

## THE COOLING POWER OF THE PIGEON HEAD

ROBERT ST-LAURENT AND JACQUES LAROCHELLE\*

*Département de biologie, Université Laval, Québec, Canada G1K 7P4*

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### Summary

Resting pigeons preheated to a stable core temperature of 43.2 °C, which is within the range of body temperatures recorded during flight, were able to cool their body at high rates if their head and upper neck were exposed to an air stream at 23.5 °C. The heat dissipation capacity of the head and neck, estimated from measurements made at a wind speed (100 km h<sup>-1</sup>) corresponding to fast flight, was 9.8 W, or 4.5 times the resting heat production. Since the greater part of this capacity, about 8 W, was attributable to the inner surfaces of the mouth, ram ventilation of the buccal cavity appears to be an important mechanism for increasing evaporative heat loss during flight. Accordingly, wind-assisted mouth cooling should be utilized by resting pigeons, since exposure to a slight breeze (approximately 10 km h<sup>-1</sup>) could augment their dissipating power by an amount equivalent to their resting metabolic rate. It is concluded that beak opening, together with a source of convection other than panting and gular flutter, is required to exploit fully the heat dissipation capacity of the buccopharyngeal mucosa of birds.

### Introduction

Flapping flight requires a very high rate of energy expenditure in birds. Since the mechanical efficiency of flight muscles is less than 25 %, most of the chemical energy used by a flying bird is converted to heat within its body rather than transduced into movement. For example, according to the results of Gessaman and Nagy (1988), homing pigeons (mean body mass 412 g) can travel 320 km in 4.25 h while maintaining an average metabolic rate (44 W) of more than 17 times the preflight level. The ensuing rate of heat production (33 W) could raise their body temperature by 1.4 °C min<sup>-1</sup>. Since pigeons cease flying when their body temperature reaches 3 °C above resting value (Aulie, 1971), powerful avenues of thermal dissipation must exist in order to allow the use of flapping flight for more than a few minutes.

Flying birds have a limited tolerance to dehydration (Biesel and Nachtigall, 1987) and, therefore, most of their heat dissipation during prolonged flights must be achieved through non-evaporative mechanisms (Torre-Bueno, 1978). This condition appears to be relatively easy to satisfy during spring and fall migrations, especially at night where the cool air and the clear sky can act as convective and radiative heat sinks, respectively. In

\*To whom reprint requests should be addressed.

such circumstances, the heat dissipation capacity (HDC) of the external surfaces of the avian body is presumably sufficient to ensure thermal balance during flight. The bare surfaces of the legs and feet (Martineau and Larochelle, 1988), and to a lesser extent the lightly feathered underwings (Craig and Larochelle, 1991), can contribute to this capacity. The role played by the head and neck surfaces is still unknown.

Intensive flight activities can take place under much less favourable conditions, for example in species breeding in warm climates where parental care may require frequent flights during the hottest part of the day. The thermal gradients between the body surfaces and the environment may then be inadequate for heat loss through convection and radiation. Under such conditions, the extent to which flapping flight can be used will depend on the ability to lose heat through evaporation while flying and to rehydrate by drinking between flights.

Little is known about the mechanisms available to birds for increasing their evaporative water loss during flight. The main site is most probably located in the head region and involves the moist surfaces of the mouth cavity. It seems obvious that the boundary layer of air over these small surfaces must be convectively renewed to achieve a high rate of evaporative heat loss. Few species have been studied, and the measurements made with respiratory masks indicate that evaporation can be enhanced during flight primarily by an increase in ventilation (Bernstein, 1987). By contrast, the information obtained during unmasked flights at high ambient temperature excludes ventilation as an important mechanism for increasing evaporative water loss in pigeons (Biesel and Nachtigall, 1987).

