VENTILATION AND OXYGEN EXTRACTION IN THE BAT *PTEROPUS GOULDII* DURING REST AND STEADY FLIGHT

By STEVEN P. THOMAS

* *Department of Biological Sciences, Duquesne University, Pittsburgh, PA 15219, U.S.A., and Department of Zoology, Duke University, Durham, N.C. 27706, U.S.A.*

SUMMARY

Tidal volume (V_T) breathing frequency (f) and oxygen consumption ($\dot{V}_{O_2}$) were simultaneously measured in the bat *Pteropus gouldii* during quiet rest at 24 °C, and oxygen extraction (E) values were calculated from these data. V_T and f were also measured at 24 °C from *P. gouldii* undertaking steady wind-tunnel flight at different speeds and angles, and this information together with appropriate $\dot{V}_{O_2}$ data reported previously for this bat were used to calculate flight E values.

The oxygen extraction of resting *P. gouldii* was similar to that of a resting non-flying mammal of comparable size but lower than that of a resting bird. *P. gouldii* increases V_T and f almost equally in going from quiet rest to level flight to achieve a 17-fold increase in minute ventilation. Compared to the resting bat, flying *P. gouldii* hyperventilates its respiratory system relative to its metabolic requirements. The level flight V_T of *P. gouldii* compares favourably with that expected for a flying bird of the same body mass, and represents almost 90 % of the total lung capacity predicted for a non-flying mammal of comparable size. Because of the increased breathing frequency during flight, the minute ventilation requirement of *P. gouldii* during level flight exceeds that predicted for a similar-sized flying bird. E values calculated for flying *P. gouldii* are significantly lower than those reported for birds flying at comparable temperatures and flight conditions.

INTRODUCTION

Animal flight is of particular physiological interest because of its high power requirements. Although flapping flight is a typical form of avian locomotion, bats are the only mammals which have evolved this ability. The rates of oxygen consumption of flying bats and birds of comparable size have been found to be basically similar. However, these rates are about 2–3 times greater than the highest rates which similarly sized running mammals appear to be capable of during heavy exercise (see Thomas, 1975).

As a result of their different evolutionary histories, the gas-exchange requirements

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* Present address and reprint requests.

of mammals and birds are satisfied by respiratory systems of very different design (King, 1966; Lasiewski & Calder, 1971; Piiper & Scheid, 1977). Various studies suggest that the through-flow avian ventilatory apparatus with its cross-current mode of gas exchange results in a higher effectiveness of gas exchange than does the mammalian lung with its dead-end alveolar ducts and its uniform pool arrangement (Tucker, 1968a; Schmidt-Neilsen et al. 1969; Scheid & Piiper, 1970; Lasiewski & Calder, 1971; Piiper & Scheid, 1972; Bernstein & Schmidt-Neilsen, 1974; Bernstein, 1976; Bouverot, Hildwein & LeGoff, 1974). Nevertheless, bats with their typical mammalian lungs can exchange O_2 and CO_2 between the atmospheric air and their pulmonary blood during flight at rates which are similar to those of the seemingly highly adapted birds. Because only a few studies of limited scope have been published in this area (Suthers, Thomas & Suthers, 1972; Thomas & Suthers, 1972), the quantitative aspects of bat flight ventilation remain poorly understood.

Reported here are the first direct determinations of the ventilatory requirements of a bat both at rest and during steady wind-tunnel flight. These data are discussed in relation to the metabolic requirements of this bat and are compared with data available from resting and flying birds in order to understand better what similarities and differences exist in the breathing patterns, ventilatory requirements, and oxygen extraction abilities of these two independently evolved groups of flying vertebrates. Bat data are also compared with those available for non-flying mammals in order to understand better the relationships which exist between the ventilatory processes of these two groups. Some of the data reported here were summarized in a brief preliminary report (Thomas, 1978).

MATERIALS AND METHODS

Experimental animals

These studies were performed on *Pteropus gouldii* (Megachiroptera, Pteropidae), a member of the flying fox family. The single male *P. gouldii* used for flight ventilation measurements (bat W) had a wingspan of 120 cm and a mean body mass of 870 g (s.d. = 10, $N = 55$) throughout this study. Subsequent measurements of resting ventilation and oxygen consumption were made from a second male member of this species (bat G) having a wingspan of 112 cm and a mean body mass of 773 g (s.d. = 13, $N = 10$). Both bats were maintained in the laboratory on a diet consisting of various types of fruits, high-protein baby cereal (Gerbers) and a vitamin-mineral supplement (Pervinal or Theralin).

Masks

The snugly fitting 3·4 g masks worn by bats W and G during ventilatory measurements were fabricated from moulded latex and celluloid (Fig. 1). The front of each mask was sealed except for a 0·7 cm aperture which was positioned directly in front of the bat's nostrils, and which passed anteriorly through a moulded latex flow probe retainer to the outside of the mask. The total effective dead space volume of each mask/probe system ($V_{D,m}$) was estimated by calculating the dead space volume of the flow probe (described later) and adding this volume to that of a projected cylinder
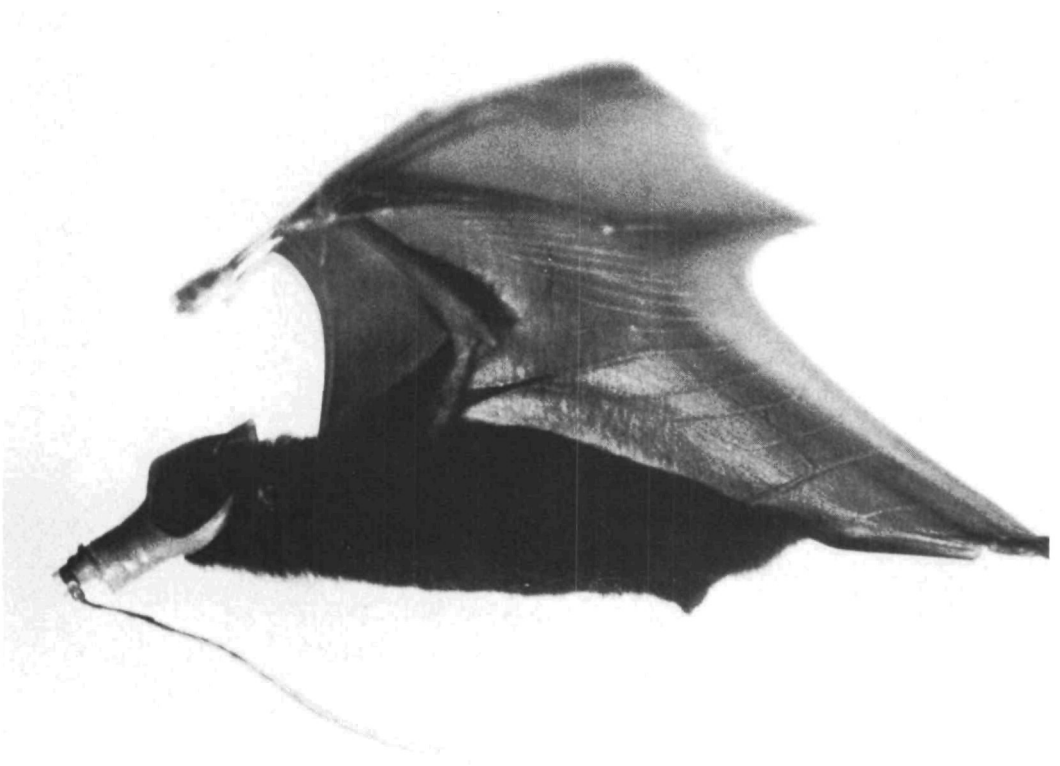
Fig. 1. *P. gouldii* flying in the test section of a wind-tunnel while wearing moulded latex mask equipped with a flow probe used for ventilatory measurements. The flow probe's cable trails below the flying bat's body.

having a diameter equal to the I.D. of the probe, and a length equal to that measured from the proximal end of the mounted probe to the animal's nostrils.

