

Pigeon flight in a wind tunnel*

III. Regulation of body temperature

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Summary. Core temperature T_c , breast temperature T_{s-br} and leg temperature T_{s-l} were measured simultaneously in pigeons during rest and flight in a wind tunnel, using thermistors.

Mean T_c at rest is 39.8 ± 0.7 °C and is independent of ambient temperature T_a (10–30 °C). In the first minutes of flight, T_c increases to 1.5–3.0 °C above resting level and remains at this higher level. This hyperthermia increases with T_a ($v = \text{const.}$). It is \pm constant in the low T_a range (10.6–13.9 °C) at flight speeds v ranging from 10–18 m s^{-1} and normal body mass, but increases with v and elevated body mass in the high T_a range (23.7–28.8 °C).

T_{s-l} is adapted to T_a at rest and increases in flight up to 3–4 °C below T_c . This increase in T_{s-l} is linear to T_a .

T_{s-br} is always lower than T_c , in extreme cases reaching resting T_c in flight.

Hart and Roy (1967) recorded T_c of 44.5 °C at T_a ranging from 4–30 °C during free flights by means of telemetry and both Aulie (1971) and Butler et al. (1977) found core temperatures of 43.3–44.1 °C at T_a above 25 °C in wind tunnel flights. These data were taken during flights of 10 min maximum duration or even at much shorter times because the birds were not able to fly longer. Flying for more than 30 min at $0 \leq T_a \leq 28$ °C, starlings maintained mean core temperatures of 44.0 or 42.7 °C (two birds), but were reluctant to fly above 28 °C and did not attain steady-state (max. $T_c = 46.8$ °C) when forced to fly at these temperatures. Only the white-necked raven (Hudson and Bernstein 1981) and the budgerigar (Aulie 1971) were able to achieve a steady-state core temperature at high ambient temperatures ($T_c = 43.5$ –44.8 °C or 42.1 °C, respectively).

In all cases during flight the birds attained core temperatures of 2–4 °C above resting levels, thus sometimes undergoing an extreme hyperthermia which may be only slightly below lethal temperatures. This paper is concerned with body temperatures (core, leg, and breast temperatures) in pigeons under the more natural conditions of real long time flights (up to 3 h) in a wind tunnel.

Materials and methods

Experimental animals and wind tunnel. Three well trained Grippler pigeons (body mass 320–350 g) were used. Details of pigeon rearing and feeding, of the training method and the aptitude of this pigeon race for wind tunnel flights as well as a detailed description of the wind tunnel, are given in Rothe and Nachtigall (1987).

Experimental methods. Body temperatures (core temperature, T_c , breast temperature T_{s-br} , leg temperature T_{s-l}) were measured using Siemens M 85 thermistor. To determine T_c a thermistor was inserted approximately 10 cm into the colon and fixed by a 3-fold layer of adhesive tape over the cloaca. T_{s-l}

Introduction

Bird flight involves a more than 10-fold increase in metabolic heat production over the resting level. This requires a corresponding increase in heat loss from the body in order to keep body temperature constant. Although there have been many studies on thermoregulation in resting birds, not very much is known about body temperatures during flight. Pearson (1964) reported core temperatures (T_c) in the range between 41.5–43.8 °C at ambient temperatures between 13 and 26 °C in pigeons shot immediately after landing. Using the same species,

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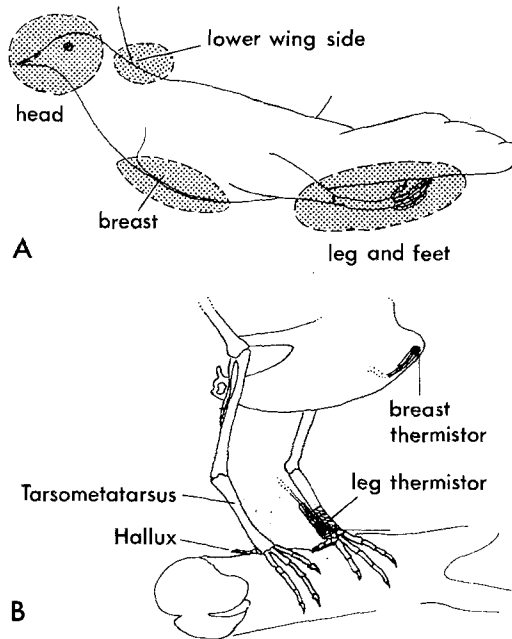


