

THE PHYSIOLOGY AND ENERGETICS OF BAT FLIGHT

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Bats are unique in being the only mammals capable of flight. The mobility, speed, and agility associated with this means of locomotion must have been an important factor in their successful radiation, which has made this diverse group the second largest order of mammals. Excluding man, and possibly rodents, bats have the widest distribution of any terrestrial mammals (Simpson, 1945; Walker, 1964; Anderson & Jones, 1967).

Despite a growing literature on the physiology of resting or hibernating bats, almost nothing is known regarding the physiology or energetics of bat flight. Mammalian flight is of particular physiological interest since recent studies of bird flight (e.g. Tucker, 1968*b*, 1969; Berger, Hart & Roy, 1970) show that it requires a metabolic rate well above the maximum of which similar size, terrestrial mammals are capable during exercise (Pasquis, Lacaille & Dejours, 1970). Furthermore, birds possess a number of adaptations for flight which are not shared by mammals. In the following research we have measured the energetic cost of flight to a bat and attempted to determine what adaptations permit these mammals to maintain the high metabolic rates for which birds seem so uniquely specialized. Some of the data which we report here were summarized in a brief preliminary report (Thomas & Suthers, 1970).

METHODS

The following experiments were conducted on *Phyllostomus hastatus* Pallas (Microchiroptera, Phyllostomatidae), a large, echolocating, neotropical bat weighing between 70 and 110 g. These animals were collected in Trinidad, West Indies, where they roost during the day in caves, abandoned buildings and hollow trees, feeding during the night on various fruits, insects and occasionally small vertebrates. Animals used in experiments were kept in the laboratory on a diet of ground beef, bananas, melons, and a vitamin-mineral supplement (Pervinal). Physiological responses to flight were studied in *P. hastatus* flying in a 6.1 × 12.2 m flight laboratory. Bats used in these experiments were kept in good physical condition by regular daily exercise. All experiments were performed at an ambient temperature (T_A) between 24 and 26 °C and a relative humidity (R.H.) between 28 and 71 % unless stated otherwise.

Deep rectal temperature (T_R) was measured to the nearest 0.1 °C on a calibrated Tri-R electronic thermometer within 10 sec after flight by inserting the rectal thermistor probe to a depth of 2 cm. An active bat was hand-held until its T_R dropped

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to 41 °C. It was then allowed to fly for a given length of time, whereupon it was caught and the deep T_R was measured again.

Respiratory rate was telemetered from quietly resting and from flying bats carrying a small 7 g FM transmitter (modified E & M Instrument Co. Model FM-1100-E3) connected to a thermistor mounted in front of the animal's nostrils as described by Suthers, Thomas & Suthers (1972).

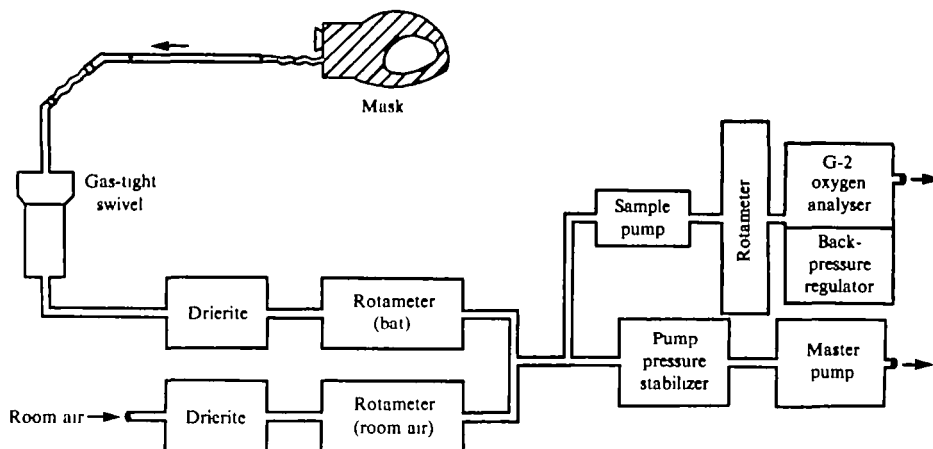
Oxygen consumption, respiratory water loss and respiratory quotient (R.Q.) were measured on bats trained to fly in a circular path along the inside of a cylindrical partition 6.1 m in diameter while wearing a 3.4 g mask connected by light-weight tubing to a vacuum pump at the centre of the circular flight path (Pl. 1). About 6–8 weeks of nightly training were required in order to accustom the bat to the mask so that long, well-coordinated flights could be consistently obtained. The posterior part of the mask was made of moulded latex which fit snugly over the bat's head. The anterior portion consisted of a short length of a cellulose centrifuge tube, sealed at the front with a taut Mylar membrane 1 μ m thick positioned several millimetres in front of the animal's nostrils. This membrane vibrated during ultrasonic pulse emission, thus permitting echolocation but preventing the escape of expired gas.

Room air entered a small opening inside an anterior directed scoop at the rear of the mask and, together with expired gases, was withdrawn at the rate of 4.14 l/min through another opening near the front on the opposite side. These gases then passed through a 0.7 m length of light-weight flexible vinyl tubing (2 mm I.D.) into a 1.6 m length of aluminium tubing. A person standing at the centre of the flight circle held this aluminium tube in front of the flying bat so that the vinyl tubing attached to the mask was kept slack and exerted no tension on the animal. The aluminium tube was connected by Tygon tubing to a gas-tight swivel junction, at the centre of the flight circle, through which the gas passed on its way to a Beckman Model G-2 paramagnetic oxygen analyser equipped with a back-pressure regulator (Text-fig. 1). This oxygen analyser gave a 10 in. deflexion for a change of 0.01 in the fractional concentration of oxygen and provided a continuous record of the bat's oxygen consumption. The high sensitivity of the oxygen analyser made it necessary to dilute the mask gases with a known volume of dry room air prior to drawing a sample of this mixture through the analyser. Gas flow was measured with rotameters that were calibrated under the pressure gradients existing during the experiment, and oxygen consumption was calculated from steady-rate oxygen analyser readings, assuming an R.Q. of 1.0, by means of the equation

$$\dot{V}_{O_2} = (F_{IO_2} - F_{EO_2}) \dot{V}_{total},$$

where \dot{V}_{O_2} is the oxygen consumption, F_{IO_2} is the fractional content of oxygen in air entering the mask, F_{EO_2} is the fractional content of oxygen in air entering oxygen analyser, and \dot{V}_{total} is the sum of flow rates through the bat rotameter and room air rotameter (Pl. 1). All oxygen consumption values in this paper are in terms of dry gas at 0 °C and 760 mmHg. If the bat's R.Q. was actually 0.7 (but see Results) the calculated oxygen consumption would be 6% too low (Despocas & Hart, 1957).

In order to make certain that there was no unintended leakage of expired gases from the mask, we measured oxygen consumption at lower flow rates. If gases were leaking out the intake opening or around the rear of the mask this leakage should increase at lower flow rates and reduce the apparent oxygen consumption of the bat.