One of the earliest signs of heat stress in birds is beak opening. This behaviour is commonly observed in overheated birds whether resting or flying, but it can be more precisely documented during flight in wind-tunnel experiments. For example, beak opening in flying pigeons (Biesel and Nachtigall, 1987) and starlings (*Sturnus vulgaris*; Torre-Bueno, 1976) begins with a slight gaping at 10–15 °C and increases with temperature until full opening is attained at 25–30 °C. Three reasons have been proposed to explain this behaviour. First, beak opening is assumed to facilitate an increase in ventilation for evaporative purposes by reducing airway resistance (Aulie, 1975). Second, by bypassing the nasal cooling system responsible for moisture recovery, it augments the amount of water vapour carried by the exhaled gases (Schmidt-Nielsen *et al.* 1970; Calder and King, 1974). These two reasons do not explain, however, why heat-stressed birds fully open their beak, since only a small gap appears to be necessary to provide an aperture much larger than that of the nasal passages and the aerodynamic drag of a fully open beak is likely to elevate the metabolic cost of flight. Finally, as beak opening increases the direct exposure of the moist surfaces of the mouth to ambient air, it has been suggested as a means for regulating evaporation during flight (Biesel and Nachtigall, 1987).

Since practical reasons preclude direct measurement of the contribution of the external and internal surfaces of the head to heat dissipation in a flying bird, we have used the indirect method that was developed to determine the cooling power of the legs and feet (Martineau and Larochelle, 1988) and of the wings (Craig and Larochelle, 1991) in the pigeon. With this method, we have measured the ability of resting pigeons to cool their

hyperthermic body when their head and neck were selectively exposed to winds covering the range of air speeds attained during flight.

## Materials and methods

### *Animals*

Domestic pigeons (*Columba livia*;  $400 \pm 29$  g; mean  $\pm$  S.D.,  $N=4$ ) were purchased from a commercial supplier and kept at approximately  $22^\circ\text{C}$  in cages measuring  $60\text{ cm} \times 50\text{ cm} \times 55\text{ cm}$ . They had free access to water and mixed grains and were given a multivitamin pill once a month. The birds were gradually accustomed to the experimental apparatus and were never subjected to any procedure that would cause them to try to flee.

### *The heating mould*

During the experiments, the body of the bird, except for the head and neck, remained enclosed within a computer-controlled heating mould (Fig. 1). This mould was similar to the one used by Craig and Larochelle (1991) and was fitted under a small wind tunnel (described by Martineau and Larochelle, 1988) so as to allow exposure of the head and upper neck to a controlled air current. An adequate seal around the pigeon's neck was obtained by drawing the head of the bird through four layers of Parafilm covering the neck hole of the mould. The absence of wind penetration was verified by monitoring the temperature within the mould just below the seal. Temperature at this location was unaffected by the wind but it closely followed the bird's body temperature.

### *Experimental strategy*

Each experiment consisted of three phases (preheating, stabilization and cooling), defined by corresponding changes in the body temperature ( $T_{\text{int}}$ ) of the bird (Fig. 2).

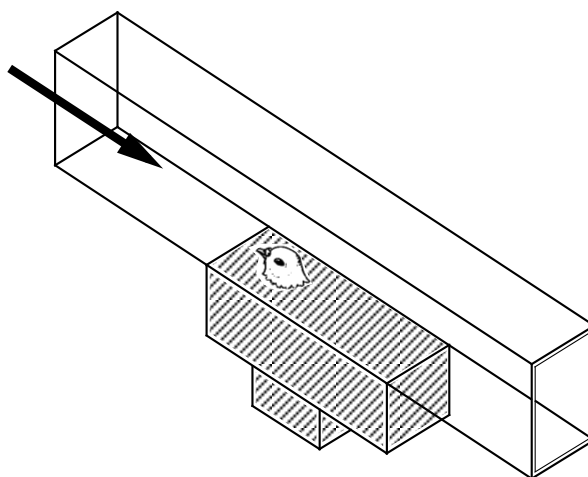


Fig. 1. A diagonal overview of the working section of the wind tunnel. Only the head and upper neck were exposed to wind (arrow), the rest of the pigeon's body being enclosed in a thermostatted mould.

