

On the importance of radiative heat exchange during nocturnal flight in birds

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Summary

Many migratory flights take place during cloudless nights, thus under conditions where the sky temperature can commonly be 20°C below local air temperature. The sky then acts as a radiative sink, leading objects exposed to it to have a lower surface temperature than unexposed ones because less infrared energy is received from the sky than from the surfaces that are isothermic to air. To investigate the significance of this effect for heat dissipation during nocturnal flight in birds, we built a wind tunnel with the facility to control wall temperature (T_{ASK}) and air temperature (T_{AIR}) independently at air speeds (U_{WIN}) comparable to flying speeds. We used it to measure the influence of T_{ASK} , T_{AIR} and U_{WIN} on plumage and skin temperatures in pigeons having to dissipate a thermal load while constrained at rest in a flight posture.

Our results show that the temperature of the flight and insulation plumages exposed to a radiative sink can be accurately described by multiple regression models ($r^2 > 0.96$) based only on T_{AIR} , T_{ASK} and U_{WIN} . Predictions

based on these models indicate that while convection dominates heat loss for a plumage exposed to air moving at flight speed in a thermally uniform environment, radiation may dominate in the presence of a radiative sink comparable to a clear sky.

Our data also indicate that reducing T_{ASK} to a temperature 20°C below T_{AIR} can increase the temperature difference across the exposed plumage by at least 13% and thus facilitate heat flow through the main thermal resistance to the loss of internally produced heat in birds. While extrapolation from our experimentally constrained conditions to free flight in the atmosphere is difficult, our results suggest that the sky temperature has been a neglected factor in determining the range of T_{AIR} over which prolonged flight is possible.

Key words: radiation, sky, temperature regulation, flight, bird, pigeon, migration, wind tunnel.

Introduction

Following the seminal work of Tucker (1966), the wind tunnel has become a common environment for the experimental study of flying animals, and its use has rapidly led to major advances in our understanding of the energetic, thermal and hydric constraints affecting avian flight (see Rayner, 1994). By 1978, it was well established that energy expenditure during flapping flight was typically an order of magnitude greater than at rest. This result, combined with estimates of the mechanical efficiency of the pectoral muscles in the 20–25% range, also implied that flapping flight was accompanied by a large increase in heat production.

Unless dissipated by convection, radiation and evaporation, this heat would lead to cessation of flight due to hyperthermia. This thermal challenge is exacerbated by the fact that only a small fraction (<10%) of the heat produced during sustained flapping flight can be lost through evaporation (Torre-Bueno, 1978). Exceeding this limit, set mainly by the rate of metabolic water production from the oxidation of lipid fuel, would lead to cessation of flight by reason of dehydration. In sum, these factors suggested that, at least in a wind tunnel, the

need to dissipate large amounts of heat by convection and radiation would make flapping flight unsustainable at ambient temperatures higher than about 10°C. This hypothesis was later confirmed by the comprehensive studies of Nachtigall's group, who nevertheless considered that it was not applicable to flight made under natural conditions, presumably because 'birds in free-range flights use a form of behavioural thermoregulation not possible in a wind tunnel' (Biesel and Nachtigall, 1987).

In view of the existence of empirical evidence showing that migrating birds can cross the Sahara by flapping flight at temperatures above 20°C (e.g. Klaassen and Biebach, 2000), the thermal constraints acting on birds during flight in wind tunnels can no longer be taken as *de facto* representative of those prevailing during natural flight, because during free flight either heat production is smaller or heat dissipation is easier, or both. Several instrumental, meteorological and biological factors have indeed been considered to explain why the metabolic rate of flying birds may be higher in a wind tunnel than in the wild (Bishop et al., 2002). However, the possibility that the radiative interface to which most birds are exposed

during migration can act as a much better heat sink than the walls of a standard wind tunnel has been neglected.

The infrared (IR) radiation emitted by the walls of a typical wind tunnel closely approximates that of a black body having a temperature equal to that of the moving air. In contrast, the atmosphere usually emits less IR energy than a black body at air temperature (T_{AIR}) and can therefore act as a radiative sink. While this property is basically due to the low IR emissivity of the atmospheric gases (see Monteith and Unsworth, 1990), it is usually expressed on a temperature scale as the temperature of a black body having the same emitting power and referred to as the (natural) sky temperature (T_{NSK}). Since the value of T_{NSK} is strongly dependent on the atmospheric water content, itself a function of T_{AIR} , it can easily be calculated using empirical formulae (Hatfield et al., 1983). The difference between T_{AIR} and T_{NSK} can range from about 40°C (cold dry air under a clear sky; Hardy and Stoll, 1954) to nearly 0°C (warm moist air under a cloudy sky; Nobel, 1991). Values around 20°C are commonly observed under cloudless skies at intermediate relative humidity. We will refer to such a difference between T_{AIR} and the equivalent black body temperature of an ambient radiative sink as a radiative temperature deficit (ΔT_{RAD}).

As shown by the occurrence of radiative freezing at T_{AIR} several degrees above zero during clear nights (Nobel, 1991), exposure of an object to the atmospheric radiative sink can reduce its surface temperature (T_{SUR}). Since the cooling effect is then proportional to $T_{\text{SUR}}^4 - T_{\text{NSK}}^4$ (Porter, 1969), radiative exchange in birds flying at night in a cloudless atmosphere may very well account for a greater fraction of the total heat loss than that reported during flight in an isothermal wind tunnel (8%; Ward et al., 1999).