Text-fig. 1. Schematic diagram showing the method used to measure oxygen consumption during flight. This system also permitted measurements of respiratory water loss and the collection of gas samples for R.Q. determinations.

The computed oxygen consumption did not begin to decrease until the flow rate through the mask was reduced to a value 20 % below that used in the actual experiments.

The relatively slow response time of the oxygen analyser prevented direct measurement of oxygen consumption during about the first minute of either flight, or rest immediately after the flight. In order to estimate the oxygen debt incurred during flight it was therefore necessary to correct the apparent oxygen consumption immediately after flight for the response time of the oxygen analysis system. This was done by preparing one gas mixture with an oxygen content identical to that of the gas sample obtained from the bat during sustained flight and another gas mixture duplicating the oxygen content of the gas sample obtained from the bat after it had levelled off to a steady post-flight value. By instantaneously switching from the simulated flight mixture to the simulated post-flight mixture, we obtained a curve on the chart of the oxygen recorder that represented the response time of the analysis system under the conditions of the experiment. The difference between the area under this curve and that obtained immediately after the bat stopped flying must be due to the gradual decrease from flight to resting oxygen consumption levels by the bat and therefore can be used to estimate the oxygen debt incurred during flight. In other words, the oxygen debt was estimated by determining how much longer it took the recorded oxygen consumption to return to a steady resting level after an actual flight than it took this record to return to the same level after a simulated flight.

The amount of lactic acid in the blood was determined by Calbiochem spectrophotometric assays. The animals were decapitated over a heparinized beaker and a 1 ml blood sample was immediately de-proteinized. Standards of known lithium lactate concentration were run simultaneously with the sample, the final analysis being performed on a Beckman DU spectrophotometer at 340 μm .

Respiratory evaporative water loss was determined by measuring within ± 0.1 mg the weight change per unit flight time of a tube of indicating anhydrous CaSO_4 (Drierite) placed in the gas flow from the mask. Care was taken to dry the interior of

the mask and tubing prior to each experiment. After the flight dry air was again passed through the system to collect any water which condensed there during the flight and include it in the computation of water loss. The water vapour collected from room air, drawn through a fresh tube of Drierite at the same flow rate and for the same length of time as the flight, was subtracted from that collected during flight to obtain the respiratory water loss.

Respiratory quotients were measured by drawing samples of the gases flowing from the mask and analysing their oxygen and carbon dioxide content on a Beckman GC-4 gas chromatograph.

Blood hematocrit was determined for the blood samples obtained by decapitation. Care was taken to be certain that the blood was well mixed before it was drawn into standard capillary hematocrit tubes and centrifuged at full speed for 5 min in a model CL International Clinical Centrifuge. Blood samples in preliminary tests which were centrifuged for an additional 5 min showed no further reduction in the hematocrit values.

Oxygen capacity was measured in blood samples obtained by decapitating a fully awake bat over a small heparinized beaker. The blood thus collected was then immediately drawn into a 2.5 ml syringe. One ml of this blood was transferred into a miniature version of a Hall tonometer having a volume of about 17 ml and similar to that described by Tucker (1967). The remainder of the blood was stored in the syringe at 5 °C for subsequent analysis. Room air was pumped at a rate of about 15 ml/min through, successively, a temperature-equilibration coil, a humidifier, and then the tonometer containing the blood sample, which was rotated at about 60 rev/min. The tonometer, as well as the tubing carrying the equilibration gas (room air) that entered it, were submerged in a water bath equipped with a stirrer which kept them at 41 ± 1 °C – about the body temperature of *P. hastatus* during flight. Blood samples were equilibrated for 30 min, after which a sample was immediately drawn into a 0.5 ml van Slyke pipette and transferred into a van Slyke manometric apparatus for oxygen-capacity determinations. Tests in which the hematocrit was determined both before and after the blood samples were equilibrated for 30 min showed that no evaporation of the sample occurred during this procedure.

Heart rate was telemetered from the flying bat by means of a small 7 g FM transmitter (E & M Instrument Co. Model FM-1100-E3) which was attached to the animal's back. This transmitter received its input from two intrathoracic leads which were insulated except at the tip, which was located close to the heart in order to minimize extraneous muscle potentials. These leads were surgically implanted under ether anesthesia a few days before the heart rate was measured.

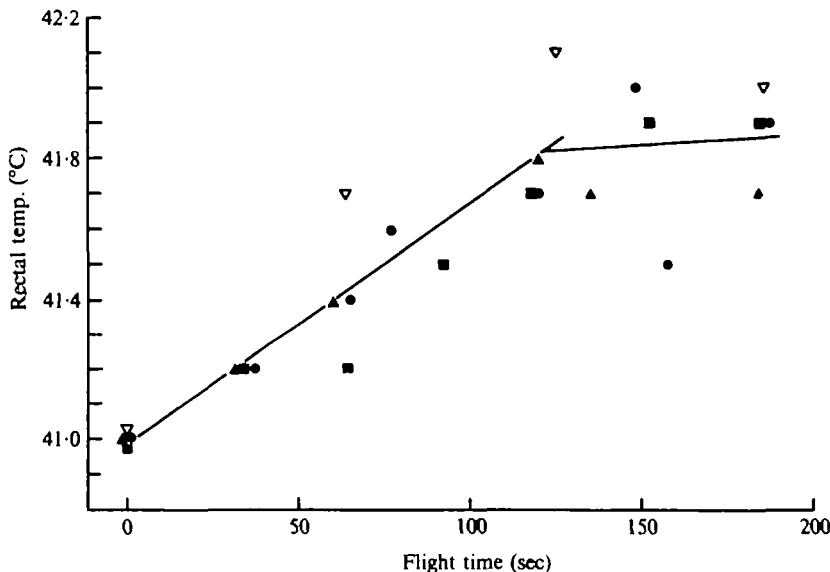
RESULTS

Deep rectal temperature

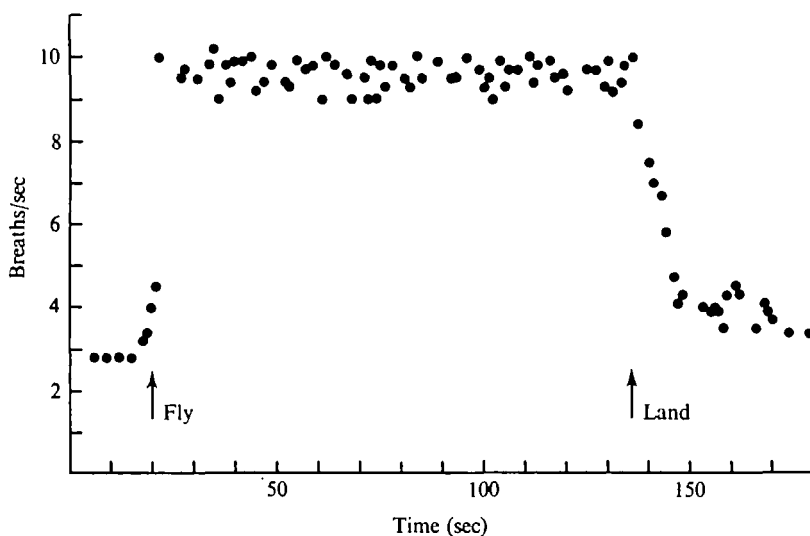
Deep rectal temperatures of four bats after flights lasting from 30–187 sec at a T_A of 24–26 °C ranged between 41.2 and 42.1 °C (Text-fig. 2). During the first 2 min of flight the T_R rose linearly at a rate of 0.4 °C/min as calculated by the least-squares equation

$$T_R = 0.0069(t) + 40.99$$

where t is the flight duration in seconds. T_R remained almost constant after the first 2 min of flight and had a mean value of 41.8 °C.