During the preheating phase, the mould served to induce heat dissipation needs similar to those that would occur in flight by raising  $T_{\text{int}}$  to a value ( $43.2 \pm 0.3$  °C) observed in flying pigeons (Hart and Roy, 1967; Aulie, 1971; Butler *et al.* 1977; Hirth *et al.* 1987). To this end, the mould thermostat was set to 5–7 °C above  $T_{\text{int}}$  and the wind tunnel was switched off, resulting in an increase of  $T_{\text{int}}$  at a rate of about  $0.1$  °C  $\text{min}^{-1}$ .

During the following phases, the mould served to minimize heat dissipation through the body surfaces, other than those under study, by keeping their temperature close to  $T_{\text{int}}$  and by minimizing loss of humidity to ambient air. During the stabilization phase, the mould thermostat was reset to the bird's  $T_{\text{int}}$  or slightly above, so as to keep  $T_{\text{int}}$  constant in the absence of wind (Fig. 2). The cooling phase was initiated by switching the wind tunnel on and programming the mould temperature to follow  $T_{\text{int}}$ .

#### *Determination of heat loss from the head and neck*

In our conditions, the birds could only gain heat through metabolic production and exchange with the heating mould. Since they could lose heat exclusively from the head and upper neck, their heat balance can be described as follows:

$$\dot{H}_{\text{head}} = \dot{H}_{\text{met}} + \dot{H}_{\text{mould}} + \dot{H}_{\text{stor}}. \quad (1)$$

In this equation,  $\dot{H}_{\text{head}}$  stands for the rate of heat loss through the head and neck surfaces,  $\dot{H}_{\text{met}}$  for the rate of metabolic heat production,  $\dot{H}_{\text{mould}}$  for the rate of heat gain from the mould, and  $\dot{H}_{\text{stor}}$  for the rate of change in the body heat content.

During the preheating phase, the sum of  $\dot{H}_{\text{mould}}$  and  $\dot{H}_{\text{met}}$  exceeded  $\dot{H}_{\text{head}}$ , resulting in an increase of  $\dot{H}_{\text{stor}}$ . To initiate the stabilization phase, the mould temperature and the bird's  $T_{\text{int}}$  were kept essentially constant and equal, reducing  $\dot{H}_{\text{mould}}$  and  $\dot{H}_{\text{stor}}$  to negligible levels and making  $\dot{H}_{\text{head}}$  essentially equal to  $\dot{H}_{\text{met}}$ . The cooling phase started with an exposure of the head and neck to wind, which increased  $\dot{H}_{\text{head}}$  and produced a net

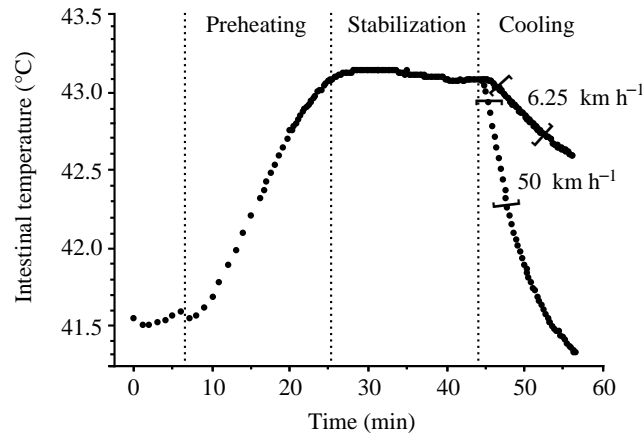


Fig. 2. Time course of the body temperature of a pigeon during the three phases of a typical experiment. During the cooling phase, the head and upper neck were exposed to a  $6.25$  or  $50$   $\text{km h}^{-1}$  wind at  $23.5 \pm 0.5$  °C. The linear portions of the curves, which were used to calculate the cooling rates, are indicated between brackets.

cooling of the body ( $\dot{H}_{\text{stor}} < 0$ ). The wind-induced cooling power was then calculated from the cooling rate ( $\Delta T_{\text{int}}/\Delta t$ ) using the following equation:

$$\dot{H}_{\text{stor}} = m \times c_p \times \Delta T_{\text{int}}/\Delta t, \quad (2)$$

where  $m$  is the body mass and  $c_p$  is the specific heat of the body ( $3.47 \text{ J g}^{-1} \text{ }^\circ\text{C}^{-1}$ ; Hart, 1951). The rate of change of  $T_{\text{int}}$  was obtained from the linear portion ( $r^2 > 0.99$  over a minimum of 3 min) of the body cooling curve.

