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TEMPERATURE REGULATION AND HEAT BALANCE IN FLYING WHITE-NECKED RAVENS, *CORVUS CRYPTOLEUCUS*

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During level flight at 10 m.s^{-1} in a wind tunnel, white-necked ravens (*Corvus cryptoleucus*, mass 0·48 kg) exhibited an increase in body temperature to steady-state levels as high as 45 °C, exceeding resting levels by nearly 3 °C. This reflects the storage of up to half of the metabolic heat produced (H_p) during 5 min of flight. During steady-state flight, body heat was dissipated in part by respiratory evaporation and convection (13–40% of H_p) evoked by increases in ventilation proportional to body temperature. Remaining heat was lost by cutaneous evaporation (10% of H_p) as well as by radiation and convection from the external body surface. The results suggest strategies that might be used by ravens during flight under desert conditions.

INTRODUCTION

During flight birds may increase their energy consumption by an order of magnitude. Up to 80% of the increase in energy expenditure, however, may involve no external work and thus constitutes an endogenous heat load on the animal. Some of the heat may be stored in the tissues of the body and thus appear as an elevation in body temperature. The remainder must be dissipated to the environment by forced convection, radiation and evaporation.

Previous reports have shown that at lower air temperatures most of the excess heat production during flight is dissipated by non-evaporative means (Tucker, 1968; Berger, Hart & Roy, 1971; Bernstein, 1976; Torre-Bueno, 1978). Since the effectiveness of non-evaporative pathways is dependent on the temperature gradient between a flying bird and its environment, reduction of this gradient should force increased reliance on latent heat transfer. In fact, most authors (Tucker, 1968; Berger *et al.* 1971; Berger & Hart, 1972; Bernstein, 1976; Torre-Bueno, 1978) have reported significant increases in evaporative water loss when air temperature was increased above 20–25 °C. The relative importance of latent heat dissipation to the overall energy balance of a flying bird may depend primarily on the bird's ability to ventilate the respiratory tract (Bernstein, 1976) although the contribution of cutaneous evaporation is unknown.

Ultimately, reliance on evaporation as a cooling mechanism creates a potential for dehydration, if continued over long periods. Long distance migrants may avoid the use of evaporative cooling by flying at high altitude where low air temperatures would facilitate convective heat loss (Torre-Bueno, 1976). However, many resident desert species, such as the white-necked raven, are often active in the presence of high ambient temperature as well as intense solar radiation. These birds may rely on latent heat loss to a greater extent and maintain water balance by replenishment from available water sources.

To determine the relative importance of the major avenues of evaporative and non-evaporative heat loss in temperature regulation during flight, we measured colonic temperature, as well as gas exchange, evaporation and ventilation in the respiratory system of white-necked ravens prior to and during steady-state, wind tunnel flights of 15–25 min duration. Complete gas exchange and ventilation data, together with an analysis of respiratory function during flight, are presented elsewhere (M. H. Bernstein and D. M. Hudson, in preparation).

METHODS

Experimental animals

Seven white-necked ravens (*Corvus cryptoleucus*) were captured as fledglings in Doña Ana County, New Mexico, during the summers of 1975–76 and maintained for two to three years on beef liver, pigeon and rat carcasses, vegetables, a vitamin supplement and water *ad libitum*. The ravens were housed together in an outdoor flight cage ($6 \times 3 \times 4$ m) partially exposed to prevailing climatic conditions. The birds appeared in good health and maintained body weight throughout the study.

Flight training

We trained the ravens to fly in an open-circuit wind tunnel similar to that described by Tucker & Parrott (1970). A downstream axial flow fan generated air flow in the Plexiglas test section ($1{\cdot}5 \times 1{\cdot}5 \times 3{\cdot}5$ m). We assumed that the angle of air velocity, θ, measured from horizontal, was parallel to the test section floor, which could be tilted from 1° above ($+1^\circ$) to 7° below horizontal (-7°). Air temperature (T_A) in the test section was controlled by a system of air conditioners and outdoor air inlets. Additional details about the construction and calibration of the wind tunnel are presented elsewhere (Hudson, 1978).

The ravens were trained to fly in the test section utilizing a collapsible perch as positive reinforcement (Tucker, 1968), but without the use of electric shock. When the birds would fly horizontally for 20 min they were trained to wear the measurement apparatus (see below). At the end of training, five ravens (mean mass, 0·48 kg) would fly horizontally, non-stop, for 20–30 min while instrumented. To keep the birds in condition it was necessary to fly them in 30-min sustained level flights three to four times a week.

Experimental methods

Deep body temperature was determined as colonic temperature (T_C), measured with welded, copper-constantan thermocouples (0·1 mm wire diameter), coated with polyvinyl and inserted approximately 7 cm into the colon. The measuring system consisted of an amplifier connected to a bucking voltage supply. The positive potentials beyond the bucked source were continuously recorded on a potentiometric recorder. These instruments were calibrated with the aid of an Eppley standard e.m.f. source, the value of which was traceable to the U.S. National Bureau of Standards (NBS). The magnitude of the bucking voltage was determined with a digital voltmeter, also checked with the standard e.m.f. source. The reference temperatures for the thermocouple were measured with a mercury-in-glass thermometer calibrated by the NBS and accurate to ± 0·1 °C. The overall systematic error of the system is estimated to be ± 0·1 °C; the time constant of the system was less than 1 s.