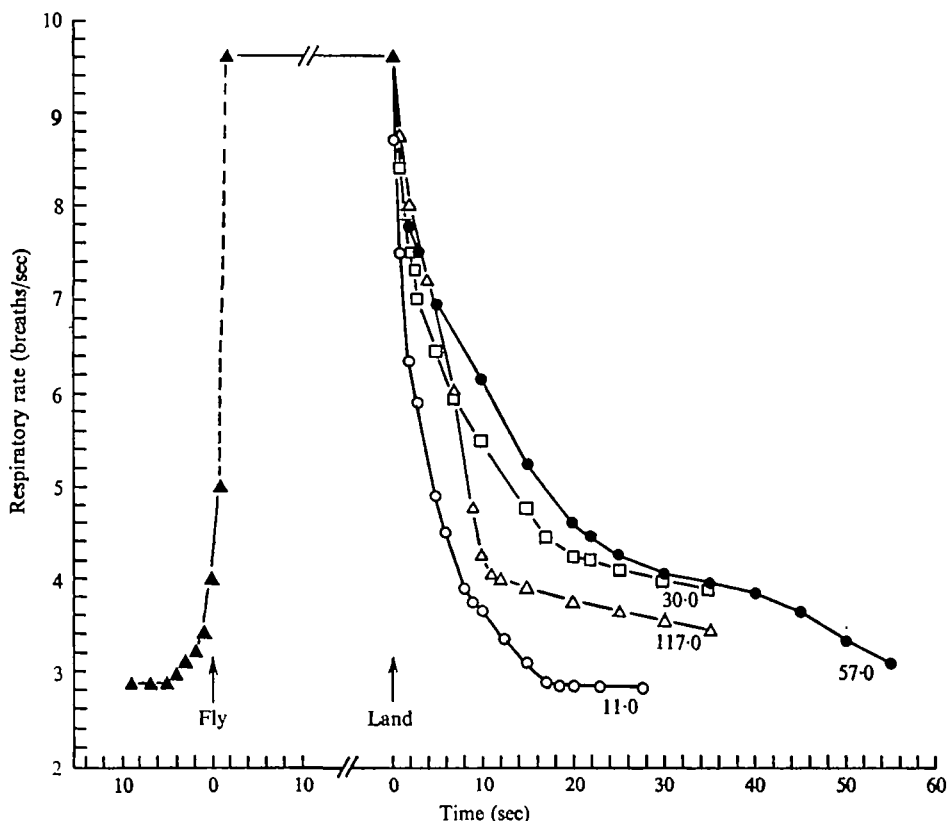
Text-fig. 2. Rectal temperature of four *Phyllostomus hastatus* as a function of flight duration. Rectal temperature was 41.0 °C at the start of each flight. $T_A = 25-26$ °C and R.H. = 54-67 %. Least-squares equation for the line fitted to the data between 0 and 125 sec is $T_R = 0.0069(t) + 40.99$. For the line fitted to the data between 120 and 180 sec this equation is $T_R = 0.0005(t) + 41.76$. ●, 106 g male; ▲, 101 g male; ■, 99 g female; ▽, 97 g male.



Text-fig. 3. Respiratory rate of a flying *Phyllostomus hastatus*. This 97 g male maintained a mean respiratory frequency of 9.6 breaths/sec (s.d. = 0.34) during this 117 sec flight. These data are similar to those obtained from other *P. hastatus* during flights longer than about 20 sec.

Respiratory rate

A typical respiratory response to flight is shown in Text-fig. 3. The respiratory rate increased within the first 3 sec of flight from an anticipatory pre-flight rate of about 2.5/sec to a mean steady-flight rate of 9.6/sec. This rate remained essentially constant



Text-fig. 4. Changes in the respiratory rate of *Phyllostomus hastatus* at the beginning of flight and immediately following flights of various durations. The abrupt increase of respiratory frequency at the start of flight is typical of the bats studied. All the recovery curves were obtained from the same bat, and the numbers indicate the duration, in sec, of the preceding flight.

throughout the remainder of the flight (s.d. = 0.314). The mean respiratory rate for many trials involving four bats varied only from 9.5 to 10.1/sec, the higher rate usually being associated with very short flights. The respiratory rate returned to its pre-flight level within 20–60 sec after the bat landed – the bulk of this recovery being completed within about 30 sec (Text-fig. 4). Recovery was rapid for very short flights (11.0 sec), slowest for intermediate length flights (30–60 sec), and became more rapid for longer flights (1–2 min).

Oxygen consumption

Even after the longest flights of 4.5 min the respiratory rate and depth of bats wearing masks for the measurement of oxygen consumption were indistinguishable from those observed immediately after similar flights without the mask. Furthermore, healthy unmasked bats could rarely be induced to fly more than about 5 or 6 min at a time in the laboratory. These observations indicate that the experimental technique by which oxygen consumption was measured did not greatly interfere with the normal metabolic functions of the bat during flight.

Table 1. *Oxygen consumption of Phyllostomus hastatus*

Bat	Mean body weight (g)	Mean flight speed (km/h)	Oxygen consumption* (ml O ₂ (g h) ⁻¹)		
			About 5 sec before flight	During flight	About 30 sec after flight
<i>F</i>	101	21	6.78 ± 0.85 (16)	27.53 ± 0.79 (16)	6.63 ± 0.95 (13)
<i>R</i>	87	13	6.12 ± 1.15 (7)	24.68 ± 1.87 (8)	6.45 ± 2.36 (8)

* Mean steady rate ± standard deviation; number of measurements (= flights) in parentheses.

Table 2. *Estimated oxygen debt incurred during flight by Phyllostomus hastatus**

Duration of flight (sec)	Oxygen Debt (ml O ₂ , S.T.P.)	Time needed to repay oxygen debt (sec)
85	5.75	28.3
92	6.75	26.2
121	5.94	24.4

* Data from bat *F*.

Oxygen consumption of two bats during flight is summarized in Table 1. Bat *F* had a mean oxygen consumption of 27.53 ml O₂ (g h)⁻¹ for flights lasting up to 4 min. The flight speed of *F* remained essentially constant during a given flight and from trial to trial so that the O₂ consumption varied only a few tenths ml (g h)⁻¹ during a flight. The response time of the oxygen-analysis system precluded reliable measurements during the first 55 sec of flight. The maximum recorded O₂ consumption from this bat was 29.10 ml O₂ (g h)⁻¹.