The aims of this study were to establish the effect of exposure to a radiative sink on the heat exchanges at the external surface of an avian plumage, and to examine the possibility that exposure to the low sky temperatures observed during clear nights may raise the maximum T_{AIR} at which flapping flight is sustainable in birds.

To simplify the task, we built a wind tunnel offering the possibility to control wall and air temperatures independently, and used it with pigeons at rest experiencing thermal constraints comparable to those observed during prolonged flight, i.e. having to dissipate a heat load in a flying posture.

Materials and methods

Animals

Domestic pigeons *Columba livia* G. (body mass $M_b = 0.366 \pm 0.038$ kg; mean \pm s.d., $N=4$) were

purchased from a commercial supplier and kept in cages measuring 60 cm \times 50 cm \times 55 cm with weekly access to an indoor aviary. They normally had free access to both water and mixed grains (Pigeon Grains, Ralston Purina Canada, Montréal, Québec, Canada), but were fasted for a 15 h period before experiments. They were gradually accustomed to the experimental setup and their behavior was continuously monitored with a camera. The birds generally remained calm, and only a few experiments were terminated because birds showed signs of restlessness or attempted to flee. The birds were used only every 3 days for no more than three experimental runs on a given day, and were offered water (and often drank) between the runs.

Our protocol was approved by the institutional Animal Protection Committee.

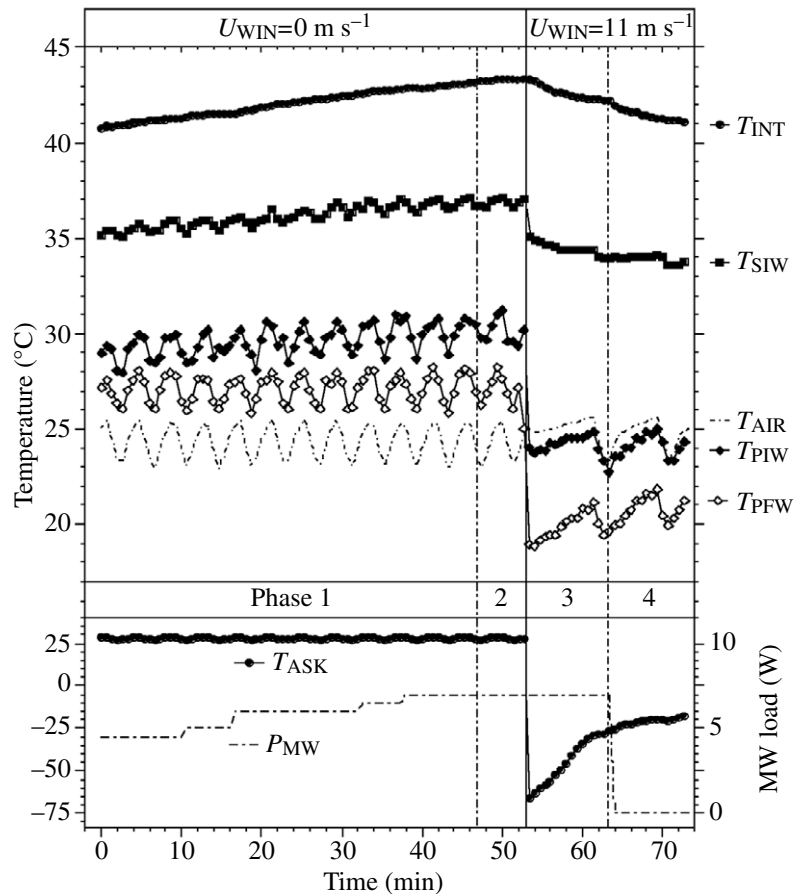


Fig. 1. Time course of four temperatures measured on a pigeon's body during a typical experimental run at a constant air temperature ($T_{\text{AIR}}=25^\circ\text{C}$): one of the body core (T_{INT}) and three of external surfaces of the wing, at level of the skin (T_{SIW}), insulation plumage (T_{PIW}) and flight plumage (T_{PFW}). Phase 1 corresponds to a period where T_{INT} is increased and phase 2 to a period where T_{INT} is stabilized, both by adjustment of the microwave load (P_{MW}). Phase 3 begins when the wind speed (U_{WIN}) is increased from 0 to 11 m s^{-1} and the artificial sky temperature (T_{ASK}) is decreased from T_{AIR} to a nominal value of -78°C . Phase 4 began by switching the microwave source off. The increase in T_{ASK} during phase 3 and 4 was due to heating of the tunnel walls by the moving air. The regular oscillations of air and other temperatures were due to the room cooling system.

Basic protocol

Each of the 96 experimental runs consisted of four phases over which T_{AIR} was constant at ca. 15°C or 25°C (Fig. 1; 25°C). During phase 1 (30–50 min), the body core temperature (T_{INT}) of the bird was raised at a maximum rate of 0.1°C min⁻¹. During phase 2 (5–10 min), T_{INT} was stabilized to a value (43.7±0.3°C) close to the maximum observed in flying pigeons (Hart and Roy, 1967; Butler et al., 1977; Hirth et al., 1987) and thus expected to elicit the use of heat dissipation mechanisms. During phase 3 (10 min), the artificial sky temperature (T_{ASK}) was set (nominally -78°C, -30°C, 0°C or T_{AIR}) and wind speed (U_{WIN}) was selected (0.3, 11 or 20 m s⁻¹) while the heating power was kept constant at the stabilizing level. During phase 4 (10 min), heating was stopped while all other parameters were kept constant.

