass as a result of the similar relationship between \dot{V}_{O_2} , M_b^{-1} and M_b .

High rates of EWL are offset to some degree by the production of metabolic water; when $R = 0.78$, metabolic water production will be $0.57\text{ g l}^{-1}\text{ O}_2$ consumed. This ratio is shown by the dashed horizontal lines in Fig. 5, indicating that average rates of EWL exceed rates of metabolic water production only at vapour pressures below $7\text{--}9\text{ Torr}$. Like most fruit bats, *P. poliocephalus* is typically found in relatively mesic habitats (Bartholomew *et al.* 1964), and evaporative dehydration during even long flights should be infrequent and easily compensated for by its diet of various fresh plant materials.

Temperature regulation

The positive relationship between T_b and T_a seen in Fig. 6 has also been reported for microchiropterans over a wide range of T_a (O'Farrell & Bradley, 1977). The variation in T_b of bats no. 6 and no. 8 appears considerable, but even at rest these bats show variation in T_b over a 4°C range (Bartholomew *et al.* 1964). Moreover, the data in Fig. 6 are from flights at various airspeeds and humidities, both of which should have some effect on a bat's steady state T_b .

The problem of temperature regulation may be more complicated for many bats and birds than for terrestrial endotherms. When these generally small animals are inactive in cold climates, there is real advantage for low thermal conductance to reduce heat loss. During flight, the enormous mass specific heat production should favour increased thermal conductance to prevent overheating. The non-evaporative thermal conductance (C) of endotherms may be calculated as follows (Tucker, 1972):

$$C = (H_1 - H_c) / (T_b - T_a), \quad (4)$$

where the heat loss (H_l) is assumed to be all of the metabolic rate at rest, or the fraction of exercising metabolic rate not represented as work, and H_e is the rate of heat loss by evaporation.

It is of interest to compare values of C for *P. poliocephalus* with those of other exercising endotherms. At $T_a = 24^\circ\text{C}$, the standard metabolic rate of *P. poliocephalus* with T_b about 37°C is 2.96 W kg^{-1} (Bartholomew *et al.* 1964), and pulmonary water loss is approximately $1.5\text{ g H}_2\text{O kg}^{-1}\text{ h}^{-1}$ (R. E. Carpenter, unpublished data). The H_e would be 34 % of the resting heat production at a rate of $2.43\text{ kJ g}^{-1}\text{ H}_2\text{O}$ evaporated ($0.58\text{ kcal g}^{-1}\text{ H}_2\text{O}$). The resting non-evaporative conductance (C_r) would thus be equal to $0.15\text{ W kg}^{-1}\text{ }^\circ\text{C}^{-1}$. If efficiency is 0.25, the heat production in flight would be 75 % of the minimum P_i of 54 W kg^{-1} (Table 2), of which about 10 % might be lost by evaporation (Fig. 5). At $T_a = 24^\circ\text{C}$, and $T_b = 39^\circ\text{C}$, the non-evaporative conductance in flight (C_f) is about $2.4\text{ W kg}^{-1}\text{ }^\circ\text{C}^{-1}$. This 16-fold increase in conductance far exceeds the four-fold increase in small exercising rodents (Tucker, 1972). The differences are doubtless the result of higher rates of convective heat loss with greater air movement across the enormous surface area of the bats.

The C_f of 0.320 kg laughing gulls is even greater ($3.4\text{ W kg}^{-1}\text{ }^\circ\text{C}^{-1}$), but their ratio of C_f/C_r is only 5.8 (Tucker, 1972). This seems to be partly the result of the relatively high C_r calculated for the gulls at rest. For example, when C_r of the gulls is calculated with their predicted basal P_i , and Tucker's values for fractional H_e (29 %), the ratio C_f/C_r (10.4) is closer to that calculated for bats on the same basis.