The mask/probe system used on bat G had a $V_{D,m}$ value of 0·18 cm³, and that for bat W was 1·90 cm³. All ventilatory volumes reported hereafter for *P. gouldii* have been corrected for the influence of $V_{D,m}$ to provide estimates of the mask-free ventilatory volumes of these bats. These corrections reduced mean ventilatory volumes by about 1·8 % (bat G), or by from 4·6–7·4 % (bat W).

Resting measurements

Breathing frequency, tidal volume and oxygen consumption measurements were simultaneously made from bat G which was trained to wear its mask equipped with a flow probe while hanging quietly for periods lasting from 30 to 60 min inside a 13 × 19 × 53 cm high open-circuit metabolic chamber equipped with a plexiglas window. Room air entered the chamber through a port, and, together with the bat's expired gases, was withdrawn from a second port and passed through a calibrated rotameter (Lab Crest, Mk III) at a mean rate of 4292 (S.D. = 24·6, $N = 5$) cm³ STPD min⁻¹ by means of a diaphragm pump. The pump then passed a continuous sample of this gas through Drierite, and finally through a paramagnetic oxygen analyser (Beckman, Model F3) whose output was continuously monitored on a potentiometric chart recorder (Perkin-Elmer, Model 56). The oxygen analyser was calibrated with room air and a Primary Standard Grade gas mixture containing 20·30 % oxygen prior to each day's measurement, and rechecked immediately following each measurement.

A total of ten different simultaneous measurements of resting oxygen consumption and ventilation were made from bat G at a mean air temperature of 24·0 °C (S.D. = 0·8) and a mean barometric pressure of 742·1 (S.D. = 4·1) mmHg. Bat G was kept in good physical condition throughout the course of these resting measurements by daily exercise flights of approximately 5 min duration inside a wind-tunnel.

Wind-tunnel

Bat W was trained to fly steadily while wearing its mask and associated flow probe for periods in excess of 15 min in the test section of a large wind-tunnel of open-circuit design (illustrated in Tucker & Parrott, 1970), whose air-flow properties have been described elsewhere (Thomas, 1975). The fan of this tunnel was equipped with a variable-speed motor, and the long axis of the tunnel could be tilted by an angle (θ) from horizontal to simulate descending ($-\theta$) flight conditions. The mean air temperature inside the tunnel's test section during these flight ventilation measurements from bat W was 24·2 °C (S.D. = 2·1, $N = 55$) and the mean barometric pressure was 758·6 mmHg (S.D. = 4·6).

Flow probes and associated circuitry

The following is a non-technical description of the flow probes and associated circuitry used in this study. A more detailed technical account of this equipment will be presented elsewhere (C. D. Mills & K. Schmidt-Nielsen, in preparation).

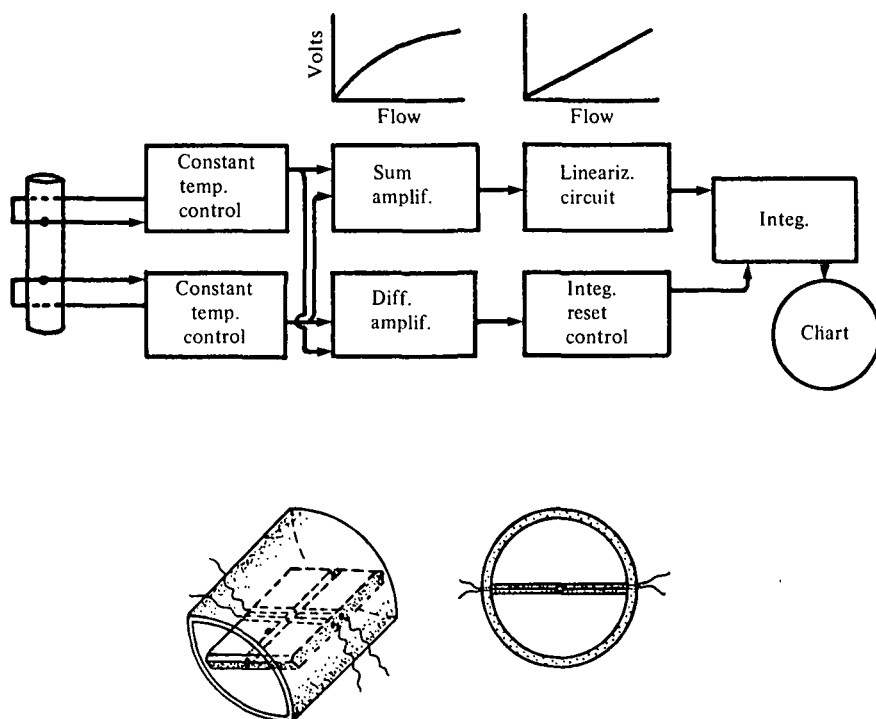The two flow probes used for ventilatory measurements from resting (bat G,

Fig. 2. Diagrammatic sketch of the flow probe and associated circuitry used for ventilatory measurements from *P. gouldii*. See text for a description of the flow-probe circuitry. Details of the flow probe are shown in the lower drawings, including the two thermistors axially aligned inside the crossmember of the cylindrical probe housing unit. I D. of flow probe 0·39 or 0·80 cm.

probe G) and flying (bat W, probe W) *P. gouldii* were similar in their basic design and operating principle, but differed in their dimensions (I.D. of probe G = 0·39 cm, I.D. of probe W = 0·80 cm). The probes operated on a principle similar to that of a hot-wire anemometer, using the rate of heat loss from heated thermistors to indicate the rate of air flow. Each probe contained two identical thermistors that were axially mounted in a cylindrical acrylic housing unit (Fig. 2), and which were heated and maintained at a constant and equal temperature by appropriate circuits (constant-temperature control circuits, Fig. 2). Two thermistors were used in order to generate a signal whose polarity indicated the direction of air flow through the probe, and this direction signal was used to control an integrator circuit (see below).

The voltage outputs from the two identical thermistor constant-temperature control circuits were summed at the summing junction of an amplifier (summing amplifier, Fig. 2) whose output was adjusted to zero from zero air-flow, and which provided a voltage output which was related in a non-linear manner to air flow rate. For a given flow rate, the input to the summing amplifier was dependent on the difference in temperature of each thermistor (maintained constant) minus that of the ambient air. If this temperature difference deviated from the original calibration value, the gain of the summing amplifier could be adjusted ('temperature compensation adjustment') to keep the non-linear output *v.* flow relationship the same.