#### *Temperature measurements and control*

Body temperature ( $T_{\text{int}}$ ) was measured with a thermistor (YSI, 402) inserted cloacally in the pigeon's intestine, to a total depth of approximately 6 cm. The thermistor resistance was read with a high-precision scanning multimeter (Keithley Instruments, 199) interfaced to a computer for data treatment. The temperature of the internal surfaces of the heating mould was read with thermistors (YSI, 409A) and controlled by a computer within  $0.3 \text{ }^\circ\text{C}$  of the desired value. 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  $0.05 \text{ }^\circ\text{C}$ .

#### *Assessment of the contribution of the various surfaces*

To estimate the contribution of the various surfaces to the total wind-induced cooling power, experiments were devised to alter the contact of these surfaces with the moving air. The wind-exposed fraction of the neck area, which was roughly 25 % at freely adopted posture, was increased two- to threefold by raising the head approximately 2 cm using a small U-shaped metal support inserted from behind, just below the lower jaw. A six- to eightfold decrease of the same area was obtained by limiting neck protrusion into the wind tunnel to a minimal value with an aureole-like support made from metal wire.

To reduce wind penetration into the buccal cavity, the beak was taped partly closed using a narrow strip (3 mm) of thin tape, leaving a 1–2 mm slit that allowed the bird to breathe normally from the sides of the mouth. In other experiments, we used a ventilated respiratory mask ( $1 \text{ l min}^{-1}$ ) carefully tailored to cover only the beak and ceræ.

When required, the eyes were covered with self-adhering felt pads (Scholl, Corn Removers), and the nasal orifices, the external upper mandible and the ceræ with dental wax. Finally, the external surfaces of the head and neck were covered by drawing the finger of a surgical glove over the beak. The tip of the finger had been punctured so as to leave only the surfaces of the bird's mandibles and ceræ directly exposed to the wind.

Data were analyzed by a one-way analysis of variance (ANOVA) followed by the Student–Neuman–Keuls *a posteriori* multiple comparisons test.

### **Results**

When only the head and the upper part (approximately 25 %) of the neck were available as heat dissipating sites, our preheated pigeons appeared to be unable in the absence of wind to lower their body temperature towards normal resting values, even while engaged in vigorous gular flutter and panting. Since their body cooling rate

remained close to zero ( $-0.005 \pm 0.002^\circ\text{C min}^{-1}$ ) and since the mould covering their trunk, wings and legs was essentially isothermic to their body core, it can be assumed that the birds were then dissipating heat from their head and upper neck at a rate approximately equivalent to their metabolic production, or 2.2 W as measured under similar conditions (Martineau and Larochelle, 1988).

*The effect of wind on the cooling power of the head and neck*

Wind exposure of the head and upper neck greatly enhanced the pigeon's ability to dissipate heat (Figs 2 and 3). With wind speeds of 75 and 100 km h<sup>-1</sup>, that is in the range of speeds used by homing pigeons (Gessaman and Nagy, 1988), panting and gular flutter ceased within 15 s but the beak remained partly open, leaving a gap of 1–2 mm. Over the following minutes, body cooling rates of up to  $0.34 \pm 0.06^\circ\text{C min}^{-1}$  were observed at a wind speed of 100 km h<sup>-1</sup>, indicating that the air movement had given to the head and upper neck a cooling power of  $7.6 \pm 1.0$  W. As the dissipating power of a heat-generating body capable of reducing its temperature equals this body's cooling power plus its calorogenic power (equation 2), we estimated the HDC of the pigeon head and upper neck to be 9.8 W in air at 23.5 °C, or 4.5 times the resting heat production.