The C_f of $2.4\text{ W kg}^{-1}\text{ }^\circ\text{C}^{-1}$ for flying bats apparently exceeds those of both pigeons and ravens, which are the largest birds whose metabolism has been measured in wind tunnels (Hudson & Bernstein, 1981; Butler, West & Jones, 1977). At an efficiency of 25 % the minimum rates of heat production of bats no. 6 and no. 8 (40.5 W kg^{-1}) are less than the approximately 50 W kg^{-1} of these birds (*ibid.*). By assuming that $H_e = 20\%$ of heat production, I calculate that C_f for pigeons and ravens at $T_a = 25^\circ\text{C}$ are, respectively, $2.3\text{ W kg}^{-1}\text{ }^\circ\text{C}^{-1}$ and $2.0\text{ W kg}^{-1}\text{ }^\circ\text{C}^{-1}$.

Despite their lower rates of mass specific heat production and apparently higher C_f values, bats show a much lower capacity to tolerate warm T_a during flight than do birds. Even with the open mouth cooling behaviour, *P. poliocephalus* quickly became severely hyperthermic at $T_a \geq 25^\circ\text{C}$, which is 10°C below the upper critical temperature of this species at rest (Bartholomew *et al.* 1964). In contrast, gulls could fly steadily at T_a as high as 30°C (Tucker, 1972), starlings and fish crows at $34\text{--}35^\circ\text{C}$ (Torre-Bueno, 1976; Hudson & Bernstein, 1981) and budgerigars flew for 5–13 min at $36\text{--}37^\circ\text{C}$ (Tucker, 1968). These differences seem to be based on the respiratory physiologies of the two groups. At T_a up to about 20°C , EWL accounts for about 10 % of heat production in both groups (Fig. 5; Torre-Bueno, 1978; Hudson & Bernstein, 1981). As T_a increased above this level, birds were able to elevate f_R , and to thereby increase H_e to 20–40 % of heat production at $T_a = 33\text{--}35^\circ\text{C}$ (Tucker, 1968; Hudson & Bernstein, 1981).

For bats, there is no evidence of a relationship between the EWL in flight and T_a , except for the unmeasured contributions of mouth opening. This apparently is because bats show an obligatory 1:1 coupling of respiratory and wingbeat cycles that restricts changes in f_R and ventilation rate to correspond to the rather small

adjustments of wing movements at moderate airspeeds (Table 2; Thomas, 1981; Thomas & Lust, 1979). This relationship appears to limit H_e in bats to such a small fraction of heat production that temperature regulation in flight is not possible at temperatures constituting most of the thermal neutral zone of these animals at rest.

A number of factors, such as ecological competition with birds or relative development of special senses, may be responsible for restricting bats to nocturnal activity. However, these data suggest that extensive daytime flying of most bats in the temperate to tropical habitats may be impossible because evaporative heat loss is restricted by the mechanics of their lung ventilation to a small fraction of their high heat production in flight.

Circulatory system

High metabolic rates in flight require corresponding adaptations of the circulatory system for adequate O_2 delivery to the muscles. The data obtained for haematocrit and haemoglobin concentration are about 30 % higher than those for terrestrial mammals (e.g. Altman & Dittmer, 1974), and 14–30 % above those of various birds (Balasch *et al.* 1974, 1976). Haematocrit and O_2 capacities of these bats agreed closely with those of *P. hastatus* (Thomas & Suthers, 1972), although O_2 capacity was much less in later measurements for *P. hastatus* (20.6 vol%) and *P. alecto* (20.8 vol%; Van Riper & Thomas, 1981).

The blood O_2 capacity can also be estimated accurately for mammals as 1.36 times the g% haemoglobin concentration (Larimer, 1959). The lower resulting value of 23 vol% for *P. poliocephalus* thus exceeds by 14–30 % both the average of 17.5 vol% reported for mammals (Larimer, 1959) and the means calculated by this method for raptors (17 %; Balasch *et al.* 1976) and marine birds (20.3 %; Balasch *et al.* 1974).

The heart mass of bat no. 6 was 36 % greater than predicted for a mammal of the same body mass by allometric equation (Stahl, 1967), and 121 % and 95 % of values predicted for birds by the similar equations of Lasiewski & Calder (1971) and Berger & Hart (1974), respectively. This large heart mass should result in correspondingly large stroke volume (SV), since this is related to heart mass (M_H , in g) of mammals over a wide range of body sizes according to the formula:

$$SV = 0.26M_H^{0.96} \quad (5)$$

(Holt, Rhode & Kines, 1968).