Tidal volume (V_T) was determined as the integral of ventilatory flow, measured by a hot-film flow transducer and associated signal conditioning apparatus (Thermo-Systems, Inc., St Paul, Minnesota). The transducer was mounted in a Plexiglas cylinder (7 mm I.D.), through which the pressure drop was specified at less than 10 Pa over the range of flows encountered. In practice the transducer assembly was mounted in a mouthpiece made of balsa wood and dental impression latex. Each mouthpiece was custom-fitted to a bird by forming a 'bite' impression in the fresh latex. During a flight, the bird's beak was taped to the mouthpiece and the nares sealed to ensure an air-tight fit. The mouthpiece was designed to minimize increases in dead space, without obstructing buccal cavity evaporative surfaces.

The transducer leads were constructed of thin, flexible, copper wire, and attached to a temperature-compensated anemometer which heated the hot-film sensor to a constant temperature and measured the power required to maintain sensor temperature, as heat was dissipated from it by airflow. The relationship between power required to maintain film temperature and airflow was electronically linearized by a polynomial function generator, the output of which was directly proportional to airflow. Linearizer output was directed to an electronic integrator connected to an oscillographic recorder.

The integrator was triggered to reset as the flow signal returned to zero between each inhalation and exhalation, such that the amplitude of the displayed signal was directly proportional to air volume for each respiratory half-cycle. The inhaled volume was distinguished from exhaled by means of a probe-mounted thermocouple, the output of which was recorded simultaneously on the oscillograph. The anemometer probe was calibrated periodically with the aid of a flow calibrator, with accuracy (± 0·2%) traceable to NBS, and the results expressed at standard temperature and pressure, dry (STPD). During experiments the effects of deviations from calibration temperature were cancelled by the use of a temperature-compensating circuit. Simultaneous measurement of body temperature permitted conversion of V_T to conditions of body temperature and pressure, saturated (BTPS).

Respiratory frequency (f) was determined by visually counting inspirations from the oscillograph trace, while the ventilation ($\dot{V}_I$, BTPS) of the respiratory tract was calculated as the product of frequency and the mean inspired tidal volume.

Respiratory gas exchange was measured in separate experiments using an individually-fitted, cone-shaped, acetate mask, open at the back, similar to that described by Tucker (1972). Air was drawn through the back of the mask and over the nares of the bird, carrying exhaled gases at a constant rate through a flexible vinyl tube (3 mm I.D.) and a flowmeter. The flow rate was chosen to preclude leakage of any expirate past the edge of the mask, such that all was drawn into the main sample stream, even during periods of maximum respiratory ventilation. An aliquot of the main sample stream was directed by an auxiliary diaphragm pump through a dewpoint hygrometer for measurement of water vapour pressure of the sample air. The hygrometer, calibrated with a precision resistance (Bernstein *et al.*, 1976), measured dewpoint to the nearest 0·25 °C. A second fraction of this aliquot was directed in parallel with the hygrometer through a calcium sulfate column to remove water vapour, through an infrared carbon dioxide analyzer, then through a paramagnetic oxygen analyzer.

All analyzer outputs were continuously monitored on recording potentiometers equipped with bucking voltage supplies. The dewpoint hygrometer recorder gave 99% response within 10 s. The oxygen analysis system responded fully within 30 s, while the CO_2 analysis system had a 45 s response time. The latter two systems resolved changes in fractional concentrations of $\pm 10^{-4}$.

The system flowmeter was calibrated with the flow calibrator for the particular pressures and temperatures at which it was to be used. The imprecision of the flowmeter readings was negligible; the difference between the flow rates obtained during the initial calibration (N = 30) and final calibration (N = 11) was less than 1%. The effect of air stream water vapour on flowmeter float deflection was also negligible over the range of ambient vapour pressures and temperatures encountered. The difference in gas flow rate, using dry air or air saturated with water vapour at 22 °C, was less than 0·06%. Temperature of flowing air was monitored at the flowmeter with a precision thermistor calibrated to an accuracy of ±0·1 °C by use of the NBS thermometer. System pressure, measured downstream from the flowmeter using a mercury manometer, was held constant by flow valves and pressure regulators. The oxygen analyzer was calibrated before and after a series of flights, either by the back pressure method (Tucker, 1972), or by depressing the oxygen concentration of ambient air by bleeding dry nitrogen into the empty mask using the flow calibrator. For calibration of the CO_2 analyzer, various calibration values were obtained by bleeding dry carbon dioxide into the empty mask at known rates using the flow calibrator. The fractional concentration of CO_2 in ambient air was assumed to be negligible.

Fractional O_2 concentration of mask inflow air was determined before and after each flight by drawing room air through the empty mask. Stabilized oxygen analyzer recordings obtained for ravens wearing the mask after at least 5 min of flight yielded fractional oxygen concentrations of mask outflow air. Information on mask inflow and outflow air, together with system flow values corrected to STPD conditions, were utilized for calculation of oxygen consumption ($\dot{V}_{O_2}$) during a steady-state flight. This was used in turn for calculation of metabolic heat production as described below. The rate of carbon dioxide production of birds in flight ($\dot{V}_{CO_2}$) was determined directly from stable CO_2 analyzer traces using calibration curves, and was used for calculation of respiratory exchange ratio ($R = \dot{V}_{CO_2}/\dot{V}_{O_2}$). Water vapour pressure (P'_W) was calculated from the dewpoint temperature of the sample air as measured by the hygrometer according to the formula of Goff & Gratch (1946). Due to transient pressure build-ups on the hygrometer sensor, it was necessary to monitor sensor pressure (P_S) and to obtain a vapour pressure (P_W) corrected to ambient (P_B) conditions as $P'_W\ P_B/P_S$. Water vapour pressure and system flow information were use to calculate respiratory evaporative water loss as done by Bernstein *et al.* (1976).