Bat *R* flew more slowly than bat *F* and its speed varied more within a given flight. It is not surprising therefore that its mean O₂ consumption (24.68 ml O₂ (g h)⁻¹) for flights lasting up to 4.5 min was somewhat lower. The highest O₂ consumption of bat *R* (27.91 ml O₂ (g h)⁻¹) was recorded during the last few seconds of a flight of more than 3 min which immediately followed several previous flights. The 'steady rate' pre-flight and post-flight O₂ consumption of bats *F* and *R* while they were resting quietly on the investigator's hand is also included in Table 1. A few measurements of flight O₂-consumption were also obtained from two other bats (*Q* and *W*) flying at speeds a little slower than that of bat *F*. Both bats *Q* and *W* consumed between 25.5 and 27.0 ml O₂ (g h)⁻¹ on these flights.

Oxygen debt and blood lactic acid

The approximate oxygen debt incurred by bat *F* on three flights ranged from 5.75 to 6.75 ml O₂ (Table 2). This debt, which would supply energy for about 8 sec of flight, must be repaid during approximately 30 sec immediately after landing when the respiratory rate remained above the normal resting level (Text-fig. 4).

Blood lactic acid was measured in a limited number of bats at rest and within 15 sec after flights of 1.0 or 2.5 min (Table 3). Resting bats had blood lactate concentrations

Table 3. *Effect of flight on blood lactic acid in Phyllostomus hastatus*

Duration of flight (min)	Blood lactate* (mg %)
0	29.6
0	29.5
0	17.4
1.0	86.8
1.0	138.0
2.5	86.4
2.5	66.4
2.5	47.2

* Assayed by Calbiochem spectrophotometric procedure.

Table 4. *Respiratory quotient of Phyllostomus hastatus at rest and in flight*

Bat	Duration of flight at time of measurement (min)	Respiratory quotient*
<i>D</i> †	0	0.83 (4) (0.80-0.85)
<i>R</i> ‡	1, 2, 3, 4	1.04 (12) (0.88-1.27)
<i>Q</i>	~1	1.04 (3) (1.01-1.06)
<i>W</i>	~1	1.12 (3) (1.07-1.18)

* Mean R.Q. followed in parentheses by *n* and range on second line.

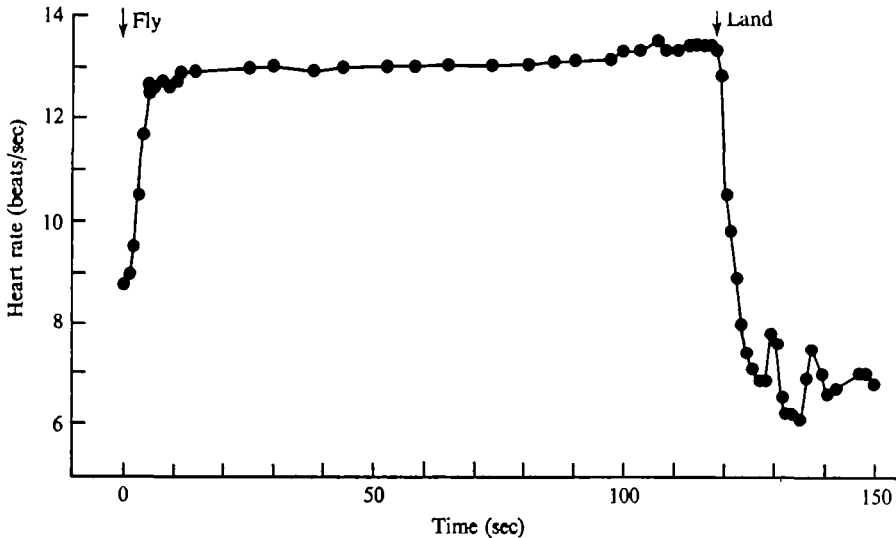
† Bat quietly resting in metabolic chamber at T_A of 29.5 °C.

‡ No significant difference in measurements made at 1 min intervals. Standard deviation of all measurements was 0.12.

between 17 and 30 mg %, whereas all but one of the flying bats had concentrations between 47 and 87 mg %. Despite the variation in values obtained from different individuals it is clear that flight resulted in an appreciable increase in the lactic acid concentration.

Respiratory quotient

Respiratory quotients during flight were determined for three bats (Table 4). The most complete data were obtained from bat *R*, where several gas samples were drawn at 1 min intervals during flights lasting more than 4 min. The mean R.Q. was 1.04 for this bat. In the cases of bats *Q* and *W* only one gas sample was drawn about 1 min after the start of each flight. The mean R.Q. for these bats was 1.04 and 1.12, respectively. Four measurements from another bat resting quietly in a metabolic chamber at a T_A of 29.5 °C gave a mean R.Q. of 0.83.



Text-fig. 5. Cardiac responses to flight by *Phyllostomus hastatus*, showing the characteristic sudden increase in heart rate at the start of flight, the nearly constant rate maintained during flight and the rapid return to a pre-flight level upon landing.

Respiratory evaporative water loss

The respiratory water loss was measured during flight in two bats. The mean respiratory water loss of bat *F* during seven flights lasting 40–157 sec was 23.8 mg H₂O (g h)⁻¹ (s.d. = 2.69, *n* = 7), while that of bat *R* for flights ranging from 65 to 266 sec was 23.6 mg H₂O (g h)⁻¹ (s.d. = 9.38, *n* = 7). The rate of respiratory water loss was not correlated with the flight duration.

Heart rate

Heart rate, like respiratory rate, rose abruptly at the onset of flight, going from an anticipatory pre-flight rate of about 8.7 beats/sec to a steady flight value of about 13.0 beats/sec (780 beats/min) in a few seconds (Text-fig. 5). This rate was maintained for about the first 100 sec of flight, and then began to increase gradually, probably due to the added burden of the FM transmitter. Upon landing, the heart rate rapidly declined and reached a post-flight rate of 6.0 beats/sec 15–20 sec after landing. The time course of this decline was almost identical for a given animal after flights lasting from 30 to 120 sec. The highest heart rate observed was 13.8 beats/sec (828 beats/min) after a particularly strenuous series of flights. Most bats landed when their heart rate reached 13.6–13.8 beats/sec. Heart rates of resting bats frightened by a sudden noise momentarily reached 12.1 beats/sec.

Blood hematocrit and oxygen capacity

Blood hematocrits of six resting bats, two bats immediately after 1 min of flight and three bats after flights of 2.5 min, are summarized in Table 5. These groups of bats had mean hematocrits of 58.8, 60.5 and 61.8, respectively. More data are needed to determine whether or not the hematocrit actually increases during flight. The mean oxygen capacity of the blood of three resting bats was 27.5 vol. % (Table 5).

Table 5. *Hematocrit and oxygen capacity of blood of Phyllostomus hastatus*

Body weight (g)	Duration of flight prior to measurement (min)	Hematocrit (%)	Oxygen capacity (vol. %)
87*	0	59	27.2
88	0	59	27.2, 26.9
79	0	62	28.0, 28.4
118	0	59, 61	—
101	0	56, 56	—
90	0	59, 58	—
89	1.0	58, 58	—
107	1.0	64, 62	—
95	2.5	59	—
106	2.5	62, 62	—
95	2.5	64, 62	—
Mean	—	60	27.5

* Female; all other bats were males.