Wind tunnel

The wind tunnel consisted of a large centrifugal blower (model 425, DELHI Industries, Delhi, Ontario, Canada) connected to a custom flow-straightening unit (length=60 cm) capable of delivering a fairly smooth and uniform air stream to a working space whose section had the shape of an equilateral triangle (Fig. 2). All surfaces of the wind tunnel were opaque and had a flat finish.

To allow control of their radiative temperature and emulate that of a natural sky, the inclined walls of the working space consisted of rectangular tanks (length×height×thickness: 48.5 cm×42.5 cm×6.5 cm; Fig. 2). These tanks were made of 6 mm thick aluminium plates and were insulated with 25 mm of styrene foam except on the air stream side, which was painted flat black. They were put in place at the beginning of phase 3. Nominal values ca. -78°C and 0°C for T_{ASK} were obtained by filling the tanks with mixtures of dry ice-methanol and ice-water, respectively. A T_{ASK} temperature of ca. -30°C

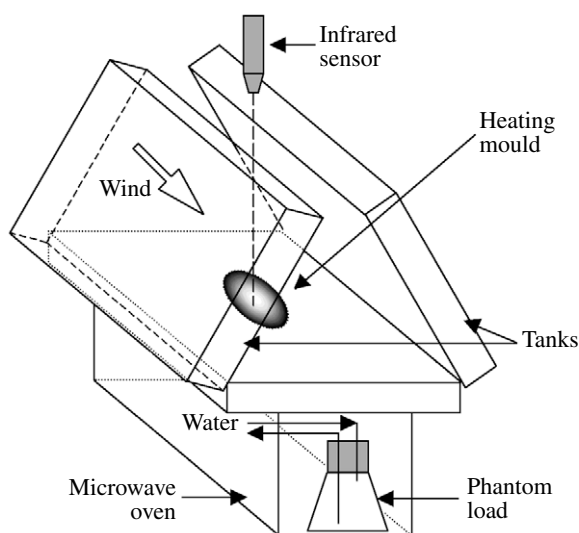


Fig. 2. Schematic view of the working section of the wind tunnel showing the position of the tanks used to control the temperature of the artificial sky.

was obtained by covering the exposed surface of the tanks filled with dry ice-methanol mixture with a 4.2 mm thick, black acrylic sheet held at 1.5 mm from the tank surface by a plastic covered metal screen. Effective values of T_{ASK} were sensitive to wind and were thus continuously monitored using an IR sensor (model OS36, Omega Canada, Montréal, Québec, Canada). The view factor of the plumage towards the artificial sky formed by the tanks was 0.72 (J.-F. Harbour and D. Rousse, unpublished data).

Maintaining the surface temperature of relatively large plates (0.21 m² each) several tens of degrees below that of air moving over them at speeds up to 20 m s⁻¹ requires a hefty cooling capacity. In our case, several tons of dry ice were used, and the tanks had to be vented out of the experimental room to avoid any significant build-up of CO₂.

A minimum U_{WIN} of 0.3 m s⁻¹ was necessary to prevent cooling of the plumage surface through natural convection by the sinking air having been in contact with the tunnel walls at low T_{ASK} . $U_{\text{WIN}}=11$ m s⁻¹ was chosen because it is close to the minimum-power speed in both pigeons (Rothe and Nachtigall, 1987) and starlings (Ward et al., 1999, 2001) flying in wind tunnels. $U_{\text{WIN}}=20$ m s⁻¹ appears close to the maximum speeds sustainable for several hours during homing flights in pigeons (Gessaman and Nagy, 1988).

The performance of our compact wind tunnel was in many respects less impressive than that of an instrument optimized for aerodynamical studies such as Lund's 21 m tunnel (Pennycuick et al., 1997). In the following comparison, values taken from their paper are shown within parentheses, together with the source figure number. At $U_{\text{WIN}}>5$ m s⁻¹, a series of freestream air speeds in our tunnel (taken at least 5 cm away from walls) gave values within 10% (<2%; fig. 3, Pennycuick et al., 1997) of the average value, with a maximum turbulence intensity of about 6% (<1%; fig. 5, Pennycuick et al., 1997). Boundary layer properties of our tunnel, however, particularly above the critical floor area covered by the bird, were quite decent. Average air speeds measured above this critical area at 1 cm from the floor (wall) were reduced by ~13% (~12%; fig. 8, Pennycuick et al., 1997) with respect to those obtained at 10 cm. Turbulence intensity at 1 cm was 7–9% (~6%; fig. 8, Pennycuick et al., 1997), an expected increase over the values observed at 10 cm.

Values of U_{WIN} were routinely measured using an air velocity meter (model 441S, Kurz Instruments, Monterey, CA, USA). No correction was applied for the small changes in air density due to barometric fluctuations (100.6±1.0 kPa). Spatial and temporal fluctuations of U_{WIN} were analyzed using a 5 μm hot-wire connected to a constant temperature anemometer (model 1750, TSI, Shoreview, MN, USA). Turbulence intensity was expressed as the percent ratio of RMS fluctuations over local average speed. Speed sensors were calibrated with a Pitot tube.