The minimal heart rates of bats no. 6 and no. 8 in flight were 90 % of the rates predicted for birds of the same mass by scaling equation (13) of Berger & Hart (1974). Depending on the values above used for relative heart size, the resulting cardiac output ($= SV \times f_H$) is 85–109 % of that expected for birds in flight. Even if the lower estimate is more accurate, the higher haemoglobin concentration and O_2 carrying capacity of the blood of bats should permit equal capacities for O_2 delivery.

Whether these circulatory adjustments are sufficient to supply the O_2 demands of flight can be seen by their use in the Fick equation:

$$\dot{V}_{O_2} = f_H \times SV (Ca_{O_2} - C\bar{v}_{O_2}), \quad (6)$$

where the last term is the arterial-venous O_2 difference (vol%). From equation (5) the SV of bat no. 6 should have been 1.48 cm^3 . Using the more conservative value of 23.0 vol% for arterial O_2 content, and assuming arbitrarily that venous blood contained a minimum of 3.0 vol% O_2 , the rate of delivery should have been about 8.51 h^{-1} , or $11.01 \text{ kg}^{-1} \text{ h}^{-1}$ for the 0.770-kg bat. If the heart rate could increase by 20% over the rates measured at V_{mp} , the circulatory system could support a \dot{V}_{O_2} of $13.21 \text{ O}_2 \text{ kg}^{-1} \text{ h}^{-1}$, which approximates the maximum rate of both bat no. 6 and no. 8 (Table 2).

Cost of transport

A useful comparison of effectiveness of the locomotion of animals is the cost of transport, which is the metabolic cost of moving an animal's weight a given distance, P_i/WV . If weight is in Newtons, this term is dimensionless. The lowest values for P_i/WV for flying animals are usually attained at, or near, their maximum flight speed (Tucker, 1973). The minimum values for P_i/WV for bats no. 6 and no. 8, at $S = 8.0$ and 8.6 m s^{-1} respectively, are 0.70 and 0.74 (Table 4). These exceed the P_i/WV of 0.63 of *P. alecto* at $V = 9.9 \text{ m s}^{-1}$, and are about 14% greater than predicted from Tucker's (1973) equation (56) for estimating minimum P_i/WV on the basis of body weight. Lower values for P_i/WV would presumably have been obtained if it had been possible to fly no. 6 and no. 8 at higher V . However, measurement of the minimum value of P_i/WV is of dubious ecological significance for this species, and perhaps for other bats, in light of the effect of V on endurance.

Endurance

The effect of velocity on endurance was so dramatic that bat no. 8 clearly could achieve its maximum range only by flying at its V_{mp} of 6 m s^{-1} . For example, at other V_i values, the mean endurance was always below the minimum endurance necessary to achieve the distance possible at V_{mp} ['endurance for equivalent distance' = $E_{mp} (V_{mp}/V_i)$; Table 4, Fig. 8A]. Put another way, the product of each V_i and its corresponding mean endurance time (in s) gives the mean distance possible at that speed; the maximum range of bat no. 8 was possible only at the V_{mp} of 6 m s^{-1} (Table 4, Fig. 8B). The endurance of bat no. 6 at 8.6 m s^{-1} was 32% of that at its V_{mp} ; its range at the higher speed would have been only 44% of that at $V = 7 \text{ m s}^{-1}$.

It is not surprising that endurance declined at velocities at which rates of O_2 and fuel consumption were higher, but it does not appear that it was simple exhaustion of energy stores that limited the endurance of this bat. One could consider the 'metabolic capacity' at each V_i as the product of the animal's endurance (in s) and its power input at that speed. If endurance were simply energy limited, the calculated metabolic capacity should have about the same value at each V_i . Instead, metabolic capacity peaks sharply (Fig. 8B) in the same manner seen for endurance and maximum possible distances.