Metabolic cost of flight

DISCUSSION

When comparing the metabolic cost of flight of bats with that of birds and with running terrestrial mammals it is important to realize that the oxygen consumption recorded from our flying specimens of *Phyllostomus hastatus* does not necessarily represent either their maximum or most efficient (ml O₂ consumed/km travelled) metabolic rate. It does, however, tell us the cost of locomotion at the speed at which these bats chose to fly under the conditions of the experiment. Their flight speed was less than that expected of wild *P. hastatus*, but the effect of velocity on the energetic cost of bat flight is unknown. A cautious comparison of the metabolic cost of locomotion by *P. hastatus* with that of birds and other mammals is worth while.

These experiments indicate that the energetic cost of bat flight is considerably greater than that of running in terrestrial mammals, and approximately similar to the cost of flight to birds. Various small rodents weighing about 25–35 g running either in an exercise wheel or on a treadmill show maximum metabolic rates of about 10–12 ml O₂ (g h)⁻¹, 6–8 times their standard metabolic rates (Hart, 1950; Segrem & Hart, 1967; Pasquis *et al.* 1970). The maximum rates reported by Pasquis *et al.* (1970) for large rodents – rats (*Rattus norvegicus*), hamsters (*Cricetus auratus*), guinea-pigs (*Cavia cobaya*) – running to exhaustion over a 1–2 min period on a treadmill ranged between 5 and 7 ml O₂ (g h)⁻¹ and were similarly 6.5–7 times the standard rates of these animals. The highest metabolic rate recorded from a running 75 g chipmunk (*Eutamias merriami*) is 7.07 ml O₂ (g h)⁻¹ (Wunder, 1970). The mean oxygen consumption of *P. hastatus* quietly resting in a chamber at a T_A of 30 °C ($T_R = 36.5$ °C) was 0.8 ml O₂ (g h)⁻¹. Although this bat is sometimes heterothermic so that its resting metabolic rate is not always comparable to the standard metabolic rate of a homeotherm, it is clear that during flight *P. hastatus* may increase its resting rate more than 34 times in contrast to the 6- to 8-fold increase observed in rodents during exercise.

Since metabolic rate is inversely proportional to body size, a meaningful comparison must take this factor into consideration. Pasquis *et al.* (1970) developed the following

equation from data on various rodents weighing 30–900 g, which predicted their maximum oxygen consumption:

$$\dot{V}_{O_2 \max} = 0.436 (\text{BM})^{0.73},$$

where $\dot{V}_{O_2 \max}$ is in ml O_2 /min and BM is body mass in grams. According to this equation a 100 g bat should have a $\dot{V}_{O_2 \max}$ of 7.54 ml O_2 (g h)⁻¹. The metabolic rate of a flying *P. hastatus* is thus about 3.7 times greater than the maximum predicted for terrestrial mammals of similar size. Even active, non-flying bats can exceed the $\dot{V}_{O_2 \max}$ predicted for rodents. A struggling vampire bat (*Desmodus rotundus*), for example, consumed 18.5 ml O_2 (g h)⁻¹ (Lyman & Wimsatt, 1966).

The metabolic rates of flying birds are roughly similar to that of *P. hastatus*. Small birds tend to be less-efficient flyers than large birds and have a higher oxygen consumption per unit body weight during flight (Tucker, 1970). Direct measurements of oxygen consumption of budgerigars (*Melopsittacus undulatus*) have been obtained by Tucker (1966, 1968*b*) during flights in a wind-tunnel. A budgerigar flying in a small recirculating wind-tunnel having turbulent air flow consumed 48.3 ml O_2 (g h)⁻¹. Subsequent experiments in a large, open, less turbulent wind-tunnel showed that the oxygen consumption of these birds (which weigh about 35 g) depends on their flight speed. The cost of flight is lowest at 35 km/h, where it averages 21.9 ml O_2 (g h)⁻¹, and increases during slower or faster flights. A budgerigar flying at 19 km/h (2 km/h slower than bat *F*) consumed 32.5 ml O_2 (g h)⁻¹. Tucker (1969) has also collected data from the laughing gull (*Larus atricilla*) flying in a wind-tunnel. Unlike the budgerigar, this 300–400 g bird consumes a rather constant 10.4–12.5 ml O_2 (g h)⁻¹ over a wide range of flight speeds extending from 24–47 km/h. Berger *et al.* (1970) reported that a 60 g evening grosbeak (*Hesperiphona vespertina*) consumed 33.7 ml O_2 (g h)⁻¹ during short flights of 7–15 sec. LeFebvre (1964), by using doubly labelled water and measuring fat loss, estimated that pigeons weighing about 380 g use 57 cal (g h)⁻¹ during long cross-country flights. This is equivalent to 11.9 ml O_2 (g h)⁻¹ assuming a flight R.Q. of 0.78 as reported for other flying birds by Tucker (1968*b*).

Birds utilize fat which has a high energy content per unit mass as their prime source of flight energy (Tucker, 1969). This apparent avian adaptation for long-distance flight is not shared by *P. hastatus*, whose resting R.Q. of about 0.8 rises to about 1.0 during flight – indicating that carbohydrates form the main energy source, as they do in other mammals during exercise. Rodents, for example, have an R.Q. of about unity during 2 min bouts of heavy exercise (Pasquis *et al.* 1970). Longer periods of exercise, however, might show a gradual shift from carbohydrate utilization to fat utilization as has been noted in dogs after about ½ h of heavy exercise (Issekutz, Paul & Miller, 1967). *P. hastatus* may not be capable of sustained flights comparable in duration to those of most birds. A colony of this non-migratory bat studied by Williams (1968) in Trinidad, West Indies, usually spent less than 10 min flying to and from their feeding areas. It would be interesting to know whether migratory bats increase their dependence on fat metabolism during migration.

Lactic acid is formed in the working muscles from pyruvate in the anaerobic breakdown of glycogen. Since lactic acid is the most abundant metabolite of anaerobic muscle metabolism, it is a useful index of the extent to which an animal utilizes anaerobic energy during exercise. Blood lactate concentrations of flying *P. hastatus* are

approximately similar to those reported for deer mice (Hart & Heroux, 1954) and white rats (Newman, 1938) during exercise. Flying *P. hastatus*, therefore, do not appear to make greater use of anaerobic metabolism than do running terrestrial mammals, even though these bats are using energy at considerably higher rates.

Pulmonary ventilation

The high metabolic cost of flight places special demands on pulmonary ventilation. Birds meet these demands in part through the unique structure of their lungs, which are composed of air capillaries which diverge from the parabronchi through which there is a unidirectional air flow during both phases of respiration (Bretz & Schmidt-Nielson, 1971), and which have an elaborate system of bellows-like air sacs. These adaptations are believed to provide a steeper diffusion gradient for respiratory gases, making gas exchange more efficient than it is in mammalian alveoli, which must be ventilated by tidal flow. However, lacking these avian adaptations, bats have succeeded in meeting the energetic cost of flight with their mammalian respiratory system.