Fig. 1. **A** Regions of maximum heat loss in the pigeon, drawn from infrared photos. **B** Points of attachment of surface (breast, leg) temperature thermistors

was measured with a thermistor fixed with tape onto the tarsometatarsus of the leg and T_{s-br} by attaching a thermistor directly onto the skin of the breast beside the sternum without disturbing the plumage (Fig. 1B). Beside these 3 areas of heat production or heat loss, the bird's head and the lower sides of its wings are of interest as can be demonstrated in infrared photos of flying birds (Fig. 1A). However, T_s in these regions was not measured in order to avoid disturbing the bird's flight.

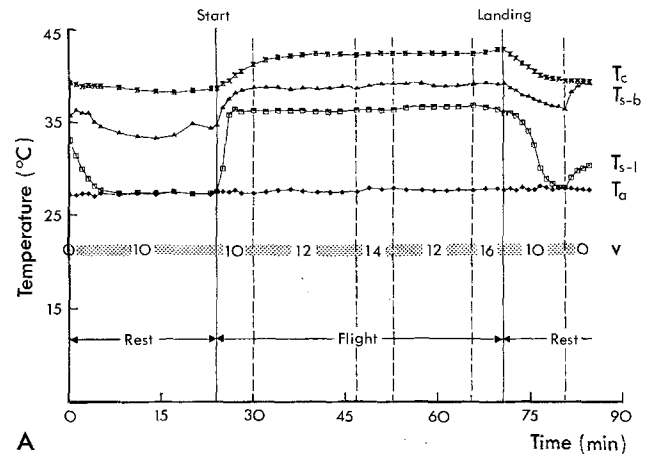
The leads from each thermistor were collected at a 'central unit' attached to the bird's back and from which only one flexible wire (containing 6 leads) led from the test section of the wind tunnel to a multiplexer. Thus, all 3 body temperatures could be recorded simultaneously with T_a by means of a bridge amplifier and a Siemens Kompensograph III pen recorder. The thermistors were calibrated to an accuracy of $\pm 0.1^\circ\text{C}$ using a mercury thermometer.

The additional mass of the measuring devices to be carried by the bird in flight was ~ 4.0 g, or $\sim 1\%$ of the body mass, which is assumed to have a negligible influence on the bird's behaviour.

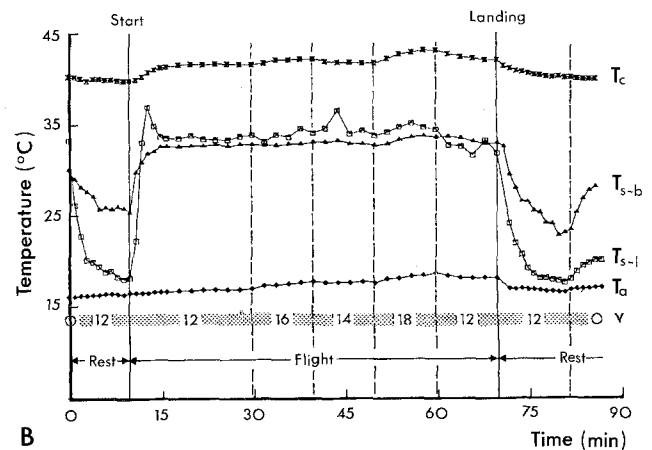
Ambient temperature could be influenced only by heating. It lay between 10.5 and 29.1°C and was measured within the test section of the wind tunnel (Siemens thermistor M 867). During a flight experiment, the ambient temperature can increase up to $\sim 3^\circ\text{C}$, due to the heat generated by the fan (Fig. 2).

Control measurements. It was found that T_c was influenced by the airstream during rest when the thermistor was not in the correct position. Therefore, in each experiment resting T_c was measured with and without wind before and after flight (Fig. 2) to control the position of the thermistor and thus to assure that real deep body temperature had been measured.