The additional drag on the bird due to the various transducer leads or gas collecting tubes was measured in the manner described by Bernstein, Thomas & Schmidt-Nielsen (1973). The wind tunnel was then tilted at an angle calculated to permit the gravitational thrust component of the cable or tube weight to cancel the drag component. Thus, the birds flew in a manner simulating unencumbered, horizontal flight.

Estimations of heat exchange

The heat production of a bird during flight may be computed from the measured oxygen uptake, the energy equivalent of oxygen for the metabolic substrate utilized and an assumption of the efficiency of conversion of metabolic energy to external work (Tucker, 1968). We assumed 25% efficiency as in mammals (Kleiber, 1961). We measured respiratory exchange ratios, but because of the uncertainties associated with their interpretation during exercise, in terms of the metabolic substrate being utilized (Hill, Long & Lupton, 1924), we used an average energy equivalent of 20·1 kJ per l O_2 STPD (4·8 kcal per l O_2 STPD). The largest error that this could engender would be 6%, but the actual error is probably lower. We then calculated heat production ($\dot{H}_p$) in W per unit body mass from $\dot{V}_{O_2}$ data (l O_2.min^{-1} STPD), as:

$$\dot{H}_p = (0{\cdot}75)\,(20{\cdot}1)\,\dot{V}_{O_2}. \qquad (1)$$

We calculated the rate of heat loss by respiratory evaporation ($\dot{H}_{re}$) from the rate of respiratory evaporation ($\dot{m}_{re}$) in g H_2O.h^{-1}.kg^{-1} body mass and the latent heat of vaporization of water (λ), assumed to be 2·43 kJ.kg^{-1} H_2O. The rate of cutaneous evaporative heat loss ($\dot{H}_{ce}$) can be estimated from the rate of loss of body mass ($\dot{m}_b$) if the change in mass due to respiratory evaporation, O_2 consumption ($\dot{m}_{O_2}$) and carbon dioxide output ($\dot{m}_{CO_2}$) are known, and if other sources of mass exchange are prevented. We thus determined $\dot{H}_{ce}$ according to:

$$\dot{H}_{ce} = (\dot{m}_b + \dot{m}_{O_2} - \dot{m}_{CO_2} - \dot{m}_{re})\lambda. \qquad (2)$$

Other sources of mass exchange were prevented by withholding food and water during experiments and by sealing the cloaca with quick drying cement.

We also calculated the quantity of heat stored by a bird experiencing an increase in body temperature, according to:

$$H_s = \Delta \bar{T}_B m_b C_t, \qquad (3)$$

where H_s is heat stored (J), $\Delta \bar{T}_B$ is the change in mean body temperature (°C), m_b is body mass (kg), and C_t is the mean specific heat of body tissues ($3{\cdot}474 \times 10^{-3}$ J.kg^{-1}.°C^{-1}; Whittow, 1976). Strictly speaking, $\bar{T}_B$ is actually the mean of a large number of temperatures measured both on the surface and deep within the body core (Whittow, 1976). Due to the difficulty in calculating the various weighting factors necessary to arrive at $\bar{T}_B$, especially for a flying bird, we have approximated $\bar{T}_B$ using T_C.

Heat is lost from the tissues as inhaled air is warmed to body temperature in the respiratory tract, although a portion of this heat may be recovered by countercurrent cooling of the exhalant (Schmidt-Nielsen, Hainsworth & Murrish, 1970). We calculated heat loss by convection from the respiratory tract ($\dot{H}_{rc}$) as:

$$\dot{H}_{rc} = \rho\, \dot{V}_E C_p (T_E - T_A), \qquad (4)$$

where $\dot{H}_{rc}$ is in W, ρ is the density of air (g.l^{-1} STPD), $\dot{V}_E$ is the respiratory minute volume (l STPD.min^{-1}), C_p is the specific heat of air (1·0 J.g^{-1}.°C^{-1}), and T_E is the exhaled air temperature (°C). T_E can be measured directly (Collins, Pilkington & Schmidt-Nielsen, 1971) or can be calculated as the dewpoint of the exhaled air, if the air is saturated and the saturation vapour pressure (P_{E_W}) of the exhaled air is known. We assumed saturation and used the fractional concentration of water in the exhaled air (F_{E_W}) and the pressure in the respiratory system (assumed equal to P_B), to calculate P_{E_W} as $F_{E_W}P_B/(1+F_{E_W})$. F_{E_W} was determined as the ratio of total exhaled water vapour ($\dot{V}_W$, l STP.min^{-1}, determined from $\dot{m}_{re}$) to $\dot{V}_E$. We assumed that $\dot{V}_I$ was the same in both the ventilatory and the gas exchange experiments. We also assumed $\dot{V}_E$ equal to $\dot{V}_I$; the use of this assumption results in an error of 1 % or less over the range of gas exchange and ventilatory parameters encountered in this study.