The minimum tidal ventilation during flight can be estimated from the respiratory evaporative water loss and respiratory frequency, assuming the expired air is saturated with water vapour at a body temperature of 41.0 °C. The respiratory rate of flying *P. hastatus* is synchronized 1:1 with the wingbeat cycle (Suthers, Thomas & Suthers, 1972) and is about 9.6 breaths/sec during relatively long flights in contrast to about 2.8 breaths/sec just before flight. The minimum tidal volume during flight is therefore about 1.46 ml (Table 6), corresponding to a minute volume of about 840 ml.

P. hastatus probably relies mostly on this increase in respiratory rate to meet the demands for oxygen during flight. Data from various birds (Tucker, 1968*b*; Berger *et al.* 1970) and from man (Dejours, 1964) show that ventilation increases in proportion to oxygen consumption in going from rest to exercise. On the basis of this assumption we can calculate that since the oxygen consumption increased about four times from rest immediately before flight to flight (Table 1) while the respiratory frequency increased about 3.4 times, the minimum resting tidal volume may be about 1.2 ml with the increase in respiratory frequency being primarily responsible for the increased pulmonary ventilation during flight. Budgerigars and evening grosbeaks increase their respiratory frequency and tidal volume about equally during the transition from rest to flight (Tucker, 1968*a, b*; Berger *et al.* 1970), the budgerigar's flight ventilation being about 5 times that at rest. Pigeons, however, like *P. hastatus*, increase their respiratory rate in preference to their tidal volume when they take to flight and also maintain a 1:1 synchrony between wingbeat and respiration (Hart & Roy, 1966).

During flight the relative pulmonary ventilation (ml air (g h)⁻¹) of *P. hastatus* is similar to that of most birds studied (Table 6). Adjustments of minute ventilation during flight to meet varying metabolic requirements could take the form of changes in respiratory rate or in tidal volume. Since, however, this bat takes one breath with each wingbeat and since the wingbeat frequency remains almost constant during flight, the respiratory rate likewise remains essentially constant. Greenwalt's (1960) finding that the wingbeat frequency for efficient flight by birds and insects is determined by the resonant frequency of their wings, which can be treated as mechanical oscillators, would seem to be true in bats and could explain the constant wingbeat frequency. *P. hastatus* must therefore rely mainly on changes in tidal volume to adjust its ventila-

Table 6. Respiratory parameters of bats and birds during flight

Species	Oxygen consumption (ml (g h) ⁻¹)*	Respiratory evaporative water loss (ml O ₂ /mg H ₂ O)	Ventilation† (ml (g h) ⁻¹)	Respiratory frequency (breaths/min)	Tidal volume‡	
					(ml (g breath) ⁻¹)	(ml/breath)
Spear-nosed bat (<i>Phyllostomus hastatus</i>)‡	24.7	1.05	592	576	0.0171	1.50
	27.6	1.16	491	576	0.0142	1.43
Budgerigar (<i>Melopsittacus undulatus</i>)§	21.9	1.08	398	199	0.033	1.15
Evening Grosbeak (<i>Hesperiphona vespertina</i>)	33.7	—	1160	294	0.066	3.95
Domestic Pigeon (<i>Columba livia</i>)¶	—	—	431	487	0.0147	5.59
	11.9	1.20	287	487	0.0098	—

* S.T.P., dry.

† Bats: gas volume at $T_B = 41^\circ\text{C}$, 760 mmHg; calculated on basis of mean respiratory water loss as described in text. Birds: gas volume at $T_B = 42^\circ\text{C}$, 760 mmHg; calculated on basis of total body water loss, except direct measurement by Hart & Roy (1966) on pigeon and Berger *et al.* (1970) on evening grosbeak.

‡ This study – bat *R* upper line and bat *F* lower line.

§ Flying 35 km/h at T_A of 18–20 °C. Data from Tucker (1968*b*).

|| Calculated from data of Berger *et al.* (1970) for a 60 g bird and corrected to gas volume at 42 °C. Short flights of up to 14 sec.

¶ Upper line: data from Hart & Roy (1966) and LeFebvre (1964). Lower line: values calculated by Tucker (1968*b*) from data of LeFebvre (1964) assuming respiratory frequency of 487 as reported by Hart & Roy (1966).

tion during flight. It may be, however, that smaller bats, like small birds, have respiratory rates lower than their wingbeat frequency. Tucker (1968*b*) has suggested that the uncoupling of respiration from high wingbeat frequencies is necessary in small birds to avoid tidal volumes so small that only the dead space is ventilated.

The varying metabolic requirements of flight might also be met if the animal can vary the amount of oxygen extracted from a given volume of tidal air. This ratio of $\dot{V}_{O_2}/\dot{V}_{air}$ indicates the efficiency of ventilation. Hart & Roy (1966) suggested pigeons may be able to control the efficiency of their ventilation. This might be accomplished in the avian lung with its parallel respiratory and non-respiratory pathways by varying the relative resistance of these channels. This mechanism is not possible in the mammalian lung however. Bats could theoretically alter their ventilatory efficiency by varying blood flow through the pulmonary capillaries, but there is no evidence that this occurs. It may also be that *P. hastatus* maintains a rather constant metabolic rate over a wide range of flight speeds as do laughing gulls (Tucker, 1969) and crows (Thomas, unpublished data).

In any case, the efficiency of ventilation is clearly an important parameter. When respiratory evaporative water loss is used to estimate ventilation, the efficiency of oxygen extraction can be expressed as ml O₂ consumed/mg H₂O exhaled. It is noteworthy that *P. hastatus* compares favourably with birds in this respect (Table 6). Perhaps the most meaningful comparisons can be made between *P. hastatus* and

Table 7. *Comparative cardiac function during exercise**

Animal	Body weight (g)	Heart rate (beats/min)	Cardiac output (l/kg hr) ⁻¹	Stroke volume (ml/kg body wt)
Spear-nosed bat 'R' (<i>Phyllostomus hastatus</i>)†	87.5	780	89.8	1.92
Spear-nosed bat 'F' (<i>Phyllostomus hastatus</i>)†	101.0	780	100.4	2.15
Deer mouse (<i>Peromyscus leucopus</i>)‡	24.0	700	59.5	1.42
Evening grosbeak (<i>Hesperiphona vespertina</i>)§	59.3	840	170.0	3.38
Hypothetical bird§	100.0	730	119.0	2.7

* Estimates of cardiac output and stroke volume are minimum values which assume $A - \dot{V}_{O_2}$ difference equals the blood oxygen capacity. Birds and bat in flight; mouse running.

† Assuming blood oxygen capacity = 27.5 vol. %. See text.

‡ Calculated from data of Segrem & Hart (1967), assuming blood oxygen capacity = 18 vol. %.

§ Calculated from data of Berger, Hart & Roy (1970), assuming blood oxygen capacity = 20 vol. %.

budgerigars, since the methods we employed to estimate minimal flight ventilation were similar to those of Tucker (1968*b*) and provide an estimate of the maximal $\dot{V}_{O_2}/\dot{V}_{air}$ ratios. It can be calculated from the data presented in Table 6 that budgerigars and *P. hastatus* have similar maximal $\dot{V}_{O_2}/\dot{V}_{air}$ ratios during flight with values of 6.2–6.6% and 5.2–6.9%, respectively. The fact that these bats operate during flight at a relative minute ventilation similar to that of a budgerigar and appear able to utilize their inspired air as efficiently as do these birds is quite an accomplishment considering the profound differences in the respiratory system of birds and mammals.