At winds of 50 km h<sup>-1</sup> and lower, open-mouth panting continued for 2–10 min, depending on the air speed. The effect of wind remained important, allowing the birds to increase the cooling power of their head and neck by  $1.7 \pm 0.4$  and  $2.4 \pm 0.4$  W at 6.25 and 12.5 km h<sup>-1</sup>, respectively. Even at the highest wind speeds, the pigeons had apparently no difficulty in controlling their head position for visual purposes. They sometimes kept their head at an angle (up to 90°) to the air current, without noticeable effects on their cooling rate.

*The contribution of the various surfaces of the head and neck*

Several observations indicate that the wind-dependent cooling power of the head is much more important than that of the neck. For example, extensive changes in the neck

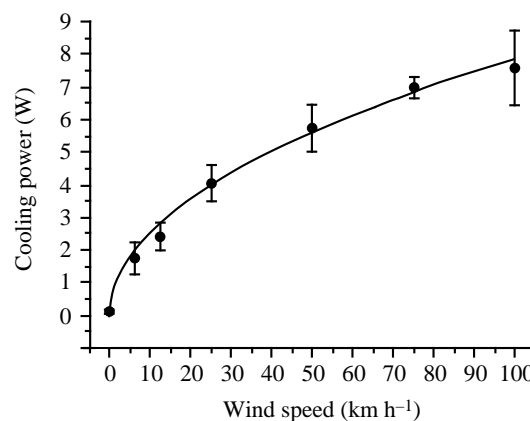


Fig. 3. The effect of wind speed (at  $23.5 \pm 0.5^\circ\text{C}$ ) on the cooling power of the head and upper neck in pigeons whose body had been preheated to  $43.2 \pm 0.3^\circ\text{C}$ . Results are expressed as means  $\pm$  S.D. for 5–9 experiments using three birds for each point. The curve corresponds to a best-fitting square root function ( $y = 0.78x^{0.5}$ ,  $r^2 = 0.99$ ).

area exposed to wind did not result in proportional changes in cooling power (Table 1). Conversely, limiting the contact between the air stream and some surfaces of the head, particularly those of the mouth cavity, had drastic effects on whole-body cooling rates. Restricting beak opening to a 1–2 mm slit, as birds do spontaneously at high wind speeds, reduced the rate of heat loss from the head and neck by nearly 50 % at low wind speed. Furthermore, fitting the bird with a ventilated respiratory mask which covered only the beak and cerae reduced the wind cooling effect by almost 80 %. In contrast, shielding the surfaces of the upper mandible, cerae and nares, or the ocular areas, with windproof material changed the wind-induced cooling power by less than 20 %, as did shielding all surfaces of the head and neck other than those of the mandibles and cerae.

These results must, however, be interpreted with caution. Enclosing the trunk of the birds in the heating mould, changing the neck extension and/or fitting a respiratory mask may interfere with the efficiency of gular flutter and panting. In our conditions, however, this effect should be minor, since birds kept their capacity to dissipate heat through their head during the stabilization phase at a rate near that of metabolic heat production. Shielding the beak and cerae with a respiratory mask may deviate the air flow and reduce the heat loss by the downstream surfaces of the head, in which case the calculated contribution (78 %) of the mouth cavity to the whole-body cooling power would be overestimated. Such an error cannot be very important since shielding the feathered surfaces of the head and neck with a tightly fitting plastic envelope that was unlikely to disturb the upstream air flow around the beak confirmed that these surfaces contribute modestly (15 %) to the whole-body cooling power. Our data are thus consistent with an estimate of about 80 %, or 6 W, for the fraction of the maximum cooling power of the head and neck that is due to wind penetration through the open beak. Taking into consideration the dissipation of the metabolic heat (see above), we evaluate the HDC of the mouth cavity to be about 8 W.