To test whether the surface temperature measured on the bird's leg was influenced by the airstream and ambient temperature, a plastic tube with the same diameter as a pigeon's leg



A



B

Fig. 2A, B. Time plots of the core temperature T_c , breast temperature T_{s-br} , leg temperature T_{s-l} of the pigeon GWH and ambient temperature T_a before, during and after flight in a wind tunnel. Flight speed v varied as indicated in m s^{-1} . **A** $T_a = 27.4^\circ\text{C}$. **B** $T_a = 16.1^\circ\text{C}$

and carrying a thermistor attached in the same way (Fig. 1B) was perfused with water of 42°C . By measuring the surface temperature of the tube in the airstream of the wind tunnel, it was found that it differed from the inner (water) temperature. The difference increased mainly with increasing wind speed v and little with decreasing T_a , e.g. at $v = 12 \text{ m s}^{-1}$ T_{s-l} may be corrected by adding 2.7°C at $T_a = 13^\circ\text{C}$ and 2.5°C at $T_a = 23^\circ\text{C}$. These correction values were obtained at complete exposure to the airstream, a state only observed at high T_a in bird's legs (Biesel and Nachtigall 1987). Thus we obtained the maximum deviation; the deviation may actually be lower at lower T_a due to the legs changing their position according to the ambient temperature.

In a single experiment, with a 75-min flight, and by comparing the temperatures measured on the skin with those measured by a thermistor implanted under the skin, it was shown that sub- and supracutaneous temperatures on the bird's breast are very similar.

Experimental procedure. The test bird was weighed, prepared with the thermistors as described and placed in the test section of the wind tunnel. Resting temperature of the bird sitting on

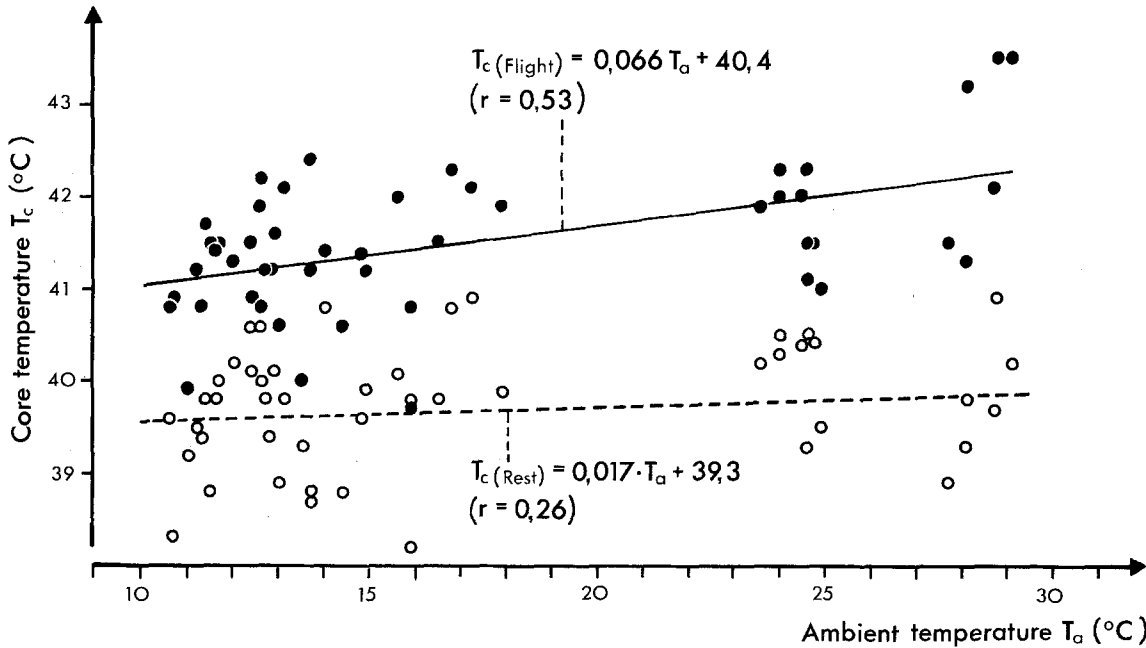


Fig. 3. Mean core temperature T_c of pigeons during rest and flight ($v=12 \text{ m s}^{-1}$) as a function of ambient temperature T_a . T_c in rest is not significantly correlated with T_a . T_c in flight increases linearly with T_a ($P \leq 0.05$)