The non-linear output was then linearized by a circuit containing analogue multipliers (Fig. 2). A separate circuit integrated this linearized flow rate signal to provide an output (integrator output) whose amplitude indicated the volume of air flowing through the probe. The integrator was turned on at the moment air-flow through the probe began in the inspiratory direction, and was turned off and instantly reset to zero when air flow in the inspiratory direction ceased (integrator reset control, Fig. 2). Since the inspired air temperature is the same as that of the ambient air, accurate determinations of the animal's inspired flow rates and tidal volumes could be made by first performing a temperature compensation adjustment on the probe circuit at this particular ambient temperature.

Probe calibration procedures

Initial calibrations were carried out inside a Forma controlled-temperature room at 23·0 (± 0·5) °C using procedures similar to those of C. D. Mills & K. Schmidt-Nielsen (in preparation). Briefly, these procedures included first determining the non-linear output *v.* flow-rate relationship for each flow probe, using this and other information to compute the values of the resistors to be used in the linearizer circuits, inserting these resistors, and finally verifying the circuits' actual linearized output *v.* flow-rate relationship for each probe. The unidirectional rates of air flow through the probes during these phases of calibration were controlled and quantified with the aid of Vol-U-Meters (Brooks Div., Emerson Electric Co., Model 1057 or 1058), which were modified to allow room air to be drawn directly through the probe and into the Vol-U-Meter without having to first pass through rubber tubing. Probe circuit outputs were displayed and monitored to the nearest millivolt on a digital voltmeter (either Heath, Model EU-805A or Keithley, Model 190). By these means, the relationships between voltage outputs and flow were established over a range of flow rates between zero and either 38 $cm^3 s^{-1}$ (probe G) or 500 $cm^3 s^{-1}$ (probe W), using increments of about 2 or 20 $cm^3 s^{-1}$, respectively. For each probe, the slope of the linearized output *v.* flow relationship was then used together with the measured integrator time constant value to calculate the conversion constant that gives the volume of air flow that corresponds to a unit chart deflexion of the integrator output signal. The integrator output was displayed on a calibrated potentiometric recorder (either Brush, Model 220 or Beckman RM Dynograph).

Probe calibration and related tests

The following series of tests were undertaken to verify the accuracy of the probe calibration procedures, and to learn the degree to which various experimental conditions would influence the performance of the probes. During these tests the probes were attached by a short length of rubber tubing to a respirator pump (Harvard Apparatus, Model 607, 661 or 681) whose valves were disabled so that air was respirated in and out of the same port.

In the first of these tests, comparisons were made of stroke volume values determined from the amplitudes of the integrator output signals generated by probes G and W ('indicated stroke volumes') and those calculated from measurements made the nearest 0·01 cm of the pump's cylinder bore and piston stroke ('actual stroke

volumes') over a range of different stroke volume settings comparable to the range of
tidal volumes obtained from the quietly resting (bat G) or flying (bat W) bats during
preliminary measurements. Results showed that the various indicated stroke volumes
agreed to within 3 % or better with their respective actual stroke volume values over
the range of stroke volumes examined for probe G ($5\cdot1$–$15\cdot7$ cm^3) and probe W
($25\cdot5$–$49\cdot9$ cm^3). No attempt was made to correct the indicated tidal volume measure-
ments obtained from the bats for these negligible discrepancies.

The influence of wind-tunnel air flow and probe orientation on indicated stroke
volume was examined by positioning the respirator pump containing probe W inside
the tunnel's test section at a point $0\cdot5$ m above its floor. After a control recording was
made with the tunnel motor off, the integrator output signal was continuously recorded
as tunnel air-speed was varied in approximately 2 m s^{-1} steps from 6 to 12 m s^{-1}. The
influence of probe orientation was assessed at a tunnel air-speed of $10\cdot8$ m s^{-1} by
slowly tilting the respirator pump containing the probe through an angle of 60° from
the axis of the tunnel air-flow vector. Neither turning on the tunnel fan motor nor
varying tunnel air-speed had any detectable influence on the integrator output signal
generated by the respirator pump when the axis of probe W was orientated directly
into the wind (i.e. probe orientation angle = 0°). Only at the highest ($10\cdot8$ m s^{-1})
tunnel air-speed when the probe orientation angle exceeded 50° did an influence
become apparent. However, whereas probe orientation angles in excess of 50° caused
the amplitudes of the individual integrator output signals to become slightly less
uniform (presumably because of turbulence generated within the probe), the mean
amplitude of several consecutive signals did not differ from that of the controls. This
consideration, together with the observation that bat W almost always maintained
the probe at an orientation angle of less than 50° during flight, were taken as
evidence that no probe orientation-related error was introduced into these ventilatory
measurements.

Unintentional leakage of gas from the posterior regions of the mask of bat W was
tested for by comparing ventilatory volumes obtained from the masked bat during
five separate flights at a constant set of tunnel conditions with those made during five
other flights at the same tunnel conditions, but with a $0\cdot9$ cm wide moulded latex
'compression band' placed over the mask at a point corresponding to the base of the
animal's snout to further enhance the mask's degree of compressive fit at this site. The
ventilatory volumes obtained from bat W flying with the compression band were
found to be indistinguishable from those obtained when the compression band was
not used. As a precautionary measure, however, a compression band was always used
during actual experiments involving bat W. For bat G, observations were made of
both the snugness of fit of the posterior (sealing) regions of the mask after it was
placed on the bat, and the condensation pattern inside the mask immediately after it
was removed from the bat at the end of each measurement period. Neither of these
observations showed evidence of unintentional gas leakage from the mask of bat G.

Compensation for mask and cable drag

In order to obtain ventilatory data which more closely approximated those expected
from bat W during unencumbered wind-tunnel flight, compensations were made for

he total force generated by the mask plus the associated probe cable which acted on the flying bat's body in the direction of the drag vector (F_{net}). F_{net} values were determined at each combination of air-speed and θ by placing the mask containing the probe and its associated cable on a wingless styrofoam model of bat W that was attached to a one-component strain-gauge flight balance described elsewhere (Thomas, 1975). The appropriate F_{net} value together with a knowledge of the combined weight of the bat's body, mask and suspended cable ($W_{b, m, c}$) were then used to calculate the additional increment by which the tunnel had to be titled in the downward (θ more negative) direction from its nominal θ value to permit the resulting increment in the thrust component of $W_{b, m, c}$ to exactly cancel F_{net} (for additional details, see Thomas, 1975).

As expected, F_{net} was found to increase with air-speed (S) at each θ. Consequently, the increment by which the long axis of the tunnel had to be tilted downward from its nominal θ value to just compensate for F_{net} also increased with air speed. Thus, when $\theta = 0°$ nominally, the tunnel was actually tilted from horizontal by an amount which ranged from $-0.6°$ (when $S = 8.02$ m s^{-1}) to $-0.9°$ (when $S = 9.86$ m s^{-1}) during the actual experiments in order to obtain ventilatory data which more closely approximated those expected during unencumbered flight at the nominal θ value.