Measurement of T_{AIR} was made in the wind tunnel using a thermocouple that also controlled the cooling unit of the room. The only light in this room came from a standard 60 W bulb unviewable from the bird position.

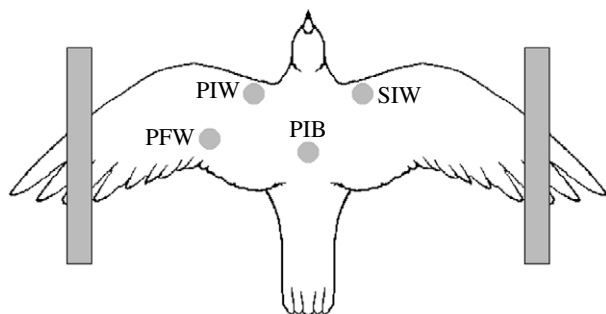


Fig. 3. Selected sites for measurement of the external surface temperature of the wing skin (SIW), wing insulation plumage (PIW), wing flight plumage (PFW) and back insulation plumage (PIB).

Posture control

Within the working section of the wind tunnel, the bird was held in a posture similar to that observed during gliding flight. The body trunk was supported by a basket-like mould, made of rubber strips. The inside of the mould was padded with a cotton liner, while the outside was covered by heating wires taken from a common heating pad. The mould was embedded in the floor of the working space of the wind tunnel at a depth such that the opened wings were positioned flat on the wind tunnel floor. To maximize heat loss by the upper facing surfaces of the bird, the mould was kept at a temperature slightly above that of the bird body, and the (unheated) floor that supported the wings was made of 7.5 cm thick insulating foam to minimize downward heat loss.

The wings were held opened by pinching the distal primary feathers between padded bars (Fig. 3). Based on measurements made in starlings by Ward et al. (1999), we estimated that the upper-facing surface of our constrained birds was 36% of the total surface exposed during free flight. The exposed frontal area of the bird (ca. 20 cm²) determined a blocking factor of about 2%, as compared with the cross-sectional area of the working space of the tunnel.

Body heating system

To simulate the heat load observed during flapping flight, the bird was exposed to a low-power microwave (MW) source located below the mould. This source consisted of an 800 W domestic oven facing upwards, with its door window removed. The MW load delivered to birds (P_{MW}) was reduced to a maximum value of about 10 W (at 100% duty cycle) by a metallic screen replacing the door window and by a bottle of water acting inside the oven as a phantom load maintained at 20°C by an external cooling circulator. The variable P_{MW} level required for adequate control of the pigeon T_{INT} was obtained by adjusting the duty cycle of the MW source *via* a computer-activated relay replacing the door switch. Supplementary metallic screens and plates were used to prevent direct MW irradiation of the underwings and legs. Since the penetration depth of 2.45 GHz MW is about 1 cm, this arrangement was expected to favour the preferential heating of the pectoral

muscles and therefore the maximum recruitment of the heat dissipation mechanisms used during flight. The pectoral skin was consistently warmer than the intestine (by up to 3°C) during MW irradiation, indicating that thermal absorption was indeed higher near the site where most of the heat is produced during flight.

The experimental birds showed no reaction to indicate any possible non-thermal effects of MW exposure. No sign of cutaneous damage was observed, even in the pectoral area where the highest temperatures were recorded.

To prevent personal exposure to MW, the wind tunnel was installed in a metal-walled room, from which leaks were found to be negligible using a MW meter (model HI-1501, HOLADAY, Eden Prairie, MN, USA).

Measurement of biological temperatures

Plumage temperature was measured using an infrared thermometer accurate to 0.1°C (model MX4, Raytek, Santa Cruz, CA, USA; bandwidth, 8–14 μm; average spot size, 2 cm; reading time: 0.25 s) through a slit between the upper edges of the side walls in the working space of the wind tunnel. Preliminary measurements were made at various points over the bird, and three locations were selected as representative of the average temperature of back insulation plumage (T_{PIB}), wing insulation plumage (T_{PIW}) and wing flight plumage (T_{PFW}), respectively (Fig. 3). In this paper, insulation plumage refers to the feather coat directly overlying the skin and flight plumage refers to the primaries and secondaries. Precise aiming of the infrared thermometer was achieved using a custom device made with two printing head carriers taken from dot-matrix printers. The stepping motors were controlled by a computer, allowing reproducible measurements both within and between the wings.

Upper wing skin (T_{SIW} ; Fig. 3) and pectoral temperatures were read with 36 gauge copper–constantan thermocouples kept in contact with the skin by gluing or tying to adjacent feathers. T_{SIW} was taken as representative of the temperature of the whole wing skin. T_{INT} was measured in the intestine using a lubricated thermistor inserted cloacally to a depth of 6 cm.

All temperatures were obtained by reading the sensors every 40 s with a computer and calculating the values from polynomial curves established through calibration against a certified thermometer over the whole experimental temperature range. IR emissivity of all surfaces was assumed to be 0.97. The MW heating was suspended a few seconds before reading the sensors to eliminate any MW interference.