RESULTS

Core temperatures

The relationship of colonic temperature to air temperature during sustained horizontal flight at 10 m.s^{-1} is shown in Fig. 1. Colonic temperature was independent of T_A from 14 to 22 °C, but increased gradually between 22 and 28 °C and sharply above 28 °C. The relationship is best described by the second order, least-squares equation:

$$T_C = 44{\cdot}63 - 0{\cdot}16\,T_A + 0{\cdot}005\,T_A{}^2, \quad r = 0{\cdot}86,\ N = 92, \tag{5}$$

where r is the correlation coefficient. Pre-flight resting T_C averaged 42·2 °C (± 0·4 SD, N = 36) at T_A between 14 and 24 °C. There was no difference in T_C between birds instrumented with the ventilation probe and birds flying with the colonic thermocouple only.

Respiratory evaporation and heat production

The rate of evaporation from the respiratory tract was measured as a function of ambient temperature at flight angles of 0 and −4 ° and at a speed of 10 m.s^{-1}. Respiratory evaporation during level flight showed a strong correlation with T_A described by the least-squares equation:

$$\dot{m}_{re} = 1{\cdot}23T_A - 12{\cdot}17, \quad r = 0{\cdot}92,\ N = 29, \tag{6}$$

where $\dot{m}_{re}$ is expressed in units of mg H_2O (g.h)$^{-1}$. The lowest recorded $\dot{m}_{re}$ was 13 mg H_2O (g.h)$^{-1}$ at 22·0 °C, while the highest was 34 mg H_2O (g.h)$^{-1}$ at 32·8 °C. Respiratory water loss at $\theta = -4$ °C was less strongly correlated with ambient temperatures; the relationship was best described by the least-squares equation:

$$\dot{m}_{re} = 0{\cdot}32\,T_A{}^{1{\cdot}1}, \quad r = 0{\cdot}63,\ N = 23 \tag{7}$$

Between the two flight angles, there was essentially no overlap in recorded respiratory evaporation over the range of temperatures utilized. In resting birds at T_A of 18–24 °C, mean evaporation of water from the respiratory tract was 2·55 mg H_2O (g.h)$^{-1}$ (±0·62 SD, N = 36).

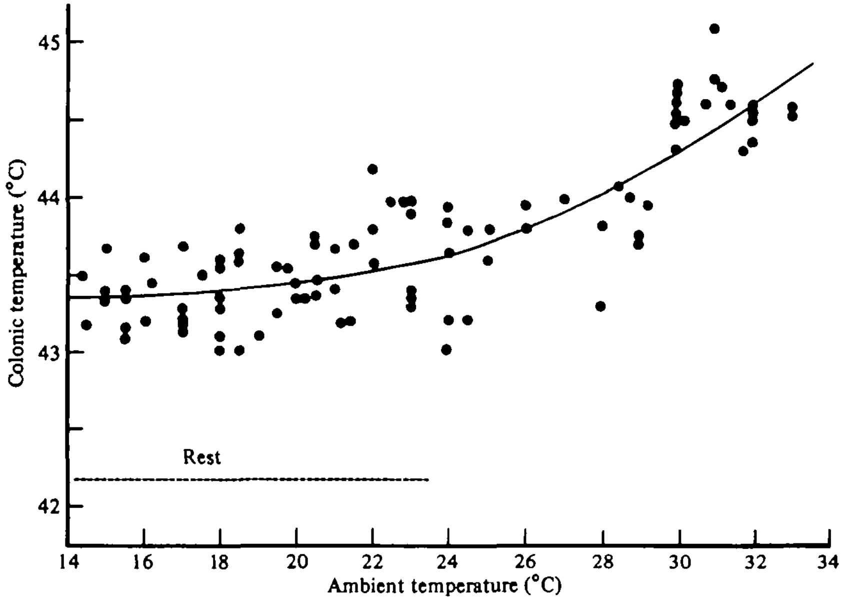

Fig. 1. Mean, steady-state colonic temperature for five white-necked ravens, during horizontal flight, in relation to ambient temperature. Points indicate the steady-state mean value after at least 5 min of flight. The line is described by equation (5).

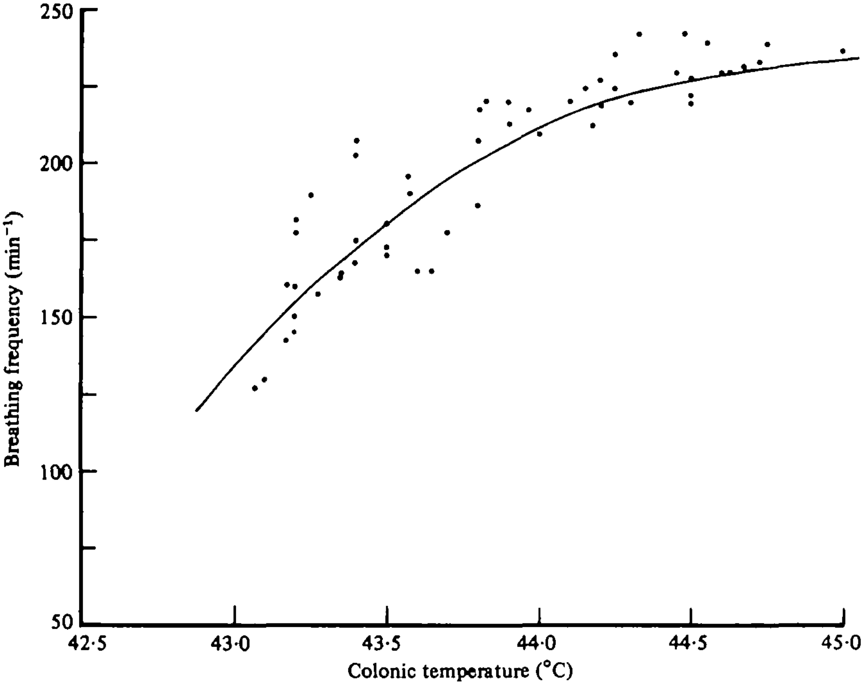

Fig. 2. Respiratory frequency in relation to mean colonic temperature during horizontal flight at 10 m.s^{-1}. Line was fit to data by the method of least-squares and is described by equation (9).