Experimental protocol

The following sequence of steps were followed during each day's measurements from *P. gouldii*.

A probe calibration continuity check was first performed at the original calibration temperature (23 °C) with the aid of the respirator pump to verify that the original input/output relationship of each probe did not change throughout the course of these experiments. The temperature compensation adjustment was then performed at the location where the experiment was to be performed by switching on the respirator pump, whose settings remained unchanged from the preceding step, and adjusting the probe circuit to bring the amplitude of the integrator output signal back to its original value. Prior tests showed that this procedure compensated to within 1 % of the full-scale linearized output voltage for temperature changes of at least ±5 °C from the original calibration temperature of 23 °C.

For bat W, the mask, compression band, and finally the probe were placed on the animal, after which it was allowed to fly for about 9 min, during which its ventilation was continuously recorded. Tunnel air temperature was also recorded to the nearest 0.2 °C at 1 min intervals throughout each flight. The bat was allowed to rest for about 5 min between flights. During this period the probe was again attached to the respirator pump and a recording was made of the integrator output signal. If either these recordings, or calculations based on tunnel air temperature changes and the probe's temperature sensitivity indicated that an error of 2 % or more induced by room-air temperature change was introduced into the tidal volume measurements, data for this particular flight were discarded. A similar procedure was used in conjunction with the resting ventilatory measurement from bat G. If needed, the probe circuit's temperature compensation adjustment was reset prior to the next flight. Bat W would usually perform two or three such flights per day.

Handling of data

For each determination made from bat G, a 1 min segment corresponding to the time when both the oxygen analyser and ventilation recordings remained both stable and of low magnitude was chosen for subsequent analysis. The mean oxygen consumption rate ($\dot{V}_{O_2}$) was calculated for each trial as described by Thomas (1975) by assuming that bat G maintained a respiratory quotient value of 0·8 throughout these measurements (Thomas & Suthers, 1972). Mean tidal volume (V_T, corrected for mask-plus-probe dead space) was computed for the 1 min analysis period of each trial. This value and the associated mean breathing frequency (*f*) were used to calculate the mean inspired minute ventilation rate ($\dot{V}_I$) for the trial. From these data, the mean oxygen extraction value was computed for each trial. Throughout this paper, oxygen extraction (*E*) is defined by the relationship $E = \dot{V}_{O_2}/(\dot{V}_I . F_{IO_2})$, where both rate terms are expressed in units of cm³ STPD min⁻¹, and F_{IO_2} is the fractional composition of oxygen in the inspired air (assumed to equal 0·2095).

The ventilatory parameters of bat W usually stabilized during the fourth minute of flight. A stable segment of the integrator output recording which consisted of 100 consecutive inspirations obtained sometime between the sixth and ninth minute of each flight was therefore chosen for analysis. From these raw data, the mean *f*, and the mean $V_{D,m}$-corrected V_T and $\dot{V}_I$ values were computed for each flight. Measurements were made for five different flights at each particular combination of tunnel air speed and flight angle investigated.

<div align="center">RESULTS</div>

Breathing frequency

The mean breathing frequency (*f*) of bat G during quiet rest was 44·75 b min⁻¹ (S.D. = 3·73, *N* = 10). For bat W, *f* tended to vary in an inverse manner with air speed (*S*) at each flight angle studied (Fig. 3). Thus, for level flight, *f* decreased in value from 192 b min⁻¹ (at 8·02 m s⁻¹) to 180 b min⁻¹ (at 9·86 m s⁻¹). At a given *S*, *f* usually did not change appreciably from one flight angle to another. Equations fitted by the method of least squares to these data from bat W are presented in Table 1.

Tidal volume

The mean tidal volume (V_T, cm³ STPD) of resting bat G was 9·77 (S.D. = 0·60, *N* = 10). In contrast to breathing frequency, V_T values for bat W increased with increasing *S* at each flight angle studied (Fig. 4, Table 1). For a given *S*, V_T decreased by about 11 % when flight angle decreased from 0° to −2°, and by about 31 % when flight angle went from 0° to −4°.

Minute ventilation

The mean minute ventilation rate ($\dot{V}_I$) of bat G during rest was 436·8 cm³ STPD min⁻¹ (S.D. = 39·7, *N* = 10). For bat W, the relationships between *f* and V_T were such that for a given flight angle, $\dot{V}_I$ tended to increase with increasing *S* (Fig.

Table 1. *Summary of the relationships between tunnel air speed* (S, $m\ s^{-1}$) *and the ventilatory parameters obtained from bat W flying at the three angles studied*

(Equations were fitted by the method of least squares to data obtained at various flight speeds which ranged from 8·02 m s^{-1} to either 9·86 ($\theta = 0°$) or 10·80 m s^{-1} ($\theta = -2°$, $-4°$).

| Flight angle (θ, deg)	Equation	S.E. of estimate	N	Text equation no.
	(A) Breathing frequency (f, breaths min^{-1})			
0	$f = 88{\cdot}99S - 177{\cdot}43 - 5{\cdot}35S^2$	4·01	15	(1)
-2	$f = 617{\cdot}46 - 82{\cdot}34S + 3{\cdot}79S^2$	9·09	20	(2)
-4	$f = 223{\cdot}69 - 4{\cdot}70S - 0{\cdot}05S^2$	8·50	20	(3)
	(B) Tidal volume (V_T, cm^3 STPD)			
0	$V_T = 109{\cdot}14 - 18{\cdot}36S + 1{\cdot}16S^2$	2·43	15	(4)
-2	$V_T = 104{\cdot}32 - 17{\cdot}61S + 1{\cdot}09S^2$	1·54	20	(5)
-4	$V_T = 121{\cdot}19 - 22{\cdot}91S + 1{\cdot}37S^2$	2·51	20	(6)
	(C) Minute ventilation ($\dot{V}_I$, cm^3 STPD min^{-1})			
0	$\dot{V}_I = 5388{\cdot}02 + 237{\cdot}00S - 2{\cdot}48S^2$	445·65	15	(7)
-2	$\dot{V}_I = 32259{\cdot}52 - 5655{\cdot}55S + 306{\cdot}55S^2$	479·08	20	(8)
-4	$\dot{V}_I = 20620{\cdot}69 - 3715{\cdot}24S + 215{\cdot}6S^2$	584·88	20	(9)
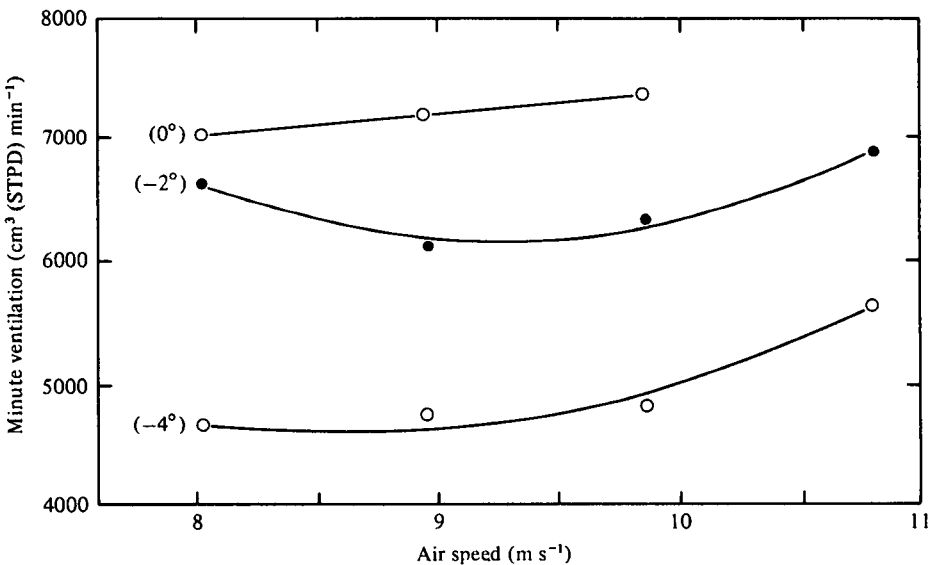
Fig. 5. The relationship between inspired minute ventilation rate and speed for *P. gouldii* flying at the three angles investigated. The minute ventilation rate for each experiment was calculated as the product of the mean tidal volume and the mean breathing frequency determined for each experiment. Each point represents the mean of five separate experiments performed at the indicated flight condition. The curved lines fitted to these data represent the equations in section C of Table 1.

