THE COOLING POWER OF PIGEON WINGS

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Summary

The rate of heat loss through the stretched wings ($\dot{H}_{wings}$) was studied in resting pigeons preheated to a body temperature (43.7°C) within the range of those recorded during flight. The experimental system was designed to allow the calculation of $\dot{H}_{wings}$ from the increase in whole-body cooling rates resulting from exposure of the wings to various wind speeds (0–50 km h^{-1}) at 23°C. The maximum value of $\dot{H}_{wings}$ was 3.8 W, less than twice the heat production of a resting pigeon. This indicates that the contribution of the wings to heat dissipation during flight may not be nearly as important as has been supposed. At low windspeeds (0–12.5 km h^{-1}), $\dot{H}_{wings}$ corresponded to about 40 % of the resting rate of heat production, and this value is discussed in connection with the various wing postures observed in hyperthermic birds.

Introduction

Birds must fly with a plumage designed primarily to keep them warm at rest under cold and windy conditions. As heat production may increase by at least one order of magnitude during flapping flight, heat disposal can pose a problem during prolonged flight even at moderate air temperatures. For example, homing pigeons (average body mass 412 g) can fly 320 km in 4.25 h at an average metabolic rate of 44 W, as calculated from their total CO_2 production (24.4 l corresponding to 670 kJ) measured by the double-labeled water technique (Gessaman and Nagy, 1988). Estimating the muscular efficiency during flight at 25 %, these pigeons were producing heat at a rate of about 33 W, or more than 13 times their resting level.

Since pigeons stop flying when their body temperature reaches 44.5°C (Aulie, 1971), or about 3°C above the resting value, one can calculate that they cannot store heat at a rate greater than 0.3 W over a period of 4.25 h in order to remain below this temperature. They must thus dissipate about 99 % of the heat produced during flight, clearly demonstrating a great need to increase their rate of heat loss through evaporation, radiation and convection.

Both theoretical considerations and experimental results suggest that a bird's rate of evaporation must be kept low during a long-distance flight. Owing to the fixed relationship between the production of metabolic water and that of heat during lipid oxidation, an evaporative heat loss exceeding 8 % of the heat

production during flight results in dehydration (Torre-Bueno, 1978). As expected from the metabolic and circulatory efforts required during flapping flight, birds are less tolerant to dehydration during flight than at rest. Biesel and Nachtigall (1987) have suggested that a 5 % loss of body water (about 4 % of body mass) forces pigeons to stop flying. This has been challenged by Gessaman and Nagy (1988), who observed mass losses of up to 7.9 % in pigeons following a 320 km flight and attributed them to dehydration. Once reinterpreted, however, their data fully support the suggestion made by Biesel and Nachtigall (1987), since the rates of CO_2 production measured by Gessaman and Nagy (1988) indicate that the depletion of lipids (assuming an energy content of $39.1 \, kJ \, g^{-1}$) may explain about half the mass loss. Assuming that these pigeons, which flew for 4.25 h at a metabolic rate of 44 W, evaporated a quantity of water equivalent to their metabolic production plus 4 % of their body mass, their total rate of evaporative cooling was about 6.1 W, or one-fifth of their rate of heat production.

These simple calculations show that the bulk of heat dissipation during long-term flight must take place through radiation and convection. Although the clear sky can play an important role as a radiation sink during high-altitude nocturnal migration, convection is expected to be largely dominant in most daytime flights where the solar load can easily offset radiation losses to the environment.

Prime candidates for the role as sites of convective heat dissipation in birds are the unfeathered and thinly feathered areas. The richly vascularized surfaces of the feet and of the bare portion of the legs possess a high capacity for heat loss to air. In the pigeon, the unfeathered part of the legs and feet, while representing only 7 % of the total skin area, can dissipate about 11 W when exposed to a $50 \, km \, h^{-1}$ wind at 15°C (Martineau and Larochelle, 1988).

Since the underwings and the flanks are generally exposed only during flight, they may also contribute to the required increase in thermal conductance. The undersides of the wings are of particular interest because of the paucity of feathers in this area. These surfaces have been suggested (Eliassen, 1962; Tucker, 1968; Biesel and Nachtigall, 1987) to be important sites of heat dissipation during flight, although their capacity for heat exchange has not been estimated.