Cardiovascular function

The high hematocrit (59–60) of *P. hastatus* is probably an important factor permitting efficient respiratory exchange and thus constitutes an important adaptation for the transport of oxygen. Similarly high values were reported by Studier & Ewing (1971) who found hematocrits of 53.7 and 56.3 in *Myotis nigricans* collected at dawn and sunset, respectively, and 59 in *M. lucifugus*. There is some evidence that inactive or hibernating bats may store red blood cells in their spleens. Blood from the spleens of hibernating *M. lucifugus* had a mean hematocrit of 75 ± 2 compared to heart hematocrits of 45 which rose to 53 when the bat was 'active' or 'excited' (Kallen, 1960). The high oxygen capacity (27.5 volumes %) of the blood of *P. hastatus* is not surprising in view of its hematocrit. Burke (1953) reported a mean oxygen capacity of 21 volumes % (range 16.4–24.8) for blood from seven *M. austroriparius*. This blood was obtained from excised hearts and the rather wide range of oxygen capacity values suggests that it was not very homogeneous.

The blood of small terrestrial mammals generally has a hematocrit of about 45 (Spector, 1956; Popovic & Kent, 1964) and an oxygen capacity of about 18 vol % (Gjønnes & Schmidt-Nielsen, 1952; Burke, 1953). To our knowledge, the only mammals whose blood hematocrit and oxygen capacity are comparable to those of *P. hastatus* (and probably of other bats) are those which are either adapted to high

Table 8. Comparison of heart and lung weights

Animal	Body weight (g)	Heart weight (g/100 g body wt)	Lung weight* (g/100 g body wt)	Reference
Spear-nosed bat (<i>Phyllostomus hastatus</i>)	103	0.94†	0.92‡	This study
Rock lemming (<i>Dicrostonyx rubricatus</i>)	50	0.59	1.59	Spector, 1956
Golden hamster (<i>Mesocricetus auratus</i>)	120	0.47	0.46	Spector, 1956
American Robin (<i>Turdus migratorius</i>)	70	1.46	2.42	Spector, 1956
Starling (<i>Sturnus vulgaris</i>)	60	1.47	1.87	Spector, 1956

* Both lungs.

† $n = 7$, S.D. 0.0035.‡ $n = 7$, S.D. 0.0038.

altitudes or are divers. Human residents living at 4540 m, for example, have a hematocrit of 59.9 and an oxygen capacity of 26 vol. % (Prosser & Brown, 1961). Diving animals such as muskrats (*Ondatra zibethica*) (Irving, 1939) and harbour seals (*Phoca vitulina*) (Irving *et al.* 1935) have oxygen capacities of 25.0 and 29.3 vol. %, respectively. Among birds, pigeons are reported to have a hematocrit of 52 (Bond & Gilbert, 1958) and an oxygen capacity of 20 vol. % (Drastick, 1928). House sparrows have a mean hematocrit of 48.8 and an oxygen capacity of 19.1 vol. % (Tucker, 1968*a*).

Oxygen transport in the blood is described by the Fick equation:

$$\text{oxygen consumption} = \text{heart rate} \times \text{stroke volume} \times A - V_o \text{ difference,}$$

where the last factor represents the difference in oxygen content of arterial and mixed venous blood. Minimal values for stroke volume, and thus for cardiac output, can be calculated for *P. hastatus* during flight by assuming the maximum value that the $A - V$ difference can attain (27.5 vol. % = blood oxygen capacity) (see Table 7).

The cardiac function of *P. hastatus* is compared with those of birds and of a small mammal in Table 7. The heart rate of a flying bat is high and comparable to that of birds of similar size. Studier & Howell (1969) telemetered a mean heart rate of 1022 beats/min from an 18 g *Eptesicus fuscus* during flights of 2–4 sec. A 28 g house sparrow (*Passer domesticus*) had a heart rate of 924–987 beats/min during flight (Berger *et al.* 1970) and a flying budgerigar had a rate of 930 beats/min (Aulie, 1971*a*). The heart rates of *P. hastatus* and *E. fuscus* during flight fall only slightly above that calculated by an equation developed by Berger *et al.* (1970) to predict the heart rate of flying birds from their body weight.

Cardiac output also depends upon the stroke volume. The estimated minimum stroke volume of *P. hastatus* is between about 1.9 and 2.2 ml/kg body weight and thus lies midway between similar estimates for deer mice during exercise and flying birds (Table 7). This estimate of stroke volume is consistent with the heart weight of this bat, which we found to lie between that of small terrestrial mammals and birds (Table 8). Berger *et al.* (1970) have pointed out that the high stroke-volume of birds in comparison to terrestrial mammals can be accounted for by the relatively large heart

of the former. These authors estimated stroke-volume/heart-weight ratios of between 0.11 and 0.23 ml/g for birds, compared to 0.22 ml/g for deer mice. In *P. hastatus* this ratio is about 0.21–0.23 ml/g.

Since birds and *P. hastatus* consume similar amounts of oxygen and have similar heart rates during flight, their oxygen pulse (i.e. stroke volume $\times A - V_{O_2}$ difference) must also be similar. *P. hastatus* must compensate for its smaller stroke volume by having a high hematocrit which enables its blood to transport a greater amount of oxygen per unit stroke volume than a bird.

Temperature regulation and heat budget during flight

The T_R of *P. hastatus* during flight is about 5 °C above its normal thermoneutral body temperature and is very close to its upper lethal temperature of 42–43 °C (McNab, 1969; Thomas, unpublished data). Morrison & McNab (1967) reported a T_R of 41 °C in the bat *Sturnira lilium* after flight. Elevation of body temperature during exercise is commonly observed in animals. For example, running chipmunks raise their temperature from 37 °C to about 40 °C (Wunder, 1970); budgerigar cloacal temperature, which is about 41 °C at rest, stabilizes at 42.1 °C after 3 min of flight (Aulie, 1971*b*); and pigeons maintain deep sternal temperatures of 44.5 °C after 2 min of flight – a temperature elevation of 1.5–2.0 °C above that at rest (Hart & Roy, 1967).

The metabolic heat that *P. hastatus* must dissipate during flight can be computed by assuming a 25 % conversion efficiency of metabolic energy to external work (Kleiber, 1961) and a stable core temperature (Fig. 3). Once this temperature is reached, no further heat is stored in the body and all the metabolic heat produced must be lost by evaporation (0.58 cal/ml H_2O), conduction, convection, or radiation. Since only respiratory evaporative water loss was measured in this study, the contribution of non-respiratory evaporative water loss to heat dissipation cannot be quantified and is lumped with heat lost via other avenues. Calculations based on these assumptions show that at a T_A of 25 °C *P. hastatus* loses about 14 % of its metabolic heat by respiratory evaporation during flight. This is comparable to the situation in budgerigars, which are calculated to lose 15–18 % of their metabolic heat by pulmocutaneous evaporation when flying 35 km/hr at 20–30 °C (Tucker, 1968*b*) and to an estimated 19 % of total heat lost by respiratory evaporation from black ducks (*Anas rubripes*) flying at T_A 's of –16 to +19 °C (Berger, Hart & Roy, 1971). It contrasts, however, with terrestrial mammals such as running chipmunks which lose 38 % (Wunder, 1970) and running dogs which can lose 59 % (Young *et al.* 1959) of their metabolic heat through their respiratory tract.