a perch in darkness was measured, at first without wind, then with the wind turned on at a speed of 10 or 12 m s^{-1} . The resting temperature was recorded until T_c became constant and $T_{s-1} \approx T_a$. Flight was then started by turning on the light and removing the perch. A single flight consists of several flight stages, each lasting up to 30 min and with a wind speed altered in steps of 2 m s^{-1} . Wind speed was changed only when temperatures had reached steady-state values. The position of the thermistors was controlled at the end of a flight by measuring the resting temperature at the same wind speed set before flight began (Fig. 2).

Results

Flight behaviour

No differences in flight behaviour due to the instrumentation could be observed. The pigeons showed their typical flight behaviour i.e. flapping flight interrupted by gliding phases in the speed range between 10–14 m s^{-1} and permanent flapping flight above 14 m s^{-1} . At high T_a ($> 24 \text{ }^\circ\text{C}$) pigeons with high body mass and/or flying at high wind speeds became increasingly reluctant to fly and tended to land. On such occasions, panting and spreading of the wings for cooling after landing were sometimes observed. Flights within the high T_a range were usually shorter (24–29.1 $^\circ\text{C}$; 32.1 min \pm 8.7 SD; $N=11$) than within the lower T_a range (10.6–16.5 $^\circ\text{C}$; 47.6 min \pm 11.2 SD; $N=22$).

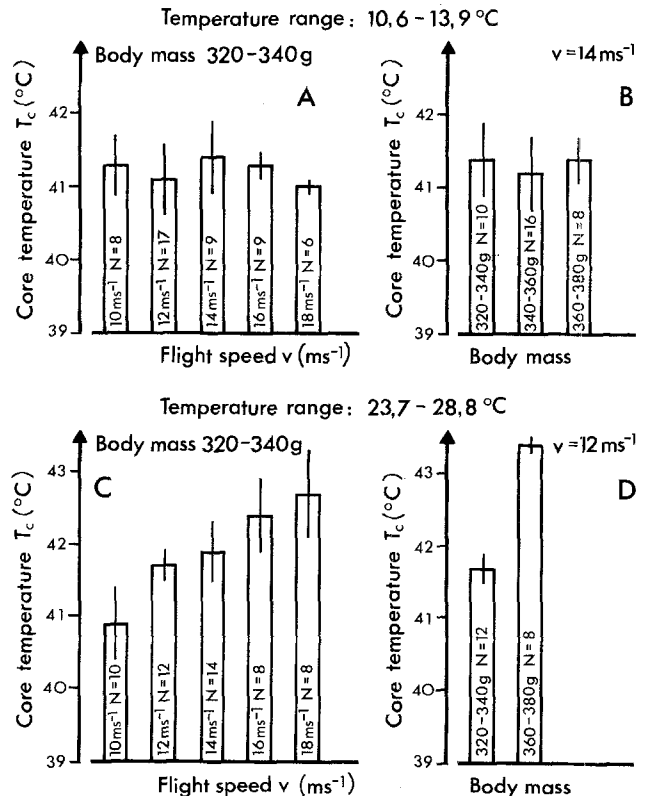


Fig. 4A–D. Mean core temperature T_c of pigeons during flight in a wind tunnel. At low ambient temperatures (10.6–13.9 $^\circ\text{C}$) mean T_c is independent of flight speed (A) and body mass (B). At high ambient temperatures (23.7–28.8 $^\circ\text{C}$) mean T_c increases with flight speed (C) and body mass (D). Bars: SD