Heat flow calculations

The level of P_{MW} was crudely estimated from measurements of the maximum value of the rate of change of T_{INT} ($\Delta T_{INT}/\Delta t$; in deg. s⁻¹) following switching the MW source off after T_{INT} stabilization:

$$P_{MW} = M_b \times c_p \times \Delta T_{INT} / \Delta t, \quad (1)$$

where a value of 3.47 J g⁻¹ K⁻¹ was used for heat capacity (c_p) of the pigeon body (Hart, 1951).

Table 1. Multiple regression models describing the effect of environmental variables and their interactions on surface temperatures of the pigeon

Dependent variables	Intercept ¹	Independent variables ²					
		T_{AIR}	$T_{\text{ASK}}^{1.6}$	$U_{\text{WIN}}^{0.5}$	$T_{\text{AIR}} \times U_{\text{WIN}}^{0.5}$	$T_{\text{ASK}}^{1.6} \times U_{\text{WIN}}^{0.5}$	$T_{\text{AIR}} \times T_{\text{ASK}}^{1.6}$
T_{PFW}	127.0	0.451	-4.64×10^{-3}	-9.80	5.09×10^{-2}	-6.09×10^{-4}	2.96×10^{-5}
r^2	0.962	0.568	0.0003	0.0026	0.0162	0.0449	0.3299
T_{PIW}	101.9	0.616	-2.66×10^{-3}	-9.58	3.77×10^{-2}	-2.28×10^{-4}	1.48×10^{-5}
r^2	0.963	0.864	0.0001	0.0037	0.0071	0.0108	0.0776
T_{PIB}	136.1	0.472	-5.96×10^{-3}	-11.96	4.94×10^{-2}	-3.43×10^{-4}	2.89×10^{-5}
r^2	0.966	0.771	0.0006	0.0054	0.0179	0.0024	0.1682
T_{SIW}	264.5	0.133	-8.04×10^{-3}	10.40	-3.00×10^{-2}	-2.35×10^{-4}	2.93×10^{-5}
r^2	0.294	0.244	0.0034	0.0053	0.0059	0.0157	0.0199

Environmental variables: T_{AIR} air temperature, T_{ASK} artificial sky temperature, U_{WIN} wind speed; surface temperatures of the pigeon: T_{PFW} flight plumage of the wing, T_{PIW} insulating plumage of the wing, T_{PIB} insulating plumage of the back, T_{SIW} insulating plumage of the wing skin. The database includes a total of 2850 values of T measured in 4 pigeons during experimental phases 3 and 4. T values are in K and U_{WIN} in m s^{-1} .

¹Full model r^2 are shown below intercept values.

²Regression coefficients (all significant at $P < 0.002$) are shown above their partial r^2 .

To quantify the heat exchanges made by the upper facing surface of the plumage with the skin and the surroundings, we considered the capacity for heat storage at this surface as well as the influence of evaporative and conductive (downward) processes to be negligible. Heat loss to the surroundings by the plumage could then be assumed to occur through convection (*via* the external boundary layer of air; subscript CP) and radiation (for the sake of simplicity, only the loss to the artificial sky was considered; subscript RP). The relative importance of these two processes in dissipating the heat gained from the skin by transplumage flow (subscript TP) could then be defined on a percent scale as $F_{\text{CP}} (=100 \times P_{\text{CP}}/P_{\text{TP}})$ and $F_{\text{RP}} (=100 - F_{\text{CP}})$, where P refers to the magnitude of a heat flow.

Since heat flow through the plumage as well as that through its external boundary layer can be described by a simple transfer law ($P = G \times \Delta T$), where G corresponds to thermal conductance, it follows that:

$$F_{\text{CP}} = 100(G_{\text{CP}}\Delta T_{\text{CP}}) / (G_{\text{TP}}\Delta T_{\text{TP}}). \quad (2)$$

At a given T_{AIR} and U_{WIN} , when G_{CP} and G_{TP} can be reasonably considered as stable, their ratio (and the percent factor) can be replaced by a constant K_{CT} to give:

$$F_{\text{CP}} = K_{\text{CT}} \times \Delta T_{\text{CP}} / \Delta T_{\text{TP}}. \quad (3)$$

The value of K_{CT} can be calculated at $T_{\text{AIR}} = T_{\text{ASK}} = 25^\circ\text{C}$ and $U_{\text{WIN}} = 10 \text{ m s}^{-1}$ from the values of ΔT_{CP} (2.0°C) and ΔT_{TP} (8.1°C) predicted by our models for pigeons (Table 1) and from a reference value for F_{CP} taken from the study of starlings flying under comparable conditions (91%; Ward et al., 1999). Values of F_{CP} for various values of T_{ASK} could then be calculated for pigeons from the relevant predicted ΔT values and used to determine the values of F_{RP} (9% under reference conditions). We assumed that doubling U_{WIN} increased G_{CP} (and thus K_{CT} and F_{CP}) by $2^{0.5}$.