Since direct measurement of the heat lost by the wings to a moving air stream is extremely difficult, we have used the indirect method developed to determine the cooling power of the legs in the pigeon (Martineau and Larochelle, 1988). This method allowed us to quantify the effect of windspeed on the heat dissipation of bird wings by measuring the capacity of the stretched wings to cool pigeons which had been heated to a body temperature in the range of those recorded during flight.

Materials and methods

Experimental strategy

The experimental system was designed to submit the pigeon to heat stress (body temperature of 43.7±0.4°C; mean±s.D.) that can be encountered during flight

(Hart and Roy, 1967; Aulie, 1971; Butler *et al.* 1977; Hirth *et al.* 1987) in order to create the need for heat dissipation similar to that of flying birds. To achieve this condition, pigeons were placed in thermostatted enclosures capable of heating their body during the heating phase or maintaining the body surfaces other than the head (and the wings when exposed) at the same temperature as the bird's core temperature (intestinal, T_{int}) during the cooling phase. Such a system can thus eliminate heat loss by radiation and conduction by these surfaces and greatly reduce their heat loss by convection and evaporation.

Heat balance during cooling

The heat balance of a bird during a cooling phase can be described as follows:

$$\dot{H}_{met} + \dot{H}_{stor} = \dot{H}_{head} + \dot{H}_{wings} + \dot{H}_{trunk} + \dot{H}_{legs} . \tag{1}$$

The left-hand term represents the heat that a bird must dissipate in order to lower its body temperature, categorized by its source. $\dot{H}_{met}$ is the rate of metabolic heat production and $\dot{H}_{stor}$ the rate of decrease in the body heat content. The right-hand term is the same heat but classified by the sites of dissipation.

Calculation of $\dot{H}_{wings}$ with equation 1 requires either measurement or elimination of the other values. Four of these other values were either negligible or almost constant. $\dot{H}_{trunk}$ and $\dot{H}_{legs}$ were virtually eliminated as the main body and the legs were enclosed in thermostatic moulds whose temperatures were maintained at the bird's T_{int}. The value of $\dot{H}_{met}$ was expected to be constant, as has been observed in similar conditions (Martineau and Larochelle, 1988). $\dot{H}_{head}$, the rate of heat loss from the head, neck and respiratory surfaces, could also be considered to be relatively constant, since the birds all used polypnea during the period over which $\dot{H}_{wings}$ was measured. These four terms were grouped as $\dot{H}_{par}$, since they resulted in a residual (parasite) cooling power in our experimental system. A practical equation for the determination of $\dot{H}_{wings}$ can now be formulated as follows:

$$\dot{H}_{wings} = \dot{H}_{stor} - \dot{H}_{par} , \tag{2}$$

where the cooling power of the wings is the difference in $\dot{H}_{stor}$ with the wings exposed and unexposed.

The determination of $\dot{H}_{stor}$ requires the determination of a true mean body temperature. We have chosen to use changes in intestinal temperature, T_{int}, as representative of changes in true body temperature since the maintenance of the bird's immediate environment (the thermostatic moulds) at its T_{int} ensured that the thermal core was in fact the whole bird.

Experimental animals

The experiments were performed on four unanaesthetized domestic pigeons (*Columba livia*) having a mass of 395 ± 25 g. The birds had free access to mixed grain and water at all times between the experiments.

All experiments were conducted in a manner intended to avoid all pain and

discomfort to the animals. The pigeons were gradually accustomed to the
apparatus and showed no signs of distress or desire to flee.

Restraining, insulating and heating of the pigeon

During all the experiments, the pigeon's body was lightly restrained in a nearly
normal resting position by a sculptured mould made of high-density polyurethane
(Fig. 1). The sides of the mould had openings permitting the wings to be stretched
out. The top, bottom and the lower half side of the mould were covered by heating
plates each made of a 1 mm aluminum sheet onto which heating pad wires and a
sensing thermistor were glued. A 6 mm layer of fiberglass wool was sandwiched
between the aluminum and a 3 mm sheet of Plexiglas on the outside.