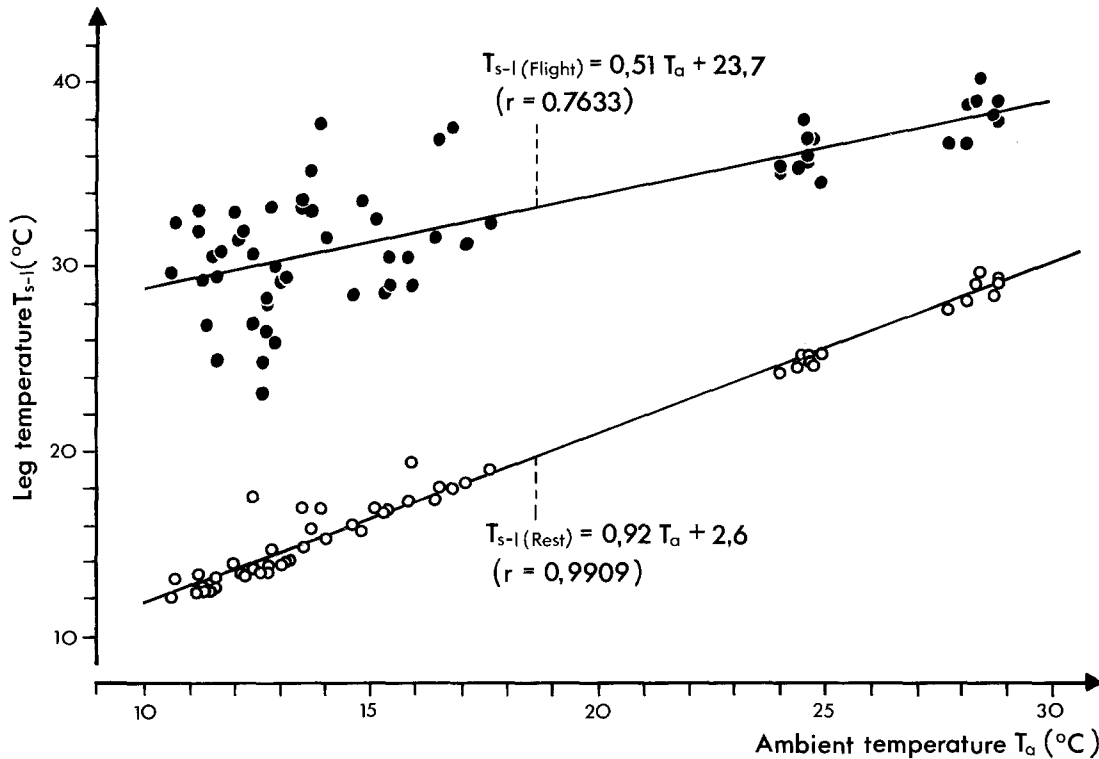


Fig. 5. Mean leg temperature T_{s-1} of pigeons during rest (but wind turned on) and flight in a wind tunnel ($v=12 \text{ m s}^{-1}$). T_{s-1} during rest adapts to T_a . T_{s-1} in flight is elevated and increases linearly with increasing T_a as indicated

Thermoregulatory behaviour, such as opening of the bill and exposure of the legs during flight, was observed as described in Biesel and Nachtigall (1987).

Body temperatures

Figure 2 presents time plots of the core temperature T_c , the breast temperature T_{s-br} , the leg temperature T_{s-1} and the ambient temperature T_a during two flight experiments with the pigeon GWH (including pre- and post-flight resting periods) at high ($27.4 \text{ }^\circ\text{C}$) and low ($16.1 \text{ }^\circ\text{C}$) T_a .

T_a rises slightly during the experiments due to the heat generated by the fan (maximum increase $\sim 2.5 \text{ }^\circ\text{C}$).

Pre-flight resting periods: T_c remained more or less constant ($\sim 40 \text{ }^\circ\text{C}$) independent of T_a , whereas T_{s-1} and T_{s-br} descend due to the cooling effect of the airstream (wind at 10 or 12 m s^{-1}). T_{s-1} approached T_a , whereas T_{s-br} declined only slightly.