It is not surprising that *P. hastatus* loses most of its metabolic heat by non-respiratory means during flight. The body-surface area of a bat is greater than that of other small mammals and birds of similar weight (Poole, 1936; Hartman, 1963). Chew & White (1960) have estimated that flight surfaces account for 80 % of the total surface area of the pallid bat (*Antrozous pallidus*). Since these surfaces are unprotected by fur and are well supplied with a fine network of blood vessels (Nicoll & Webb, 1955), they appear well adapted for heat dissipation, particularly during the forced convection of flight. Cowles (1947) observed that *Myotis yumanensis* dilated its wing vessels at a T_A ($= T_B$) of 40–41 °C. Bartholomew, Leitner & Nelson (1964) reported a similar pattern

of dilation in three species of Megachiroptera. These studies of resting bats suggest that constriction and dilation of the wing vessels aid in thermoregulation. Kluger & Heath (1970) internally heated *Eptesicus fuscus* with a thermode and showed that vasodilation in the wing is a thermoregulatory adjustment which can be initiated by receptors which are presumably in the CNS, as well as by the peripheral receptors described by Nicoll & Webb (1955). Thermoregulatory dependence on convection and radiation from the large naked surfaces of the flight membranes might make bats susceptible to overheating in direct sunlight, but this possibility is avoided by their nocturnal habits. Evaporative cooling may likewise be inefficient during tropical nights when the humidity is often near the dew-point.

SUMMARY

1. The energetics and physiological responses to flight of the echolocating bat *Phyllostomus hastatus* were studied to determine the energy requirements and physiological adaptations for mammalian flight.

2. The metabolic cost of bat flight is approximately comparable to that of bird flight and requires a metabolic rate appreciably greater than has been reported for terrestrial mammals during exercise. During flight *P. hastatus* consumed between 24.7 and 29.1 ml O_2 (g h)⁻¹, which is about four times its metabolic rate immediately prior to flight and more than 30 times its oxygen consumption while resting with a T_R of 36.5 °C in a small chamber.

3. The onset of flight is accompanied by an abrupt increase in both the heart rate, from about 8.7 to 13 beats/sec, and the respiratory rate, from 3 to about 9.6/sec. Rectal temperature is elevated during flight and maintained at about 41.8 °C. The respiratory quotient, which averages 0.83 in a quietly resting bat, rises to a little over 1.0 during the first few minutes of flight.

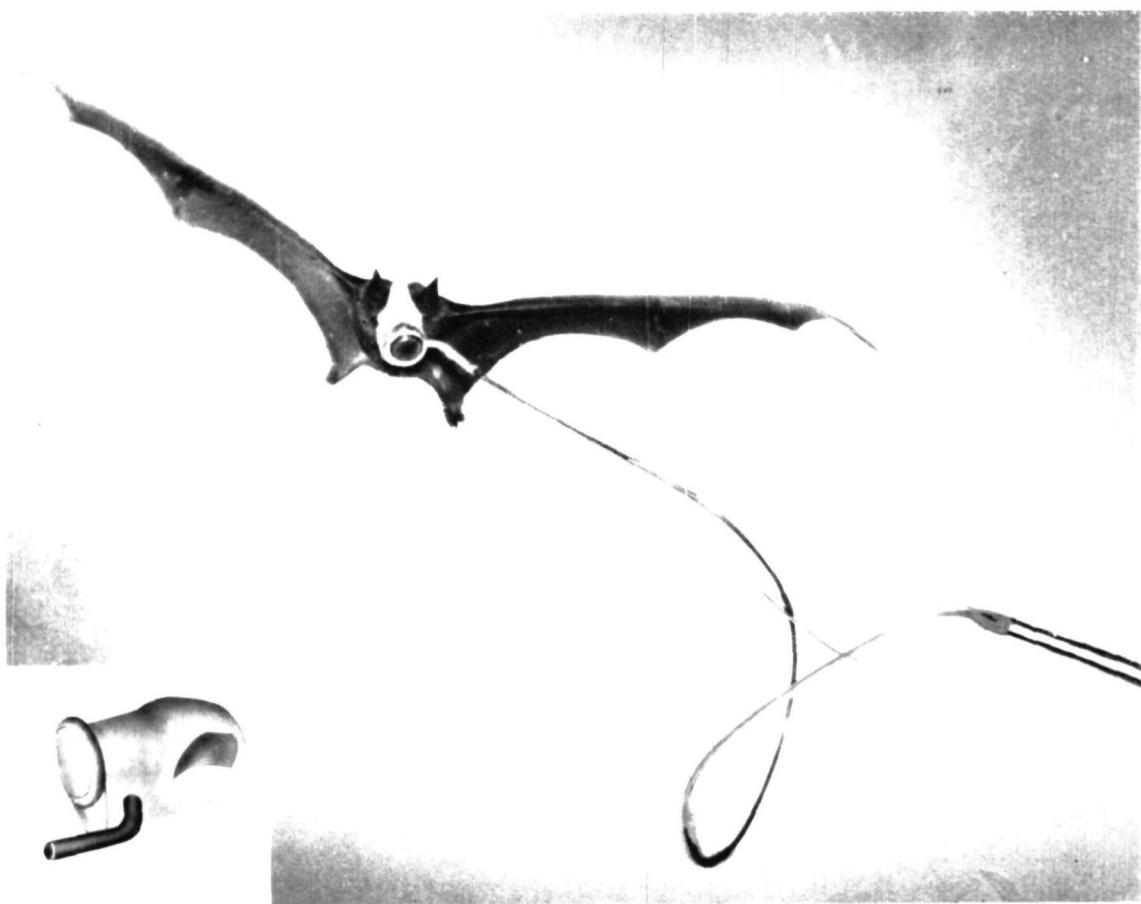
4. The minimum estimated tidal volume during flight is about 1.4 ml. One respiratory cycle occurs with each wingbeat, corresponding to an estimated minute volume of 840 ml, which is comparable to that reported for the flying budgerigar. The amount of oxygen extracted by *P. hastatus* from a given volume of tidal air is also comparable to the efficiency of ventilation reported for this bird.

5. High hematocrit values of about 60%, and a high oxygen capacity of 27.5 vol % of *P. hastatus* blood, must represent important adaptations for enabling the flying bat to maintain such a high metabolic rate.

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EXPLANATION OF PLATE

Phyllostomus hastatus in flight wearing the latex mask used in measuring oxygen consumption. Inset shows details of the mask, including the Mylar membrane stretched over a ring at its anterior end to allow the orientation pulses to be transmitted through the mask during echolocation.