The upper half of each side of the mould consisted of a 10 mm thick wooden slab
whose bottom edge had been tailored and covered with a foam strip in order to
make a hermetic contact with the upper surface of the wing. The lower half of the
side, which covered the flanks of the bird, consisted of a heating plate fitted with
appropriate foam strips making a windproof junction with the wing and the upper
slab. These sides most resembled a guillotine with a crescent-shaped hole into
which the wings were lightly pinched. In controls, where the wings were kept
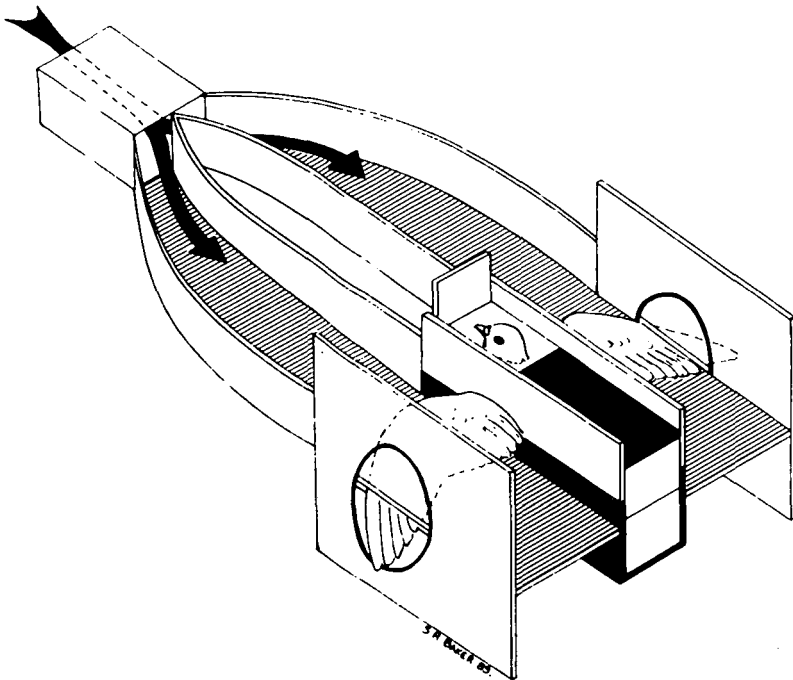inside the mould, the bottom edge of the wooden slab was flat.

Fig. 1. A diagonal overview of the wind tunnel and thermostatted body mould
showing the pigeon with its wings in their retaining devices. The dark surfaces
correspond to the heating plates. A Plexiglas cover (not shown) identical to the floor
was placed over the airways to retain the wind.

The naked portions of the legs and the feet were placed in a polyurethane box containing its own heating plate. During the heating phase, the body temperature of the pigeon was increased to the desired value by keeping the heating plates and a pectoral heating pad at a temperature of 50–55°C. The wings, when stretched, were insulated between 2 cm layers of foam. During the cooling phase, the thermostat controlling the heating plates and pectoral pad was continuously reset to the bird's T_{int}.

Temperature measurements and control

Temperatures were measured with thermistors placed on the heating plates and inserted cloacally in the pigeon's intestine, to a total depth of approximately 6 cm. The thermistor resistance was read *via* a high-precision scanning multimeter (Keithley Instruments, 199) interfaced to a computer for data treatment. All sensors were calibrated with a certified mercury thermometer and their response was described with an appropriate polynomial equation. The inaccuracy of the temperature measurements did not exceed 0.05°C.

The temperature of the five heating plates and the pectoral pad was read and controlled by a computer within 0.3°C of the desired value.