Data analysis

The experimental sequence among the 4 birds and the 24 conditions was chosen randomly. Multiple linear regression models (SAS, 1994) were prepared using the forward procedure of SAS (version 8) applied on all raw measurements made during phase 3 and 4 of each experiment. Best-fit exponents for U_{WIN} and T_{ASK} were determined as those maximizing r^2 values when calculating the regression with the variables raised to powers between 0 and 4 by 0.1 steps. This procedure gave 0.5 for the exponent of U_{WIN} , a value commonly observed in both inert objects (Holman, 1990) and living animals (Goldstein, 1983). It gave 1.6 for the exponent of T_{ASK} , a value theoretically expected to be smaller than the commonly observed one (4; Holman, 1990) as only 72% of the total ambient surface emitting IR towards the upper surface of the bird was at T_{ASK} , the remaining part being at T_{AIR} .

Results

Our results show that the upper surface temperature of the flight (T_{PFW}) and insulation (T_{PIW} and T_{PIB}) plumages of a pigeon constrained in a flight posture can be described by multiple regression models based on measurements of only three environmental variables (T_{AIR} , T_{ASK} and U_{WIN}). As expected from their r^2 values (>0.96 ; Table 1), these models faithfully account for the trends observed in the experimental data sets (Fig. 4). None of the other measured variables (T_{INT} , T_{SIW} , M_{b} and P_{MW}) was retained as significant in the models, likely because their changes were relatively small and noisy. The models allow easy and accurate prediction of the combined effects of environmental variables on the plumage surface temperatures, and they were therefore used to calculate the predicted values reported below.

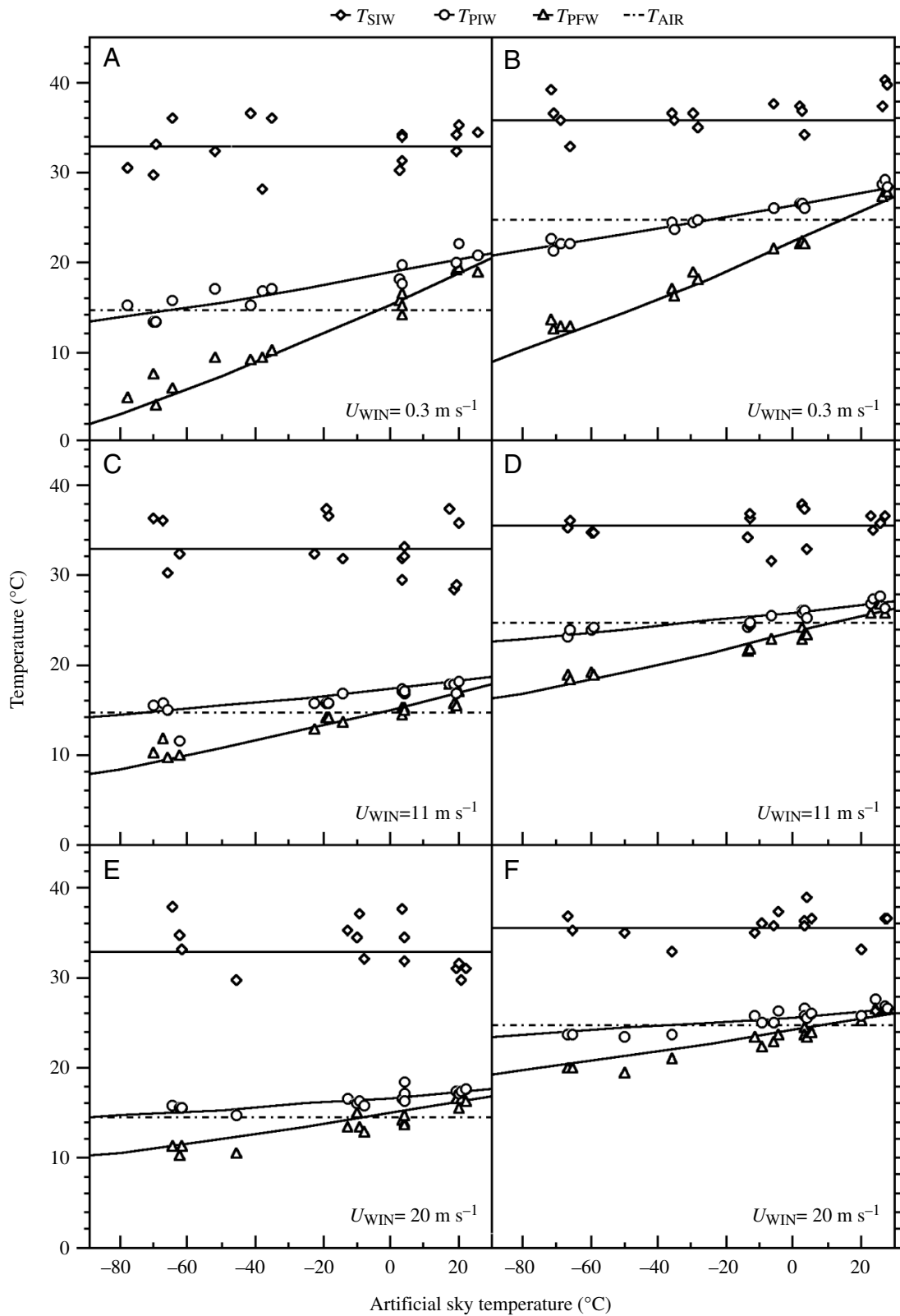


Fig. 4. Influence of artificial sky temperature (T_{ASK}) on the temperature of the external surfaces of the skin (T_{SIW}), insulation plumage (T_{PIW}) and flight plumage (T_{PFW}) according to air temperature (T_{AIR} ; 15°C in A,C,E, 25°C in B,D,F) and wind speed (U_{WIN} ; 0.3 m s^{-1} in A,B; 11 m s^{-1} in C,D; 20 m s^{-1} in E,F) during experimental phases 3 and 4. Dotted lines show observed mean values ($N=4$) while solid lines show values predicted from the regression models based on all measurements (Table 1).