If the endurance of a flier were limited at all speeds by energy stores, as has been implied for birds (Pennycuik, 1968; Tucker, 1971), then the time aloft would be maximized if the animal flew at the V_{mp} , but range would be maximized at the speed (V_{mr}) at which the cost of transport (P_i/WV) is minimal. But the endurance

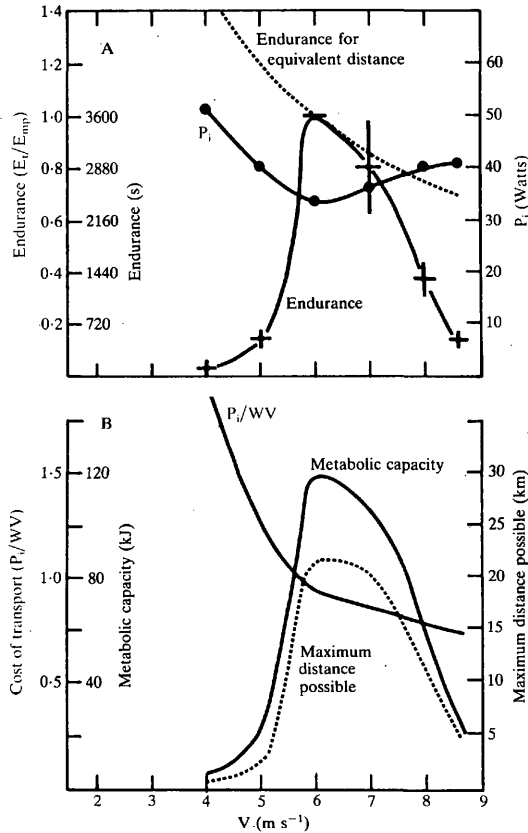


Fig. 8. (A) Effect of airspeed (V) on power input (P_i ; right ordinate) of bat no. 8 and on its endurance (left ordinate), which is expressed both as the ratio of endurance at test speed (E_t) to endurance the same day at V_{mp} of 6 m s^{-1} (E_{mp}), and as actual time by setting $E_{mp} = 3600 \text{ s}$. Horizontal lines are mean values; vertical lines indicate mean ± 2 s.e.m.; curved lines fitted by eye. Actual endurance at $V = 6 \text{ m s}^{-1}$ was variable, but was always treated as the reference point in calculating endurance as E_t/E_{mp} ; hence, there was no statistic calculated. Dotted line indicates the endurance necessary (as fraction of E_{mp} or in s) at each velocity to achieve the distance possible at $V = 6 \text{ m s}^{-1}$. (B) Effect of airspeed on three calculated indices of performance. The declining value for cost of transport (P_i/WV) indicates that minimum cost occurred at the maximum speed flown (8.6 m s^{-1}). Products of endurance (in s) at each V_t and corresponding power input indicate the 'metabolic capacity'. Products of endurance and velocity give the maximum distance that could be flown at each V_t (dotted line, right ordinate).

of bat no. 8 at the velocity where P_i/WV was minimum (8.6 m s^{-1}) was only 13.6 % of its endurance at 6 m s^{-1} (Table 4, Fig. 8A). Thus, despite the lower cost of transport available at any V above V_{mp} (see line P_i/WV , Fig. 8B), the bat could fly

only 4.22 km at the 'speed of maximum range' when capable of a distance of 21.6 km at $V = 6 \text{ m s}^{-1}$.

There seem to be no obviously correct alternative explanations for the observed effect of velocity on endurance and metabolic capacity. At V_{mp} , endurance may actually be limited by the availability of energy reserves. At the minimum and maximum velocities, flight durations were sometimes as brief as 1–2 min, and the animals usually breathed vigorously with closed mouths for a minute or two after landing. At the higher metabolic levels required at these airspeeds endurance was perhaps limited by rates of O_2 delivery to the flight muscles. However, at moderate speeds (e.g. $5\text{--}8 \text{ m s}^{-1}$) the flights were long enough (7–20 min) to suggest that the anaerobic contribution to flight was unimportant, and the lack of heavy breathing after bats landed suggested that the O_2 debt was insignificant.

The endurance of endotherms may be limited by severely elevated body temperatures (Aulie, 1971; Taylor & Rowntree, 1973). To avoid possible effects on endurance bats were not flown with thermocouples or other apparatus to monitor T_b in these flights. However, the flights to measure endurance were all made at T_a below those normally causing heat stress (24°C), and the behavioural cooling responses described previously were not seen in any of these flights, although they were looked for.