Table 1). For a given S, $\dot{V}_I$ decreased by about 20% when flight angle decreased from 0° to $-2°$, and by about 45% when flight angle went from 0° to $-4°$.

Resting metabolism and oxygen extraction

The mean $\dot{V}_{O_2}$ and associated E values determined for bat G during quiet rest were 14·16 cm^3 STPD O$_2$ min^{-1} (S.D. = 0·93, $N = 10$) and 0·16 (S.D. = 0·0] $N = 10$), respectively.

Table 2. *Comparison of resting ventilatory parameters obtained from a 777 g P. gouldii (bat G) with those predicted from allometric equations for a 722 g non-flying mammal (mammal X) or a non-passerine bird (bird X) of the same body mass*

	Bat G	Mammal X*	Bird X†	(a) Ratio (bat G/mammal X)	(b) Ratio (bat G/bird X)
f (breaths min^{-1})	44·8	57·2	18·6	0·78	2·41
V_T (cm^3 min^{-1})	9·8	5·9	10·0	1·66	0·98
$\dot{V}_I$ (cm^3 min^{-1})	436·7	308·1	232·7	1·42	1·88
$\dot{V}_{O_2}$ (cm^3 min^{-1})	14·2	9·5	9·4	1·49	1·51
Oxygen extraction (E)	0·16	0·15	0·19	1·07	0·84

* Stahl (1967).   † Lasiewski & Calder (1971).

DISCUSSION

Resting ventilation and oxygen extraction

It is worthwhile to compare ventilatory data obtained from bat G with the theoretical values predicted from the allometric equations of Stahl (1967) for a typical non-flying resting mammal of similar size (hereafter referred to as 'mammal X'), and with values predicted for a 722 g resting non-passerine bird ('bird X') by the allometric equations of Lasiewski & Calder (1971). Such comparisons show the following relationships (Table 2).

The mean resting $\dot{V}_{O_2}$ determined for bat G was about 1·5 times greater than the 'standard metabolic rate' (SMR) values calculated for both mammal X and bird X. This difference is not unexpected since bat G was equipped with the mask and flow probe during these $\dot{V}_{O_2}$ measurements, and was therefore probably not as fully relaxed as it would have been under truly SMR measurement conditions. This interpretation is consistent with the findings of Bartholomew, Leitner & Nelson (1964), who reported that the SMR values of the three species of Australian flying foxes they studied (*Pteropus poliocephalus*, *Pteropus scapulatus* and *Syconycteris australis*) approximated those expected for non-flying placental mammals of their size. The higher resting $\dot{V}_{O_2}$ of bat G was associated with a higher $\dot{V}_I$ than was predicted for mammal X. Nevertheless, $\dot{V}_I$ was essentially proportional to $\dot{V}_{O_2}$ in these two mammals as indicated by the similar magnitudes of their $\dot{V}_{O_2}$ and $\dot{V}_I$ ratios (column (a), Table 2) and their similar E values. The E of bat G is also similar to that of the dog resting at 23 °C (0·17, Bouverot, Candas & Libert, 1973), but appreciably lower than the E of resting man (0·26, Asmussen, 1965).

Results indicate that resting *P. gouldii* requires a greater volume of inspired air per unit of oxygen removed by its lungs than does a resting bird. Thus, Table 2 shows that while the resting $\dot{V}_{O_2}$ of *P. gouldii* was about 1·5 times greater than that expected for bird X, its $\dot{V}_I$ was almost 1·9 times greater than that of bird X. This relationship is also indicated by the fact that the E of resting *P. gouldii* ($=0·16$) is about 15 % lower than the value predicted for bird X (Table 2), and about 20 % or 40 % lower than the E values reported for the fish crow (*Corvus ossifragus*, a passerine) resting quietly at 20 °C (where $E = 0·20$) or 25 °C (where $E = 0·28$), respectively (Bernstein & Schmidt-Nielsen, 1974). Also, a limited number of measurements made from bat G resting at different air temperatures between 20 and 31 °C showed no indications

of hyperventilation due to heat stress during rest at 24 °C (S. P. Thomas, unpublished data). These findings for resting *P. gouldii* are therefore consistent with those of other studies which suggest that the through-flow avian ventilatory apparatus results in a greater effectiveness of gas exchange than does the mammalian system with its blindly ending alveolar ducts (Scheid & Piiper, 1970; Bretz & Schmidt-Nielsen, 1971; Lasiewski & Calder, 1971; Piiper & Scheid, 1972; Bernstein & Schmidt-Nielsen, 1974; Bernstein, 1976).

Available data also suggest that differences may exist in the resting breathing patterns of these animals. Although the $\dot{V}_I$ of bat G was 1·4 times greater than the value expected for mammal X, the f of this bat was about one-fifth less than that of mammal X, indicating a tendency for bat G to utilize disproportionately deeper but less frequent breaths than mammal X. It remains to be seen whether other species of bats share this type of a resting breathing pattern with *P. gouldii*. Also, one can see that the *P. gouldii*/bird $X f$ ratio (column (*b*), Table 2) exceeds that for $\dot{V}_I$ while the V_T ratio in this column is lower in magnitude than the $\dot{V}_I$ ratio. These relationships suggest that for a similar $\dot{V}_I$, *P. gouldii*, like mammal X (Lasiewski & Calder, 1971), would be expected to have a higher f and a lower V_T than a resting bird of the same body mass. The extent to which these differences in the breathing patterns of resting mammals and birds reflect the different mechanical features of their unsimilar ventilatory apparatus and/or possible differences in the central neurogenesis of breathing in these two independently evolved groups and/or other factors still remains unclear (reviewed by Bouverot, 1978).