Flight: All temperatures rose when flight started. T_c rose a few degrees ($1.5 \text{ }^\circ\text{C}$ or $3.0 \text{ }^\circ\text{C}$) and reached a new steady-state level after 6 or 10 min of flight. Raising or lowering of the flight speed was always followed by small increases or decreases of T_c . T_{s-br} and T_{s-1} showed increases

in the range between 6 to $17 \text{ }^\circ\text{C}$ each coming to a new \pm constant level. Changes in flight speed were followed by slight changes in T_{s-br} and T_{s-1} .

Post-flight-period: All temperatures declined more or less to pre-flight values. An increase in T_{s-br} and T_{s-1} could be observed when the wind was turned off.

Core temperature T_c . Resting T_c had a mean value of $39.8 \text{ }^\circ\text{C}$ ($\pm 0.7 \text{ SD}$, $N=48$). In the T_a range studied, no statistically significant ($P \leq 0.05$) correlation between T_c and T_a could be found (Fig. 3). Thus T_c is independent of T_a and not influenced by the cooling effect of the airstream in the wind tunnel.

In flight, pigeons raise their T_c as shown in Figs. 2 and 3. At a flight speed v of 12 m s^{-1} , T_c ranges between $39.7 \text{ }^\circ\text{C}$ and $43.3 \text{ }^\circ\text{C}$ (minimum and maximum record). T_c in flight increases with T_a . In the T_a range studied, the increase is significant ($P \leq 0.05$) and can be approximated by a linear function (Fig. 3). Increasing T_c in flight leads to an increasing difference to the resting T_c (hyperthermia) from a mean value of $1.4 \text{ }^\circ\text{C}$ at $T_a = 10 \text{ }^\circ\text{C}$ to $2.3 \text{ }^\circ\text{C}$ at $T_a = 30 \text{ }^\circ\text{C}$.

Mean T_c in flight is independent of the flight speed v (10 – 18 m s^{-1}) in the low T_a range between 10.6 – $13.9 \text{ }^\circ\text{C}$ (no significant correlation between T_c

and v), whereas it increases with v in the high (23.7–29.1 °C) T_a range (Fig. 4A, C). The positive correlation is significant ($P \leq 0.05$) and can be described by the linear function $T_c = 0.22 v + 38.8$. Furthermore T_c in flight is influenced by the body mass (artificially increased by feeding), but only in the high T_a range (Fig. 4B, D).

Leg temperature. T_{s-1} . During rest, T_{s-1} approaches T_a within the whole T_a range tested as indicated by the slope (≈ 1) of the regression line (Fig. 5). In flight T_{s-1} lies between 23.1 °C and 40.3 °C, increasing with T_a . The relationship can be described by a linear function (Fig. 5). The values plotted have not been corrected for the cooling effect of the airstream in flight.

Discussion

Core temperature

The resting core temperature of our pigeons was 39.8 ± 0.7 °C, i.e. in the range of T_c 's measured by Bernstein (1974) on the same bird species, and by Torre-Bueno (1976) on the starling, but clearly below the values found by Hart and Roy (1967), Aulie (1971) and Butler et al. (1977) in pigeons.

The T_c 's of pigeons obtained during flight by the same authors, ranged from 43.3–44.5 °C and were clearly higher too. All those measurements were made during flights of less than 10 min and in some cases less than 2 min, because the birds refused to fly longer. Upon landing, the typical signs of overheating such as panting, gular flutter and spreading of the wings were reported (Butler et al. 1977). Other bird species such as the starling (Torre-Bueno 1976) and the white-necked raven (Hudson and Bernstein 1981), which performed much longer flights underwent the same extreme hyperthermia up to a T_c of 46.8 °C at T_a above 28 °C in the starling. In these cases no steady-state core temperature could be observed and the birds were unwilling to fly and had to be chased to remain in the air.