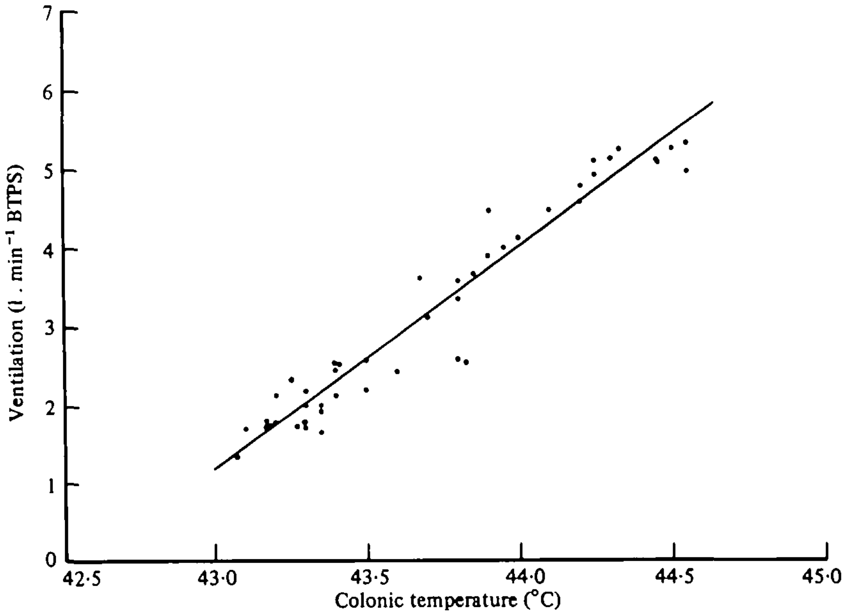

Fig. 3. Ventilation in relation to colonic temperature during steady-state horizontal flight. Each point was calculated as the product of measured tidal volume (BTPS) and frequency. Line was fit to the data by the method of least-squares and is described by equation (10).

In contrast to respiratory evaporation, metabolic heat production ($\dot{H}_p$) did not increase with T_A, averaging 49·8 W.kg^{-1} (±4·0 SD, N = 28) during horizontal flight. Resting $\dot{H}_p$ averaged 11·9 W.kg^{-1} (±1·8 SD, N = 96). Mean respiratory exchange ratio for all five birds during steady-state flight was 0·77 (±0·025 SD, N = 250), compared to a mean preflight value of 0·80 (±0·088 SD, N = 20). Complete data for $\dot{V}_{O_2}$ and $\dot{V}_{CO_2}$ will be presented in a subsequent paper (D. M. Hudson and M. H. Bernstein, in preparation).

Ventilation

Tidal volume and frequency were measured simultaneously with body temperature during level flight at 10 m.s^{-1}. Over the range of ambient temperatures tested (22–34 °C), T_C increased from 43·1–44·5 °C. Tidal volume increased linearly with T_C over this range from 10·4 cm^3 BTPS to 22·4 cm^3 BTPS. The least-squares equation describing this relationship is:

$$V_T \text{ BTPS} = 8{\cdot}67\, T_C - 363, \quad r = 0{\cdot}95, \text{N} = 46 \qquad (8)$$

The mean resting tidal volume at T_A of 22 °C (T_C of 42·2 °C) was 10·5 cm^3 BTPS (±2·4 SD, N = 20).

Respiratory frequency also increased with increasing body temperature (Fig. 2) but the relationship was not linear over the entire range of T_C, so a least-squares polynomial equation was used to describe the data:

$$f = -55866 + 2499{\cdot}9\, T_C - 27{\cdot}85\, T_C^2, \quad r = 0{\cdot}91, \text{N} = 53, \qquad (9)$$

where f is given in units of min^{-1}. Breathing frequency ranged from 125 min^{-1} to 240 min^{-1}, while mean resting f was 32·5 min^{-1} ($\pm$ 6·2 SD, N = 20).

As a result of the variation of V_T and f with T_C, $\dot{V}_I$ also increased with T_C over the range of ambient temperatures used (Fig. 3). This relationship was strongly linear despite the non-linearity of the frequency relationship, and is described by:

$$\dot{V}_I \text{ BTPS} = 2{\cdot}84\, T_C - 121, \quad r = 0{\cdot}96, \text{N} = 46. \tag{10}$$

Ventilation ranged from 1·3 to 5·3 l.min^{-1} BTPS. Resting ventilation calculated from the pre-flight values of f and V_T was 0·34 l.min^{-1} BTPS.

DISCUSSION

Temperature regulation

Sustained flight at ambient temperatures of between 22 and 33 °C resulted in a marked increase in the body temperature of the white-necked raven, even though this T_A range approximates the zone of thermal neutrality for the resting bird. The range of core temperatures measured (43·5–44·8 °C) may be only slightly below the lethal temperatures for many avian species (Dawson & Schmidt-Nielsen, 1964; Dawson & Bennett, 1973). Thus ambient temperatures that are low for resting birds may be correlated with hyperthermia during flight.