During all the measurements, the inner surfaces of the mouth, which appeared to be

Table 1. *The effect of various treatments on relative heat loss (%) by the head and neck in preheated pigeons, at two wind speeds ( $T_{air} = 23.5 \pm 0.5$  °C)*

Treatment	Wind speed (km h <sup>-1</sup> )	
	6.25	50
None (control groups)	100 (7)	100 (5–7)
Neck exposure increased (two- to threefold)	–	82±14 (6)
Neck exposure decreased (six- to eightfold)	–	98±17 (5)
Restricted beak opening	52±13 (9)*	88±18 (9)
Respiratory mask fitted	–	22±7 (9)*
Feathered area covered	–	85±21 (5)
Eyes covered	82±29 (8)	93±19 (9)
Nares, beak and cerae covered	–	108±14 (7)

Results are expressed as means ± S.D. followed by the total number of measurements in parentheses.

Three birds were normally used for each treatment. Asterisks indicate the significant differences ( $P < 0.05$ ) with respect to the appropriate control values.

engorged with blood, remained copiously moist, indicating a possible contribution to the bird's capacity for evaporative water loss.

### Discussion

The present results have important implications with respect to current models of temperature regulation in birds. They demonstrate that beak opening does more than just reduce the airway resistance or bypass the nasal recovery of humidity during expiration. They show that the buccopharyngeal mucosa, an area well-provided with the vascular structures found in tissues specialized in heat exchange (Midtgård, 1984), has the potential to dissipate heat at a rate much higher than that observed when panting and/or gular flutter are the only sources of convection over its surface. Full exploitation of this potential at 23.5 °C apparently depends on complete beak opening, except in the range of wind speeds corresponding to fast flight (75–100 km h<sup>-1</sup>). At these speeds, the wind-assisted ventilation of buccal surfaces is probably sufficient to allow the bird to close its beak partly and thus to reduce aerodynamic drag. The external air current may then supersede the one created by panting and/or gular flutter and lead to a rapid cessation of these energy-consuming and heat-generating activities. This cessation may well be explained by enhanced brain cooling resulting from increased cooling of the mouth and other surfaces of the head.

This study also shows that the sensitivity of birds to ambient convection is markedly increased by beak opening, and this should be taken into consideration whenever thermoregulatory behaviour and heat dissipation are to be assessed in the wild as well as in metabolic chambers. For example, the rates of respiratory heat loss measured with a mask can affect estimates of the effective rates under conditions where the amount of ambient air movement around the mouth would be smaller (e.g. at rest in calm air) or greater (e.g. during swift flight) than that prevailing inside the mask. The reduction of evaporative heat loss due to wearing a mask in flying birds should, however, be less striking than that observed in this study, since ventilation of both the respiratory tract and the mask should then be higher than at rest.

We do not think that the validity of our main conclusions is limited by the fact that experimental birds were restrained in a mould isothermal to their body, rather than resting or flying freely. There is no reason to believe that our results overestimate the HDC of the head surfaces, because other sites normally involved in heat dissipation were not functioning. Before engaging in heat-producing and water-consuming mechanisms, such as gular flutter and panting, hyperthermic birds can be expected to vasodilate all their cutaneous dissipation sites fully. There is no evidence that birds can sense local heat flow and focus their blood to the most effective sites. Under conditions leading to maximum vasodilation, all dissipation sites, which are connected in parallel to the arterial pool, should then have the potential to reach their maximum HDC simultaneously. We can therefore expect that the HDC of the head surfaces in heat-stressed birds would be, at a given body temperature, unchanged by exposure of the skin of the trunk and legs. What would be changed in that case would be the rate at which the birds can cool their body.



*Wind-speed-dependence of the cooling power of the head and neck*

Interestingly, the influence of wind on the cooling power of the head and upper neck is very well described by a function of the square root of the wind speed (Fig. 3). Within the range of Reynolds numbers (2700–44 000) corresponding to our conditions, convective heat losses limited by the thermal resistance of the boundary layer are expected to depend on wind speed to a power 0.5–0.6 in the case of smooth cylinders and spheres (Kreith and Black, 1980). Our results suggest that changes in beak opening and head orientation have little effect on the relationship between wind speed and heat dissipation through the head and neck of pigeons. This hypothesis is further supported by a study of convective heat loss from simple models of animal shapes, namely smooth cylinders, arcs and cones having a relevant diameter of 2.5 cm (Wathen *et al.* 1974). It was found that the thermal dissipation of the models was little affected by geometry, amount of closure and orientation with respect to wind.