According to our experiences with pigeons, these symptoms of reluctance to fly and overheating can be referred to insufficient flight training and/or to using birds less suitable for wind tunnel flights (Rothe and Nachtigall 1987). In our pigeons which were able to fly non-stop for as long as 3 h under optimum conditions ($v \approx 12 \text{ m s}^{-1}$; normal body mass), only a slight increase of T_c in flight in the T_a range from 10 to 30 °C could be observed (Fig. 3). 'Unphysiologically' high T_c and symptoms of overheating occurred only in the high temperature range with additional stress related to

higher flight speed (Fig. 4C) and/or 'artificially' elevated body mass e.g. if the birds flew with a full crop (Fig. 4D). Even then, the core temperatures (maximum value 43.5 °C) do not attain those found by other authors in pigeons and other bird species.

Nevertheless, in this as in all other studies of T_c in flight, a clear rise from rest to flight was found. T_c becomes more or less constant in a broad range of T_a (0–28 °C, Torre-Bueno 1976; 14–22 °C, Hudson and Bernstein 1981), or shows slight increases (1.5–2.5 °C) with temperature as in his study between 10–30 °C (Fig. 3).

A possible function of this hyperthermia during flight is heat storage. As has been shown by Torre-Bueno (1976) and Biesel and Nachtigall (1987) heat storage could be an important means for thermoregulation only during short flights and thus cannot explain the elevated T_c kept during long distance flights.

On the other hand, elevated T_c may influence the evaporative heat loss (Biesel and Nachtigall (1987)). It increases the non-evaporative heat flow by increasing the temperature gradient between the bird and the environment. Thus the rise in T_c could be a thermoregulatory adjustment to the heat load during flight. Nevertheless, it is questionable whether it is used entirely or mainly as a means for increasing heat loss, since in a broad T_a range T_c is independent of T_a . Even at temperatures below 0 °C at which the birds were unwilling to fly, the same increase was found if they did. Anyway it is difficult to understand, why a bird should raise its body temperature in order to facilitate heat loss when it is actually too cold for it to fly (Torre-Bueno 1976).

A possible explanation for the occurrence of a constant hyperthermia in flight, is given by Torre-Bueno (1976) by comparing with studies on humans. Maximum power output and muscle efficiency in humans increase with higher muscle temperature. If the bird's muscle would respond in the same way – comparative tests have not been made – this would be very advantageous. The bird could then fly with less muscle mass, and this in turn would enable it to fly longer distances with the same energy reserves. The elevation of T_c during flight in birds under physiological conditions would, in this sense, not be the result of insufficient thermoregulatory abilities, but an adaptation to the extreme exercise during flight. However, a T_c above physiological flight T_c (as can be found under unphysiological stress, see above), can only be explained as being a mechanism of heat dissipation – within the tolerated range (Hudson and

Bernstein 1981) – or as being the result of inadequate thermoregulation.

Skin temperature (breast and legs)

Breast temperatures T_{s-br} in flight were always found to be lower, by a few degrees, than T_c , but they reached values of resting T_c at high T_a (Fig. 2A). At the present stage the data have not been analyzed further, due to their extreme variability which may have been caused by irregular attachment of the thermistors, disturbing of the plumage or by differences in the plumage of the different individuals.

Steen and Steen (1965) have shown, that “the naked legs of the birds serve as controlled heat conduits of great importance in thermoregulation”.

The legs conserve heat by adapting their temperature to the ambient temperature in rest (Fig. 5). Heat loss via the legs is enhanced by increasing blood flow and thus increasing the temperature gradient between the legs and the environment. The presence of a good blood supply is suggested by the relatively quick heating up of the legs (Fig. 2). Anatomical evidence shows that they possess a well developed blood vessel system right down to their toes (Hyrtl 1864; Bernstein 1974). According to Baudinette et al. (1976) the blood flow in the legs of the herring gulls can be increased 5-fold within the temperature range of 10–35 °C.

In fact, as shown in Fig. 5, the mean leg temperature in pigeons is higher in flight compared to resting conditions and increases with ambient temperature, but the raise in T_{s-l} is only half as great (indicated by the slope of the regression line) as necessary to keep the temperature gradient constant. This apparent decrease in heat loss capacity of the legs might be compensated by changing the leg posture (from hiding under the feathers at low

T_a to complete exposure to the wind at high T_a) as described by Biesel and Nachtigall (1987), who have shown that these behavioural reactions are correlated to changes in the thermal conductance found in the flying pigeons.

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