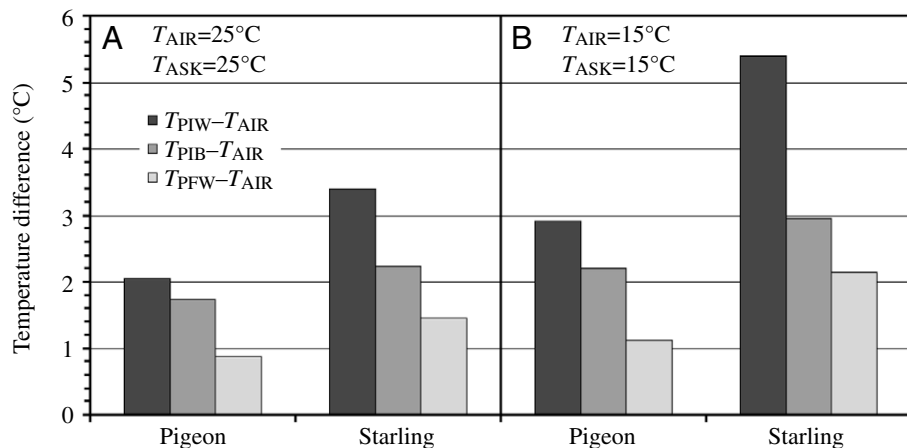


Fig. 5. Predicted effects of air temperature (T_{AIR}) at equal artificial sky temperature (T_{ASK} ; A, 25°C; B, 15°C) on the temperature differences influencing dry heat loss from three corresponding plumage surfaces in a pigeon (present study) and a starling (calculated from table 3 in Ward et al., 1999), all under a 10 m s^{-1} wind. The surface temperatures are T_{PIW} for the insulation plumage of the wing (dorsal brachials), T_{PIB} for the insulation plumage of the back and T_{PFW} for the flight plumage of the wing (dorsal secondaries).

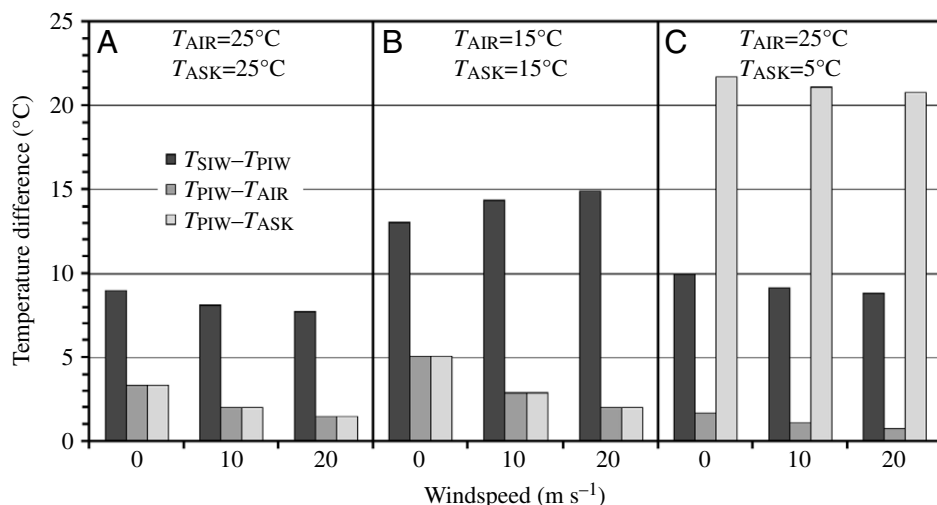


Fig. 6. (A) Temperature differences influencing the heat gained from the skin by the external surface of the insulation plumage on a pigeon's wing ($T_{SIW}-T_{PIW}$) and the loss of this heat to the surroundings by convection ($T_{PIW}-T_{AIR}$) and radiation ($T_{PIW}-T_{ASK}$) at $T_{AIR}=T_{ASK}=25^\circ\text{C}$. (B,C) Predicted effects of lowering both air (T_{AIR}) and artificial sky (T_{ASK}) temperatures (B) or only T_{ASK} (C). The wing temperatures are those of the external surface of the plumage (T_{PIW}) and of the skin (T_{SIW}).