A 0.5 power relationship between whole-body heat loss and wind speed also fits the data obtained from several avian species (see Goldstein, 1983). However, in many cases, a higher exponent is required, presumably because penetration and/or mechanical disruption of the plumage by the moving air increases with wind speed (see Bakken, 1991).

*Possible contribution of the head to thermoregulation during flight*

Mouth opening provides birds with a ram-ventilated site capable of greatly improving their ability to fly under heat-stressing conditions. In the pigeon, the mouth, together with the other surfaces of the head, has an HDC that corresponds to 30–50% of the heat production during flight. The lower estimate would apply to high-speed flights (approximately  $75 \text{ km h}^{-1}$ ), where heat production would be about 33 W (see Introduction), while the higher value could be associated with the heat produced (about 19 W) during flights made at minimum power speed (approximately  $35 \text{ km h}^{-1}$ ; calculated by Martineau and Larochelle, 1988).

As the greater part of the HDC of the head and neck is correlated to the exposure of moist surfaces in the buccal cavity, wind-assisted mouth cooling is likely to be an important mechanism for increasing evaporative heat loss during flight. The cooling power of other moist surfaces of the head, such as those of the eyes and nasal cavity, though significant for the regulation of brain temperature in pigeons (Bernstein *et al.* 1979), was not important at the whole-body level, as suggested previously (Pinshow *et al.* 1982).

The wind-induced cooling power of the mouth region in pigeons is comparable to that estimated for legs and feet when they are trailed (Martineau and Larochelle, 1988), a behaviour also displayed by many birds in reaction to heat stress when flying in the wild (Frost and Siegfried, 1975; Bryant, 1983) and in wind tunnels (Torre-Bueno, 1976; Biesel and Nachtigall, 1987). The buccal site offers several advantages, since it is better located for brain cooling and less likely to increase aerodynamic drag than the trailing legs and feet. The aerodynamic factor should be particularly meaningful, given the high speeds ( $75\text{--}90 \text{ km h}^{-1}$ ) commonly sustained by homing pigeons (Gessaman and Nagy, 1988) and since the beak need gape only a small amount to utilize the HDC of the mouth.

Because of its potential for evaporation, the buccal mechanism can also be expected to retain a heat dissipation capacity at high air temperatures, whereas that of the dry surfaces of the legs and feet should decrease in proportion to the body-to-air temperature gradient. However, the loss of water associated with mouth opening should restrict its use to flights of limited duration.

Compared with a panting-like reaction to enhance evaporation, wind-assisted mouth cooling is unlikely to cause pulmonary hyperventilation and thus to disturb acid–base balance. This should be particularly important for birds such as the pigeon, in which breathing and flapping are synchronized (Tomlinson and McKinnon, 1957), so that a ventilation increase would imply a larger tidal volume and a higher risk of hyperventilation.

*Possible contribution of the head to thermoregulation during rest*

Resting birds should also take advantage of wind-assisted mouth cooling. For example, just by opening their beak into a wind as low as  $10 \text{ km h}^{-1}$ , pigeons could increase their HDC by an amount equivalent to their resting rate of heat production. This suggests that exposure to wind may be an important thermoregulatory behaviour during heat stress, by delaying the use of muscle-driven gular flutter and panting or enhancing their effect. Birds could, for example, profit from wind-assisted mouth cooling to shorten the cooling periods between bouts of intense activity or to stay cool when incubating eggs in a hot climate (Thomas and Robin, 1977).

As the buccal surfaces are kept moist and well-perfused in most vertebrates, it can be expected that many species make use of wind-assisted mouth cooling. Likely candidates are those employing mouth gaping, such as alligators, to reduce the rate of heat gain through the head (Spotila *et al.* 1977). However, animals with buccal surfaces well-adapted for whole-body cooling, such as panting homeotherms, are probably the most efficient users of this mechanism, and particularly if, like overheated dogs (Krönert *et al.* 1980), they conspicuously expose their mouth cavity and tongue to ambient convection.

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