Determination of heat loss from the wings

The effect of windspeed on the rate of heat loss by the wings was determined by positioning the preheated bird in a specially built wind tunnel (Fig. 1). The airstream (23.0±0.5°C) from a cage blower was channeled so as to provide two equivalent air currents into which the wings of the bird could be extended in a position similar to that occurring in flight. Adequate airspeed distribution and low turbulence were obtained in the working section (10 cm wide by 6 cm high) by careful use of upstream deflecting plates and gauze screens. Airspeeds, as measured in the empty working section with a hot-wire anemometer (Datametrics, 100 VT), were uniform (within 3 % of average) in both space and time at all points more than 0.5 cm from the walls. The position of the wings was established by pinching the distal primary feathers into an adjustable foam-covered slit in the sides of the tunnel. The wing's angle of attack was fixed at about 15° to the wind direction, as preliminary experiments showed that birds would choose this angle when allowed to rotate their wings. Because of the width of the mould wall, only 73±4 % (determined by silhouette tracings) of the skin surface of the wings was exposed to the wind.

The heat dissipation by the wings was determined with equation 2. $\dot{H}_{stor}$ was calculated as the product of body mass, tissue specific heat (3.47 J g^{-1} degree^{-1}; Hart, 1951) and the rate of change of T_{int} obtained from the slope of the linear portion (minimum r^2 value of 0.995 and duration of at least 10 min) of the cooling curve.

Three pigeons were tested at each windspeed, each individual being tested, with one exception, at least twice.

Results

Our results show that exposure of the wings to wind enhances the ability of a preheated pigeon to dissipate heat (Fig. 2). For example, pigeons with wings exposed to a 50 km h^{-1} wind (at 23°C) were capable of cooling their body at a rate $(0.159\pm0.024°\,min^{-1})$ three times faster than that $(0.051\pm0.013°\,min^{-1})$ observed in control birds, whose wings were shielded from the wind.

Under our conditions, the cooling power of pigeon wings was a complex function of windspeed, with data points showing noticeable deviations from a smooth curve (Fig. 3). This complexity may result from changes in feather arrangement, wind penetration and/or local flow regime. A maximum value of 3.58 ± 0.60 W was observed at 50 km h^{-1}, which was the highest available windspeed in our apparatus. Using a simple correction for the exposed fraction of the wing fleshed surface $(73\pm4\,\%)$ and for the residual cooling power measured when the wings were kept inside the mould $(1.13\pm0.34$ W), we estimate the net cooling power of the pigeon wings exposed to a 50 km h^{-1} wind at 23°C to be about 3.8 W. At low windspeed (0–12.5 km h^{-1}), this value averaged about 0.9 W.

The residual cooling power $(\dot{H}_{par})$ observed in control birds, which was independent of wind speed, indicated that the heat loss in the head area exceeded the metabolic heat production. This loss can be attributed to the birds' panting as well as to convective and evaporative dissipation taking place from the head surfaces and through the opening for the head in the top of the mould.
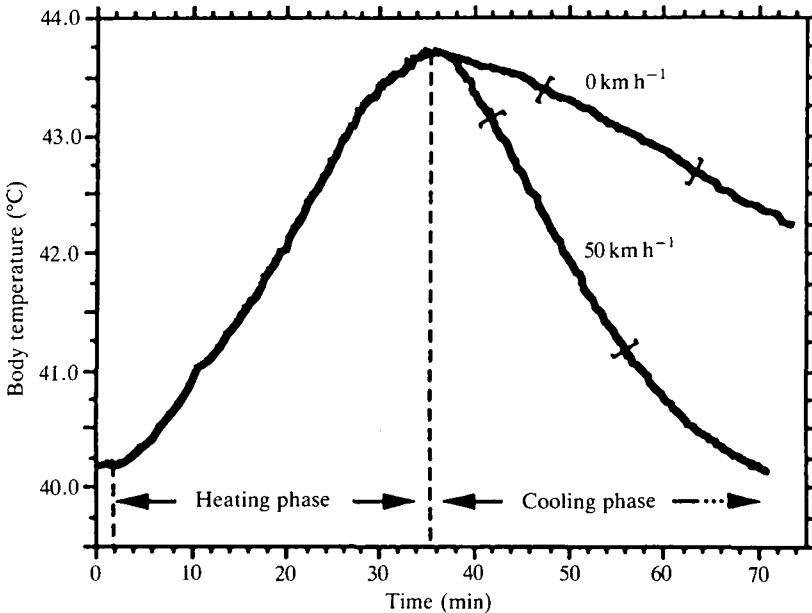