In theoretical considerations of flight metabolism and costs and times of migrations, it has been assumed that birds fly at the most economical speed, V_{mr} (Pennycuik, 1969; Tucker, 1971), and the minimum values for P_i/WV (at V_{mr}) have been the basis for comparison of the metabolic effectiveness of fliers with that of animals travelling by other methods (Tucker, 1975). Attempts to determine whether birds actually fly at either of these speeds have proved inconclusive. Free-flying laughing gulls flew at speeds that matched their top speed and V_{mr} as measured in a wind tunnel (Tucker & Schmidt-Koenig, 1971). Free-flying barnacle geese flew for only 10 s at their maximum speeds (Butler & Woakes, 1980), and budgerigars flew in a wind tunnel for no more than 5 min at top speed, although capable of 25-min flights at lower speeds (Tucker, 1968). Some small migratory birds flew at speeds below their predicted V_{mr} (Larkin, Griffin, Torre-Bueno & Teal, 1979), and shorebirds appeared to select speeds that were compromises between calculated V_{mp} and V_{mr} (Schnell & Hellack, 1979). Starlings preferred to fly in a wind tunnel at about the midrange of their possible flight speeds, and therefore below their measured V_{mr} (Torre-Bueno & Larochelle, 1978).

Data on free-flying *Pteropus* are even more scarce. Ratcliffe (1932) estimated that Australian flying foxes (species not identified) flew at 'about 25 mph' ($>11 \text{ m s}^{-1}$), without reporting wind speeds or methods of measurement. This velocity is higher than the maximum attained by any bat in a wind tunnel.

None of the other wind tunnel studies of vertebrate flight metabolism mentions any effect of airspeed on endurance. Nevertheless, this pattern can be so easily overlooked in well conditioned tunnel fliers that it may well exist in many species. Most workers have trained animals to fly at several velocities for the time desired for a particular measurement (e.g. Tucker, 1968; Thomas, 1975; Hudson & Bernstein, 1983). Any effect of V on endurance is not likely to be noticed unless flights at

different V are made the same day, in which case variations in performance might casually be attributed to fatigue.

In light of these data, and in the absence of specific measurements indicating that the endurance of fliers at their V_{mr} is at least as great as the endurance required for an equivalent distance at their V_{mp} , one cannot assume *a priori* that fliers travel at their most economical speed, or that their endurance at that V is limited solely by available fuel. Should V later prove to affect similarly the endurance of most birds and bats, it would have the following implications.

(i) Fliers probably optimize their time aloft, rather than minimizing their cost of transport.

(ii) They should travel at their V_{mp} to achieve maximum distances.

(iii) The velocity where the ratio P_r/WV is minimum should more accurately be designated the speed of maximum economy (V_{me}), rather than V_{mr} ; the latter would actually be the same as the V_{mp} .

(iv) In long distance flights the metabolic rates should be lower, but times and costs of migration higher, than predicted by the aerodynamic models or simplified allometric equations for estimating flight metabolism at V_{me} (Tucker, 1973).

(v) Comparisons of the minimal values for the cost of transport at V_{me} of various species show that the costs for fliers are approximately 25–50 % of those of terrestrial species (Tucker, 1975). If fliers actually travel at their V_{mp} , there will be an increase in their actual costs of transport, and the locomotory economies of bats and birds will be less advantageous relative to those of terrestrial species than presently assumed.

(vi) Finally, if animals typically fly at their V_{mp} , this should answer the question of how they 'know' at which speed to fly, and how this speed is determined (Tucker & Schmidt-Koenig, 1971). These could easily be determined if the animal simply flew at the velocity that is least strenuous, the V_{mp} .

Although there is interest in the actual air and ground speeds of fliers, there need to be systematic studies that measure the endurance and freely chosen airspeeds of different species, as well as their metabolic rates and values for V_{mp} and V_{me} . It would be particularly interesting to know whether the proficient migrants come closer than non-migrants to achieving the endurance at their V_{me} that is necessary to result in the range that would be possible when flying at their V_{mp} . This would justify the earlier assumptions that fliers travel at their most economical speeds.

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