Both Aulie (1971) and Butler *et al.* (1977) reported that during sustained, horizontal, wind tunnel flight pigeons produced more than 8 times the heat of birds at rest, underwent severe hyperthermia (T_C of 43·3–44·7 °C) at ambient temperatures between 25 and 29 °C and were not able to fly for more than 10 min. Starlings flying at ambient temperatures between 25 and 35 °C (Torre-Bueno, 1976) also experienced extreme hyperthermia, with core temperatures ranging from 43·5 to 46 °C. These authors all reported that their birds appeared reluctant to fly at ambient temperatures above 28–30 °C, and often failed to attain steady-state. Flights were either stopped when T_C approached lethal levels (Torre-Bueno, 1976) or the birds simply refused to fly (Aulie, 1971). In contrast, the budgerigar was apparently able to increase heat loss sufficiently to prevent over-heating during flight at ambient temperatures of 25–29 °C (Aulie, 1971). The highest T_C of a budgerigar was 42·7 °C at the end of a 7 min flight (mean T_C = 42·1 °C). The ravens in this study continued to fly despite their hyperthermia, and were able to achieve steady-state in all but a few cases.

At the lower range of ambient temperatures (14–22 °C), the ravens flew with a core temperature of 43·3 °C (1·1 °C above resting) regardless of ambient temperature. Torre-Bueno (1976) also noted this independence of core and ambient temperatures in starlings, which persisted down to 0 °C.

Heat storage

Heat storage for an exercising bird can amount to a sizeable fraction of heat production, depending in part upon the mass of the bird, the magnitude of the rise in T_C from the resting level and the duration of the exercise period. For example, Taylor *et al.* (1971) found that heat storage accounted for up to 75% of H_p in a rhea running [illegible]t ambient temperature of 43 °C for 20 min. From the mean $\dot{H}_p$ for horizontal

Table 1. *Net heat storage for a flying, 0·48 kg white-necked raven, calculated as the product of body mass, tissue specific heat, and the difference in T_C (ΔT_C) between resting and flying, according to equation* (3)

(Total heat production was calculated as the product of the rate of heat production and flight duration (min). The fraction of heat produced that is stored for a particular T_C is given as a percentage.)

			Flight time (min)			
		Heat	5	10	15	20
T_C, °C	ΔT_C, °C	stored (kJ)	Heat production stored (%)			
43·3	1·2	1·9	27	14	9	7
43·5	1·3	2·2	30	15	21	26
44·0	1·8	3·0	42	21	14	10
44·5	2·3	3·8	52	26	17	13
45·0	2·8	4·6	64	32	21	16

flight, we have calculated the total amount of heat produced (kJ) for flights of various durations and the total amount of heat stored (kJ) by a 0·48 kg raven as T_C rises from resting to flight values (from equation 3). The results (Table 1) indicate that for short flights, H_s can amount to a relatively large percentage of total H_p. For example, H_s represents 27% of H_p for 5 min of horizontal flight if T_C of 43·3 °C is reached. When T_A is elevated so that T_C reaches 45 °C, H_s can account for up to 64% of the heat produced during a 5 min flight. Even during a 10 min flight, up to 32% of the heat produced could be stored, if T_C reached 45 °C. Such a bird could cover ground distances of 3 and 6 km for these flight durations provided that the bird flew horizontal at 10 $\mathrm{m.s^{-1}}$ in still air.

Our estimates of H_s (Table 1) are probably the maximum possible, since we assumed that T_B was equal to T_C at rest and during flight. In fact, skin surface temperatures were probably lower than T_C. Torre-Bueno (1976) has measured sub-cutaneous temperatures over breast muscle as being 1·5–2 °C below T_C in starlings flying over a T_A range of 18–27 °C.

Partition of heat transfer

The data for heat storage apply to a bird not in steady-state. The energy balance equation for bird in thermal steady-state is given by:

$$\dot{H}_p = \dot{H}_{re} + \dot{H}_{ce} \pm \dot{H}_{rc} \pm \dot{H}_d, \qquad (11)$$

where $\dot{H}_p$ is the rate of heat production (equation 1), $\dot{H}_{re}$ and $\dot{H}_{ce}$ (equation 2) are the rates of heat loss due to respiratory and cutaneous evaporation, $\dot{H}_{rc}$ (equation 4) is the rate of heat lost or gained by respiratory convection and $\dot{H}_d$ is the rate of heat lost or gained by radiation and forced convection from the external body surfaces.

The fraction of metabolic heat dissipated by respiratory evaporation, $\dot{H}_{re}/\dot{H}_p$, shown in Fig. 4 as a function of T_A during horizontal flight, increased from a minimum of 0·19 at 22 °C to a maximum of 0·40 at 33 °C. The relationship is described by the least-squares equation:

$$\dot{H}_{re}/\dot{H}_p = e^{(0.0559\,T_A - 2.8)}, \quad r = 0.89,$$

(12

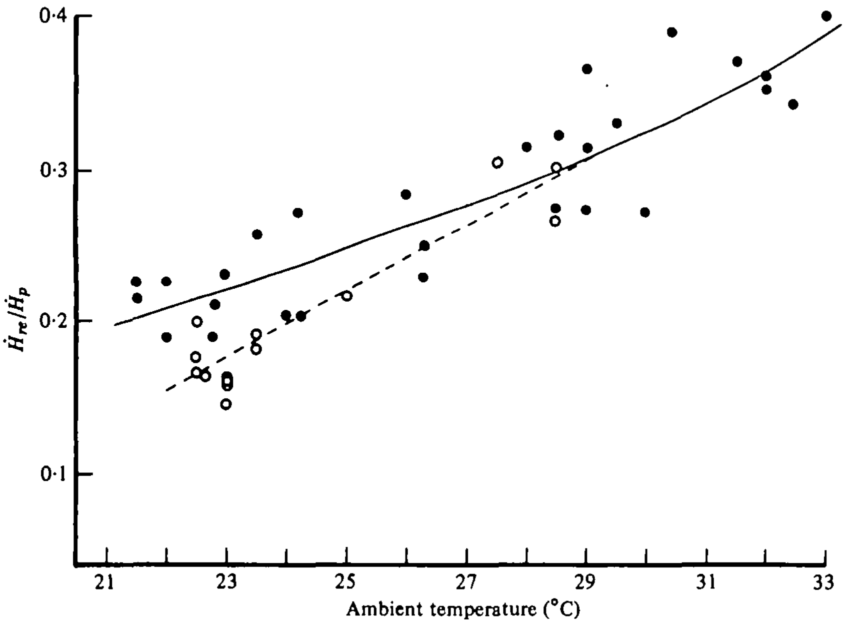

Fig. 4. The ratio of heat loss from the respiratory tract to heat production during flight as a function of ambient temperature. Points indicate ratios calculated from simultaneous measurements of respiratory water loss and oxygen consumption for horizontal flights at 10 m.s^{-1}. Solid line fit to the raven data (shaded circles) by the method of least-squares is described by equation (12), while data for fish crow *Corvus ossifragus* (unshaded circles, dashed line), recalculated from Bernstein (1976), are described by equation (13).

where *e* is the base of natural logarithms. The contribution of $\dot{H}_{\rm re}$ at rest was 14% of $H_{\rm p}$ at a $T_{\rm C}$ of 42 °C. From equation (12) we have calculated $\dot{H}_{\rm re}/\dot{H}_{\rm p}$ for a hypothetical 0·48 kg raven during level flight at five temperatures; these are presented in Table 2. Cutaneous evaporative heat loss was estimated for two birds during four, 25 min flights at 22 °C. The mean ratio of $\dot{H}_{\rm ce}$ to $\dot{H}_{\rm p}$ was 0·10 (±0·05 SD) for these flights. This result agrees closely with the data of Hoyt, Hudson & Bernstein (1976) and of R. W. Hoyt and M. H. Bernstein (in preparation). We assumed the rate of cutaneous evaporation to be constant over the ambient temperature range used in this study and have calculated $\dot{H}_{\rm ce}$ for a 0·48 kg raven during horizontal flight and at rest. We then added $\dot{H}_{\rm ce}$ to $\dot{H}_{\rm re}$ to obtain the total rate of heat lost by evaporation. The results are shown in Table 2. The total rate of heat loss by evaporation increased from 23% of $\dot{H}_{\rm p}$ at 43·3 °C to a maximum of 50% at 45 °C, while total resting evaporation dissipated about 27% of $\dot{H}_{\rm p}$.

The ratio of respiratory heat dissipation to heat production at the same $T_{\rm A}$ was similar in the 0·48 kg raven and in the 0·28 kg fish crow (*Corvus ossifragus*). The data for fish crows, originally reported by Bernstein (1976) in his Fig. 6, were miscalculated, but have been recalculated and are presented in our Fig. 4, along with those for the raven. The mean ratio of $\dot{H}_{\rm re}$ to $\dot{H}_{\rm p}$ for level flight at $T_{\rm A}$ of 28 °C was 0·29 in the raven, while the maximum observed ratio for the fish crow was 0·28 at the same

Table 2. *Calculated values for partition of heat loss, ventilation (STPD) and exhalant temperatures for a* 0·48 *kg white-necked raven at rest and during steady-state, level, wind tunnel flights at* 10 $m.s^{-1}$

(The percentage of heat loss through various avenues at the T_0 indicated is given in parentheses.)

	Resting	Flying				
Ambient temperature, °C	22·0	18·0	22·2	27·8	31·3	34·2
Colonic temperature, °C	42·0	43·3	43·5	44·0	44·5	45·0
Exhaled air temperature, °C	40·6	41·4	41·8	41·0	39·3	37·9
Ventilation, l STPD.min^{-1}	0·30	1·20	1·78	2·74	3·70	4·6
Heat loss, W						
Respiratory evaporative	0·8(14)	3·2(13)	4·8(20)	7·1(30)	8·4(35)	9·6(40)
Total evaporative	1·5(27)	5·5(23)	7·1(30)	9·4(39)	10·8(45)	12·0(50)
Respiratory convective	0·1(2)	0·6(3)	0·8(3)	0·8(3)	0·6(3)	0·4(2)
Total cutaneous non-evaporative	4·1(71)	17·2(74)	15·6(67)	13·7(58)	12·8(52)	12·0(48)

ambient temperature. The highest ratio measured for the raven was 0·38 at 33 °C. The data for fish crow are described by:

$$\dot{H}_{re}/\dot{H}_p = 0\cdot0220\ T_A - 0\cdot330, \quad r = 0\cdot93. \tag{13}$$