Fig. 2. Typical changes of the intestinal temperature (T_{int}) of a pigeon during the preheating and cooling phases. During the cooling phase, the wings were exposed to a 0 or 50 km h^{-1} wind at 23°C. The linear portion of the curves used to calculate the cooling power is indicated between brackets.
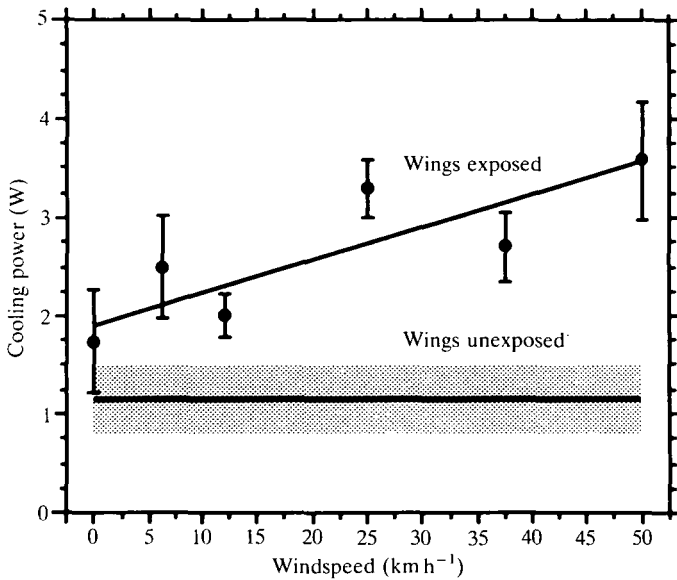
Fig. 3. The effect of wind speed (T=23°C) and wing exposure (corresponding to 0 or 73±4% of the wings' fleshed portion) on the cooling power of pigeons preheated to 43.7±0.4°C. Results are expressed as mean±S.D. (vertical bars or patterned area), for 5–6 experiments using a minimum of two different birds for each point. The equation for the upper line is $y=1.9+0.033x$ (r^2=0.55, N=40).

Unfortunately, the birds would not accept a tight fit around the neck when in a spread-wing position.

Discussion

Our results show that the loss of heat by the wings is not nearly as important as has been supposed (Eliassen, 1962; Tucker, 1968). The exposure of the wings to a 50 km h^{-1} wind increased the bird's cooling power by about 3.8 W. This corresponds to only 11% of the heat production calculated from the data of Gessaman and Nagy (1988) for a pigeon engaged in a prolonged (4.25 h) flight.

The possibility exists that an underestimation resulted from the failure of our preheating treatment to stimulate the full recruitment of the wings as heat dissipators. Although this cannot be ruled out, it appears unlikely that pigeons would not fully exploit the dissipating power of their skin before engaging (typically at T_{int}>42.6°C) in open-mouth panting, a manoeuver with important metabolic and respiratory consequences.

It is possible that our experimental conditions, in comparison with free flight, limited the heat transport to the wings. Although the data collected by Butler *et al.* (1977) indicate that the arterial pressure is not greater in flying than in resting pigeons, blood flow to the inner tissues of the wings should be much higher during flight than at rest. Since these tissues are chiefly muscles contributing to the wings'

movements, the advantage of their increased perfusion is likely to be counterbalanced by a rise in their heat production. Wing flapping will also create pulsating centrifugal effects likely to add an oscillatory component to the blood pressure in the wings' vasculature. This may possibly promote heat exchange by causing a reversible distension of the blood vessels in the superficial tissues. These and other deformations occurring during a flapping cycle may also assist blood pumping.

It is also possible that our restraining device hindered heat transport to the wings by increasing the resistance to blood circulation. This is, however, unlikely in view of the light pressure exerted on the wings by the sealing foam strips. A slight penetration of air through the wing seal appears to be a more probable problem, even though careful installation of the seal eliminated any detectable draught. This might have led to an overestimation of the cooling power of the wings, since preliminary tests showed that slight draughts into the mould could produce much higher rates of cooling.