Transition from rest to flight

In order to provide a better understanding of this bat's ventilatory adjustments to flight, resting data from bat G are compared in Table 3 with level flight ventilatory data from bat W. The flight $\dot{V}_{O_2}$ value indicated in this table for bat W was calculated from an equation (equation 2 of Thomas, 1975) which summarizes metabolic data previously reported for this particular *P. gouldii* undertaking steady level flight at the indicated air-speed. Since the same wind-tunnel and a similar mean air temperature and drag compensation principle was utilized in both the flight-metabolism (Thomas, 1975) and the flight-ventilation studies on bat W, corresponding data from these two separate studies have been combined both here and elsewhere in this paper for the purpose of calculating E values for *P. gouldii* flying at specified wind-tunnel conditions.

P. gouldii shows a 17-fold increase in $\dot{V}_I$ in going from quiet rest to steady flight, and this increase results from almost equal increases in V_T and f (Table 3). Similar ventilatory adjustment patterns have been reported for certain species of birds. For example, the evening grosbeak (*Coccothraustes vespertinus*) and the black duck (*Anas rubripes*) (Berger, Hart & Roy, 1970), and also the fish crow at 25 °C (Bernstein, 1976) all increase both V_T and f by factors which range from 3 to 5 in going from quiet rest to flight. The pigeon (*Columba livia*), however, increases $\dot{V}_I$ primarily by increasing f in going from rest to flight (Hart & Roy, 1966).

Table 3 also shows that *P. gouldii* hyperventilates its respiratory system with respect to its metabolic requirements in going from rest to flight as is indicated by the fact that its flight/rest $\dot{V}_I$ ratio is considerably greater than its $\dot{V}_{O_2}$ ratio. Consequently, the level flight E of *P. gouldii* is about 40% less than that for the resting bat. I

Table 3. *Resting data from bat G (body mass = 773 g) are compared with level flight data from bat W (870 g) in order to show the ventilatory and metabolic adjustments of P. gouldii to flight*

	Quiet rest (bat G)	Level flight *at 9.8 m s^{-1} (bat W)	Ratio (flight/rest)
f (breaths min^{-1})	44·8	180·9	4·0
V_T (cm^3 STPD)	9·8	40·6	4·1
$\dot{V}_I$ (cm^3 STPD min^{-1})	436·7	7372·4	16·9
$\dot{V}_{O_2}$ (cm^3 STPD min^{-1})	14·2	151·3†	10·7
E	0·16	0·10	0·63

* Ventilatory data calculated from equations presented in Table 1.
† Calculated from equation (2) of Thomas (1975) as described in text.

contrast to *P. gouldii*, man adjusts his minute ventilation in proportion to his metabolic requirements in going from rest to submaximal exercise (Robinson, 1974). Only during work severe enough to exhaust man in 3 min or less in his ventilation stimulated out of proportion to his metabolic requirements, apparently due to the accumulation of acid metabolites (Robinson, 1974). Avian data reviewed by Berger & Hart (1974) indicate that flying birds have oxygen extraction values which are about one-half those predicted for resting birds by the allometric equations of Lasiewski & Calder (1971). Oxygen extraction of the fish crow does not change between rest and flight at 20 °C (Bernstein & Schmidt-Nielsen, 1974; Bernstein, 1976), and estimates suggest that this may also be true for the starling (*Sturnus vulgaris*) at 19 °C (Torre-Bueno, 1978). At a T_A similar to that of the present study on *P. gouldii* (i.e. 25 °C), however, the E of the flying fish crow was similarly about one-half that of the resting crow due to the elevated flight ventilation associated with heat stress (Table 2 of Bernstein, 1976). The flight/rest $\dot{V}_I$ ratio of 14·4 reported for the fish crow at 25 °C is also not appreciably different from the value of 16·9 for *P. gouldii* at 24 °C (Table 3).

Ventilatory adjustments and oxygen extractions during flight at different speeds and angles

The wing movement and respiratory systems of flying vertebrates are of course controlled by different factors and must satisfy different requirements. Most birds show no obligatory coordination between their wing-beat and respiratory cycles during flight (reviewed by Berger & Hart, 1974) so their wing-beat and breathing frequencies can be adjusted independently of one another in a manner which presumably best satisfies the flying bird's aerodynamic and gas exchange/thermoregulatory requirements, respectively (e.g. see Tucker, 1968*b*; Aulie, 1975). A more rigid relationship has been found for *P. gouldii*, however. *P. gouldii*, like the Neotropical bat *Phyllostomus hastatus* (Suthers, Thomas & Suthers, 1972), maintains what appears to be an obligatory 1:1 synchronization between its breathing and wing-beat cycles during wind-tunnel flight over a range of different speeds and angles, with inspiration accompanying each downstroke of the wings (S. P. Thomas, unpublished data). This phase relationship suggests that some form of neural, rather than mechanical, linkage exists between the ventilatory and wing-beat movements of this bat. In view of this 1:1 synchronization, it is worthwhile to examine in more detail the manner in which *P. gouldii* adjusts its ventilatory parameters to help satisfy its different metabolic requirements of flight at various speeds and angles.
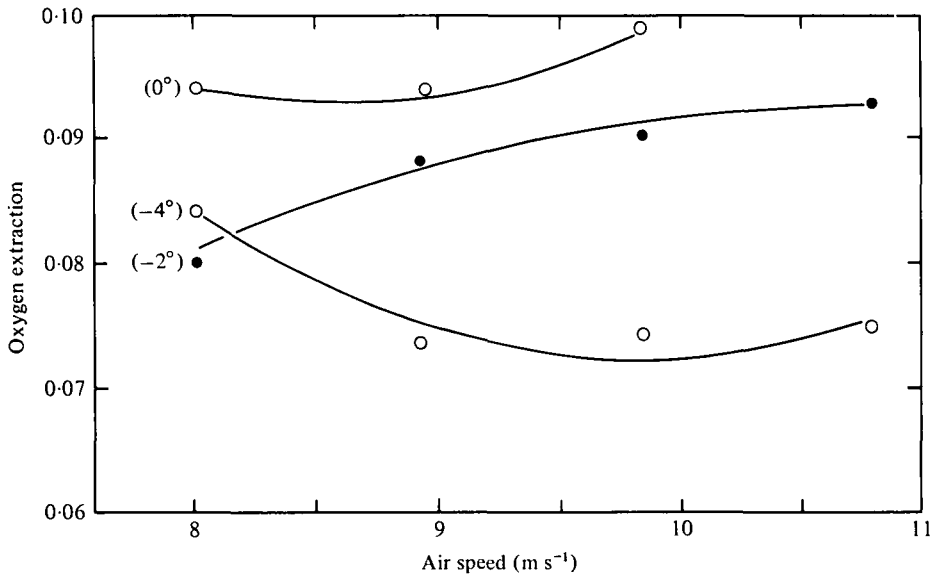
Fig. 6. Oxygen extraction [E, $= \dot{V}_{O_2}/\dot{V}_I.F_{IO_2}$] of *P. gouldii* as a function of air speed and flight angle. For each flight, E was calculated using the mean $\dot{V}_I$ determined for the flight and a $\dot{V}_{O_2}$ value calculated for bat W flying at the same speed and θ using an appropriate equation (equation 28, 29 or 30 of Thomas, 1975) previously reported for this particular *P. gouldii*. Each point represents the mean of five separate determinations made at the indicated flight condition. The curved lines associated with these points were fitted by the method of least squares.