The only other comparative data on fractional latent heat loss during steady-state forward flight are for budgerigars (Tucker, 1968), and for starlings (Torre-Bueno, 1978). In budgerigars the ratio of total evaporative heat loss to heat production was 0·15 at 20 °C and rose to a maximum of 0·47 at an ambient temperature of 37 °C. Values calculated from Torre-Bueno's (1978) ratios of evaporative heat loss to total energy expenditure, assuming 25% efficiency of converting metabolic energy to external work, were also 0·15 at 20 °C, rising to 0·29 at 28 °C. These values may have included a significant cutaneous component (Tucker, 1968; Torre-Bueno, 1978). We estimated the ratio of total evaporative heat loss to heat production to be 0·48 in the raven flying at 33 °C. Thus it appears that the larger raven must rely on its full evaporative capabilities at lower flight T_A than must the budgerigar, although similar maximal ratios of total evaporative heat loss to $\dot{H}_p$ are reached in both species.

The increase in respiratory evaporation with T_A during flight in the ravens was effected by a four-fold increase in ventilation. The ventilatory increase, in turn, was met by roughly equal increases in both f and V_T. This contrasts with the fish crow, where increased ventilation was primarily caused by increases in V_T as ambient temperature was raised above 23 °C during flight (Bernstein, 1976).

Kilgore *et al.* (1973, 1976) have demonstrated that birds under external heat loads can maintain brain temperature significantly below that of the body core. This is true in some birds during flight as well (Bernstein *et al.* 1979*a*). Prevention of respiratory evaporation reduced the temperature difference between the brain and the rest of the body (Bernstein *et al.* 1979*b*). Thus, respiratory evaporation may be critical for maintaining a low brain temperature during flight, although it may play a lesser role is dissipating heat from the body as a whole.

Exhaled air temperature during flight decreased with increasing T_A (Table 2) as probable consequence of respiratory surface cooling due to the increased rate of evaporation. Berger *et al.* (1971) reported a T_E of 31·5 °C for the black duck flying at a T_A of 19 °C, but did not report the core temperature. Several authors (Lasiewski & Bartholomew, 1966; Calder & Schmidt-Nielsen, 1968; Lasiewski & Snyder, 1969; Schmidt-Nielsen *et al.* 1969) have recorded gular surface or tracheal temperatures in various heat-stressed, resting birds. They reported surface temperatures 1 to 5 °C below T_C, and Lasiewski & Bartholomew (1966) showed that the temperature of at least the gular surface decreased as T_A was increased. All of these birds had elevated T_C and panted or gular fluttered extensively.

Assuming the density of air to be 1·29 g.l^{-1} STPD, we calculated convective heat transfer in the respiratory tract from equation (4) and from estimates of T_E and $\dot{V}_E$. $\dot{H}_{rc}$ was 3% or less of $\dot{H}_p$ under all conditions, ranging from 0·8 W at T_C of 44 °C to 0·4 W at 45 °C. In fact, the maximum $\dot{H}_{rc}$ that would be possible would be only 4·4%, if T_E were equal to T_C at the highest ventilation rate.

The remainder of the heat unaccounted for by evaporation or respiratory convection must be lost by radiation and convection from the plumage surface. Direct determination of the rates of heat loss through the skin and appendages by radiation and forced convection requires a detailed knowledge of surface temperatures and effective exchange areas. The relationships can be complex and difficult to determine, especially in a flying bird (for example, see Veghte, 1976). We have therefore had to calculate $\dot{H}_d$ as an indirect approximation from equation (11); the results are shown in Table 2. $\dot{H}_d$ was 74% of $\dot{H}_p$ at a T_C of 43·3 °C, but only 48% of $\dot{H}_p$ at T_C of 45 °C. The preflight level of dry heat loss was 71% of $\dot{H}_p$. The decrease in $\dot{H}_d$ with increasing T_C during flight represents roughly half the decrease in the overall temperature difference during heat exchange. The ability of the birds to maintain relatively high rates of dry heat transfer under these conditions is probably related to the raven's capacity to alter effective exchange area by leg and foot extension, feather erection and changes in peripheral circulation.

In our experiments we eliminated most sources of short-wave radiation flux and ignored long-wave radiant exchange between the raven and the wind tunnel walls. Since intense solar radiation is characteristic of the white-necked raven's natural environment during much of the year, it is important to know whether solar irradiation would constitute an excessive load on the raven's thermoregulatory mechanisms during flight. Although no data have been reported for flying birds, Marder (1973) estimated the net heat conduction inward through the plumage shell of a resting, brown-necked raven (*Corvus corax ruficollis*) with its back exposed to a solar irradiance of 884 W.m^{-2} in still air at 38 °C. Net absorption at the plumage surface was calculated to be 11·8 W; however, the net conduction inward through the shell was estimated to be between 0·7 and 1·8 W. The latter values are of the same order of magnitude as the rate of convective heat dissipation in the respiratory tract of our ravens during flight. Thus it is conceivable that even intense solar radiation may not add significantly to the endogenous heat load.

White-necked ravens during horizontal flight at 33 °C may be approaching the upper limits of their ability to dissipate the endogenous heat load, since the birds were not always able to achieve a steady-state T_C at or above this temperature. The ravens in their natural habitat in southern New Mexico normally encounter ambient temperatures several degrees above this level during the summer. The ravens could remain airborne and maintain heat balance under these field conditions by reducing power input requirements through soaring and gliding, ascending to more favourable thermal regimes, or by simply making shorter flights.

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