To measure the cooling power of the wings independently from that of the sides of the body, we had to insulate the flanks of the pigeons from winds of up to $50 \, \mathrm{km \, h^{-1}}$. Although the lateral heating plates provided active and passive insulation which was adequate for this purpose, they prevented a significant fraction ($27 \pm 4 \, \%$) of the wing surface from contacting with the moving air. Should the proximal part of the wings have greater specialization for heat dissipation than the other parts, our estimate of the cooling capacity of the wings would be too low. Although the vascular anatomy of the wing skin is largely unknown in birds, the available information indicates an absence of the structures (superficial venous plexuses and/or arteriovenous anastamoses) usually associated with skin areas possessing a high capacity for heat dissipation, such as those of the legs and feet (Arad et al. 1989). This indicates that the thermal resistance of the skin and subcutaneous tissues may be the limiting factor of the heat dissipation capacity of avian wings.

The heat exchange between the moving air and the wing skin in our study might not have been representative of that taking place in flight, because of differences in airflow regime or wing position and movements. Even if the angle of attack was favorable to heat exchange in our conditions, the air movements prevailing around the wings may have been, to an unpredictable extent, less efficient for heat exchange than those encountered during flapping flight. The transient aerodynamic effects associated with the various alternating movements of the wings may have significant influences on their heat-exchange capacity. Although difficult to quantify, these effects are likely to promote the mixing of ambient air with that contained in the plumage and its adhering boundary layer, and thus to reduce the local thermal resistance. As these effects appear to be very difficult to control, their influence on heat exchange should be relatively small since they would otherwise severely limit the ability of a bird to fly at cold temperatures. The fact that our maximum windspeed is near the lowest speed used by freely flying pigeons (Michener and Walcott, 1967) may also contribute to an underestimation of the wings' cooling capacity.

Although a hypothermic resting bird is admittedly an imperfect model of a flying bird, even for the study of a thermoregulatory phenomenon, we do not think that the cumulative effect of the factors discussed above invalidates the conclusion that wings are heat exchangers of minor importance during flight. This is consistent with the known arteriovenous arrangements in birds' wings, which indicate a greater specialization for heat conservation than dissipation (Arad *et al.* 1989). When compared to the bare portion of the legs and feet under similar conditions (Martineau and Larochelle, 1988), the wings are found to dissipate less than one-third as much heat, even if their fleshed portion corresponds to 27% of the pigeon's total cutaneous surface, compared with 7% for the non-feathered areas of the legs and feet (Walsberg and King, 1978). Per unit surface, the wings' dissipating capacity is thus one order of magnitude less than that of the legs and feet. This is perhaps related to the inevitable exposure of the wings during flight while that of the legs and feet can be adjusted from essentially none to full, as observed in pigeons by Biesel and Nachtigall (1987).

While the wings appear to contribute modestly to heat dissipation during flapping flight, their capacity for heat loss at rest is likely to be important, as birds display various forms of thermoregulatory behaviour associated with the wings, such as spreading, drooping and/or fanning (Kahl, 1971; Larochelle *et al.* 1982; Hirth *et al.* 1987; Arad *et al.* 1989). In our conditions, the cooling power of the wings at low windspeeds (0.9 W at 0–12.5 km h^{-1}) corresponds to about 40% of the resting rate of heat production. This value may overestimate the direct contribution of the wings to heat dissipation at rest since hyperthermic pigeons do not fully stretch their wings. In contrast, our experimental system excludes other heat dissipation mechanisms that may benefit from the natural wing postures. Exposing of the underwings also uncovers other surfaces (the flanks and axillae) which may have a capacity for convective and/or evaporative heat loss. Wing drooping or spreading may also create a chimney effect which increases heat loss by natural convection along the legs. Similarly, the slow wing fanning observed in overheated black vultures (Larochelle *et al.* 1982) may augment their heat loss by forced convection at the level of legs and feet. These behaviours should be particularly beneficial to birds which urinate on their legs to increase their thermolytic capacity during heat stress (urohidrosis; Kahl, 1963). Interestingly, many of the Ciconiidae and Cathartidae which have been reported as using this peculiar evaporative mechanism are also known conspicuously to droop, spread or fan their wings when overheated (Kahl, 1971; Larochelle *et al.* 1982).

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