Although the tendency for *P. gouldii* to decrease its wing-beat frequency with increasing S is not surprising from an aerodynamic viewpoint, the concomitant decline in f at the higher flight speeds (Fig. 3) might at first appear to be an inappropriate response from the viewpoint of gas exchange, since the metabolic requirements of this bat tend to increase somewhat at the higher flight speeds (Fig. 6 of Thomas, 1975). This is not the case, however, because at each θ, *P. gouldii* increases V_T with increasing S in a manner that more than compensates for the decline in f (Figs. 4, 5). For a given θ, this ventilatory strategy would result in both a decrease in tracheal dead-space ventilation and an increase in alveolar ventilation with increasing flight speed, and would therefore favour an enhanced effectiveness of pulmonary gas exchange at the flight speeds where the metabolic requirements of this bat are the greatest.

In order to understand better the relationships between these ventilatory adjustments and the metabolic requirements of *P. gouldii*, flight E values have been calculated for bat W at different combinations of θ and S (Fig. 6). Except for $-4°$ flight at the lowest air speed, E tends to be greatest when the metabolic requirements of bat W are highest (i.e. at the highest S at each θ, and during the most horizontal θ for each S; see Fig. 6 of Thomas, 1975). The tendency for E to increase somewhat with increasing S is consistent with the relationships discussed in the preceding paragraph. The substantial decline in E as θ becomes more negative is more difficult to interpret from a homeostatic viewpoint, and reflects the failure of this bat to reduce $\dot{V}_I$ by as much as $\dot{V}_{O_2}$ declines as θ becomes progressively more negative. For example, whereas bat W reduces $\dot{V}_I$ by about 30% in going from 0° to $-4°$ flight

Table 4. *Comparison of level flight ventilatory parameters obtained from* P. gouldii *with those predicted for a flying bird of the same body mass by the allometric relationships summarized by Berger & Hart* (1974)

	Actual value for 870 g *P. gouldii*	Predicted value for 870 g 'bird Y'	Ratio bat/bird Y
f (b min^{-1})	180·9	133	1·36
V_T (cm^3)	40·6	44·2	0·92
$\dot{V}_I$ (cm^3 min^{-1})	7372·4	5876·2	1·25

9·9 m s^{-1} (Fig. 5) its $\dot{V}_{O_2}$ falls by about 50 % (Fig. 6 of Thomas, 1975). Most of this reduction in V_I results from a decline in V_T, since at a given S, the breathing (= wing-beat) frequency of bat W usually showed only a modest change with θ, presumably for aerodynamic (v. gas exchange) reasons (Fig. 3). Thus, the absence of gliding behaviour in the wind-tunnel (v. what may be the case during descending flight in nature) along with the apparent inability of bat W to uncouple its breathing and wing-beat frequencies during flight seem to be factors that contribute to the decline in E as θ became more negative. Although tracheal dead-space ventilation would account for a higher proportion of bat W's $\dot{V}_I$ at $-4°$ than at $0°$ flight, the estimated alveolar ventilation per unit of metabolism (i.e. $\dot{V}_A/\dot{V}_{O_2}$ ratio) of bat W would nevertheless be appreciably greater during $-4°$ flight than during level flight. This latter consideration together with the low E values associated with descending flight suggest that bat W was able to deal with a substantial degree of hypocapnia and respiratory alkalosis during these $-4°$ wind-tunnel flights.

Flight ventilatory parameter magnitudes

How do the magnitudes of the ventilatory parameters determined for *P. gouldii* undertaking level flight compare with those expected for a flying bird of the same body mass? Such a comparison is complicated by the fact that almost all the detailed avian flight ventilation data available have been obtained from birds undertaking brief flights where physiological transients might be expected to exist (reviewed by Berger & Hart, 1974). It is therefore not clear how accurately the allometric equations fitted to such avian data by Berger & Hart (1974) reflect steady (v. transient) avian flight values. The steady flight $\dot{V}_I$ reported more recently for the fish crow at 25 °C (table 2 of Bernstein, 1976), however, differs by only 3 % from the value predicted for a flying bird of the same mass by equation (1) of Berger & Hart (1974), although the V_T of the flying crow is less accurately predicted by the appropriate allometric equation. Despite the foregoing complications, the avian allometric equations of Berger & Hart (1974) provide the only practical means by which flight ventilation data obtained from *P. gouldii* can presently be compared with those expected for a flying bird of the same body mass ('bird Y'). Such a comparison shows the following relationships (Table 4) and permits the following tentative conclusions to be made.

The flight $\dot{V}_I$ of *P. gouldii* exceeds that expected for bird Y due to the higher flight f of this bat. Although allometric equations indicate that a three-fold difference exists in the total respiratory system volumes of birds and non-flying mammals (Laskiewski & Calder, 1971), the flight V_T values of *P. gouldii* and bird Y are not very different

(Table 4). It is interesting to note that the flight V_T value shown for *P. gouldii* represents almost 90% of the total lung capacity predicted for a non-flying mammal of this size (Stahl, 1967). For comparison, man undertaking heavy exercise rarely uses more than 50% of his vital capacity because deeper breaths require exhausting activity of the respiratory muscles (Lambertsen, 1974). These relationships suggest that in addition to the need for very powerful and fatigue-resistant respiratory muscles, *P. gouldii* may also have a greater total lung capacity than does a non-flying mammal of comparable size. Still unknown is whether or not this bat's ability to achieve high V_T values during flight is in some way dependent on the $1:1$ synchronization which it maintains between its breathing and wing-beat cycles.

The higher flight f of *P. gouldii* (Table 4) is consistent with the observation that this bat maintains a $1:1$ synchronization between its breathing and wing-beat cycles. In contrast to *P. gouldii*, most birds have flight f values which are substantially lower than their wing-beat frequencies (Lord, Bellrose & Cochran, 1962; Tomlinson, 1963; Tucker, 1968*b*, 1972; Berger, Roy & Hart, 1970; Torre-Bueno, 1975; Torre-Bueno & Larochelle, 1978). The higher flight f of *P. gouldii* compared to bird Y is also consistent with the substantial differences which exist in the tracheal dead-space volumes (V_{tr}) of mammals and birds (Hinds & Calder, 1971; Lasiewski & Calder, 1971). Allometric equations summarized by Lasiewski & Calder (1971) indicate that a 870 g non-flying mammal would have a V_{tr} of 0·7 cm³, which is less than one-fourth the V_{tr} value of 3·2 cm³ estimated for bird Y. Unfortunately, V_{tr} data are not presently available for *P. gouldii*. On the assumption that bat W has a V_{tr} which is the same as that expected for a similar-size (870 g) non-flying mammal, however, one can estimate from the data in Table 4 that the minute tracheal dead-space ventilation rate $(\dot{V}_{tr} = f.V_{tr})$ of *P. gouldii* during flight would be less than one-third that estimated for bird Y. Thus, whereas bat W would have an estimated flight $\dot{V}_{tr}$ of 127 cm³ min⁻¹ (or about 2% of its flight $\dot{V}_I$), bird Y would have a flight $\dot{V}_{tr}$ value of 426 cm³ min⁻¹ (or about 7% of its predicted flight $(\dot{V}_I)$). Similar estimates based on steady flight f and $\dot{V}_I$ data reported for the fish crow at 25 °C (table 2 of Bernstein, 1976) indicate that $\dot{V}_{tr}$ may account for about 5% of this bird's flight $\dot{V}_I$. If the assumption concerning the V_{tr} value of *P. gouldii* proves to be valid, the foregoing considerations would indicate that, despite the higher f of flying *P. gouldii*, a smaller proportion of this bat's flight $\dot{V}_I$ would be wasted ventilating the non-exchange tracheal region of its ventilatory apparatus than would be the case for a flying bird of comparable size.

Flight oxygen extraction magnitude

The level flight E value calculated for *P. gouldii* is compared with E data reported for flying birds and running mammals in Table 5. Available data indicate that E is independent of body mass in flying birds (Berger & Hart, 1974), a finding which greatly facilitates comparisons. The steady flight E of *P. gouldii* is only about two-thirds as great as the mean E of 0·14 calculated for five species of birds undertaking brief flights at the indicated temperatures (Table 5). Of these five species, only the ring-billed gull (*Larus delawarensis*) had a flight E as low as that of *P. gouldii*. As was indicated previously, however, the very short durations of these avian flights make it difficult to assess how accurately these data reflect the steady-flight E values of the

Table 5. *Oxygen extraction (E) value calculated for flying* P. gouldii *in relationship to those of flying birds and running mammals*

Species	T_A (°C)	Body mass (g)	E	Source
		Birds, short flights		
Amazila fimbriata	35	6	0·13	Berger & Hart (1972)
Coccothraustes vespertinus	22	60	0·16	Berger *et al.* (1970*a*)
Columba livia	20	380	0·17	LeFebvre (1964), Hart & Roy (1966)
Larus delewarensis	22	420	0·10	Berger *et al.* (1970*a*)
Anas rubripes	19	1000	0·13	Berger *et al.* (1970*a*)
		(Mean E 0·14)		
		Birds, steady level flights		
Corvus ossifragus	12–22	280	0·19	Bernstein, 1976
C. ossifragus	24	280	0·15	Bernstein, 1976
		Bat, steady level flight at 9·86 m s^{-1}		
Pteropus gouldii	24	870	0·10	(present study)
		Running mammals		
Dog (intermediate exercise)	19	15000–19000	0·12	Flandrois *et al.* (1971, 1974)
Man				
Submaximal work	23	—	0·25	Asmussen & Nielsen, 1958
Maximal work	23	—	0·22	Asmussen & Nielsen, 1958

birds. Also, air temperature has been shown to influence $\dot{V}_I$ and thus E in both resting and exercising birds (e.g. Bouverot *et al.* 1974; Bernstein, 1976) as it can in mammals (e.g., Hammel, Wyndham & Hardy, 1958; Hellstrom & Hammel, 1967) so this variable should be taken into consideration. The relationship between air temperature and E, however, has not been studied for flying bats. For these reasons, I feel that the most meaningful flight E comparison is between *P. gouldii* and the fish crow flying at the same temperature. As Table 5 shows, the steady level flight E value for *P. gouldii* at 24 °C is only about two-thirds as great as that of the fish crow flying at this temperature. As was the case during rest (Table 2), flying *P. gouldii* also requires a greater volume of inspired air per unit of oxygen removed from its lungs than does a bird flying under comparable conditions.

Two different interpretations are consistent with the latter finding. On the one hand, the relative hyperventilation of *P. gouldii* compared to the fish crow may simply reflect this bat's greater dependence on respiratory evaporative heat loss at this particular temperature to help satisfy its thermoregulatory requirements during flight. Although respiratory evaporative water loss data are not available for flying *P. gouldii*, measurements from the smaller Neotropical bat *Phyllostomus hastatus* do not lend support to this contention. *P. hastatus* has been found to lose about the same percentage of its total flight metabolic heat load through its respiratory tract as do birds flying at comparable temperatures (Thomas & Suthers, 1972). Nevertheless, until information concerning the influence of air temperature on the $\dot{V}_I$ and E values of flying *P. gouldii* becomes available, one cannot accurately assess the extent to which the differences in the flight E values of *P. gouldii* and the fish crow reflect differences which may exist in the thermoregulatory adjustments of these two animals.

On the other hand, the lower E value of flying *P. gouldii* may reflect a lower gas

exchange effectiveness capability of the mammalian v. avian respiratory apparat
during the metabolic stress of flight. As was mentioned previously, data point to the
presence of a cross-current gas exchange arrangement in the throughflow avian lung
(Scheid & Piiper, 1970; Abdalla & King, 1975, 1976; Meyer, Worth & Scheid, 1976),
and several studies along with the resting data obtained from *P. gouldii* in the present
study suggest that this arrangement results in a greater effectiveness of gas exchange
than the uniform pool arrangement in the mammalian lung (Lasiewski & Calder, 1971;
Piiper & Scheid, 1972; Bernstein & Schmidt-Nielsen, 1974; Bernstein, 1976; also see
Piiper & Scheid, 1977). Assuming this is the case, the relative hyperventilation of
P. gouldii with respect to the fish crow could be viewed as a means by which this bat
compensates for the less effective arrangement of its respiratory apparatus. Thus, the
high alveolar ventilation/$\dot{V}_{O_2}$ ratio which would be associated with the low flight *E* of
P. gouldii would favour an enhanced diffusion gradient for respiratory exchange
between its alveolar gas and pulmonary blood. Since metabolic data indicate that
flying bats and birds of comparable size have similar rates of oxygen delivery to their
pulmonary blood (Thomas, 1975), this enhanced diffusion gradient might help
P. gouldii compensate for what may be the less effective functional disposition of its
mammalian respiratory apparatus. Whereas this latter interpretation is consistent
with the relatively low *E* values obtained in this study for both resting and flying
P. gouldii, it is important to keep in mind that not all species of bats have *E* values
which are less than those of birds (Thomas & Lust, 1979).

The level flight *E* of *P. gouldii* is not very much less than that shown in Table 5
for the dog which was allowed to run at a somewhat cooler temperature in order to
avoid excessive thermal polypnea which would further reduce its running *E* value.
As was the case at rest, however, *E* of flying *P. gouldii* is substantially less than that of
man who has an *E* during maximal sustainable exercise which exceeds even that of
the flying fish crow (Table 5). One must remember, however, that the weight-specific
metabolic requirements of both exercising dogs and man are considerably less than
those of flying *P. gouldii* and the crow due to their different body sizes and their
different modes of locomotion (see Schmidt-Nielsen, 1975; also Thomas, 1975).

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