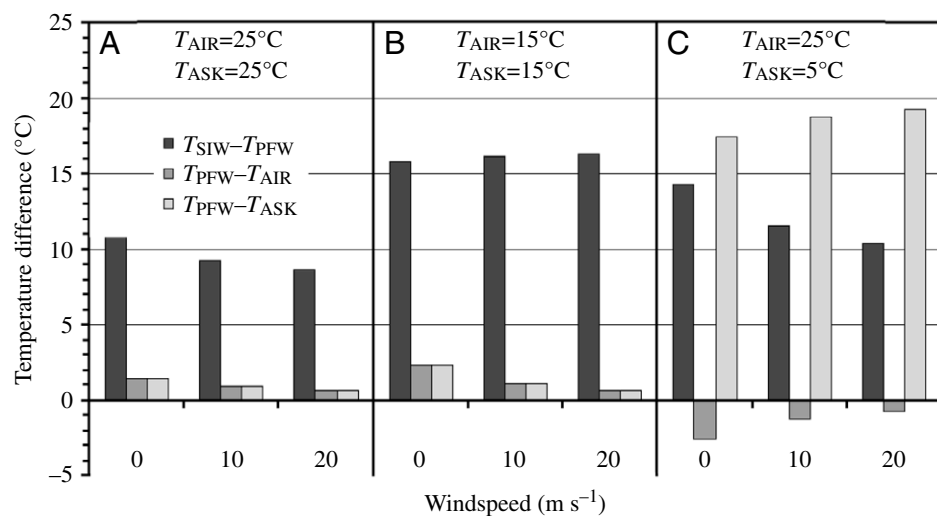
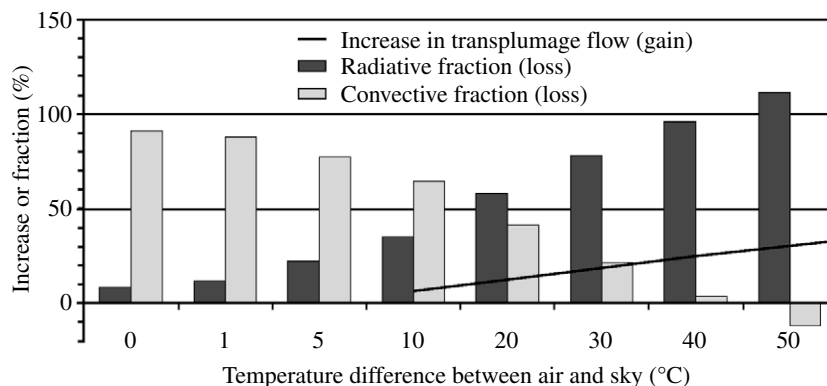


Fig. 7. (A) Temperature differences influencing the heat gained from the skin by the external surface of the flight plumage on a pigeon's wing ($T_{SIW}-T_{PFW}$) and the loss of this heat to the surroundings by convection ($T_{PFW}-T_{AIR}$) and radiation ($T_{PFW}-T_{ASK}$) at $T_{AIR}=T_{ASK}=25^\circ\text{C}$. (B,C) Predicted effects of lowering both air (T_{AIR}) and artificial sky (T_{ASK}) temperatures (B) or only T_{ASK} (C). The wing temperatures are those of the external surface of the plumage (T_{PFW}) and of the skin (T_{SIW}). At low values of T_{ASK} ($T_{AIR}-T_{ASK}>7^\circ\text{C}$), the temperature difference across the boundary layer of air ($T_{PFW}-T_{AIR}$) is reversed and now favors heat gain by the plumage surface through convection.

Fig. 8. Predicted effects of increasing the temperature difference between air (T_{AIR}) and artificial sky (T_{ASK}) on the thermal budget at the external surface of the insulation plumage in pigeons exposed to a T_{AIR} of 25°C and a wind speed $U_{\text{WIN}}=10 \text{ m s}^{-1}$. The line shows the increase (%) in transplumage heat gain by this surface. Black bars, fractions of the heat loss attributed to radiation (F_{RP}); grey bars, fractions attributed to convection (F_{CP}), expressed relative to the transplumage gain (solid line; taken as 100%). At very low values of T_{ASK} ($T_{\text{AIR}}-T_{\text{ASK}}>42^\circ\text{C}$), F_{RP} exceeds 100% because radiation also accounts for the dissipation of the heat gained by the plumage surface from the air through convection.



Our models facilitate comparison with the results of Ward et al. (1999) on starlings at flight in a thermally uniform wind tunnel ($T_{\text{ASK}} \approx T_{\text{AIR}}$). These authors also found that the plumage surface temperatures can be described precisely by multiple regression models based on T_{AIR} and U_{WIN} ($r^2 > 0.91$; table 3 in Ward et al., 1999). The three sites used to measure plumage temperature in our study are comparable to equivalent sites in Ward et al. (1999). But although the temperatures recorded at these sites reacted similarly to T_{AIR} (Fig. 5) and U_{WIN} (data not shown) in both studies, the temperature differences (ΔT) between plumage and air were often larger in the starling, putatively reflecting the higher thermal load imposed by flapping flight with respect to that imposed by our artificial heating system.

Effects of T_{AIR} on plumage temperature

Our data show that the superficial temperatures of the upper-facing plumage were very responsive to T_{AIR} , with T_{PIW} , T_{PIB} and T_{PFW} decreasing by 9–10°C following a 10°C reduction of T_{AIR} ($=T_{\text{ASK}}$) at flight U_{WIN} (10–20 m s^{-1} ; Fig. 4). The effect was slightly greater in T_{PFW} and at higher U_{WIN} . In flying starlings (table 3 in Ward et al., 1999), a reduction of 10°C resulted in decreases of 8.0°C in the area corresponding to T_{PIW} (dorsal brachials) and 9.3°C in those corresponding to T_{PIB} (back) and T_{PFW} (dorsal secondaries).

In pigeons, the largest proportion of the total ΔT responsible for dry (non-evaporative) heat loss from skin to environment ($T_{\text{SIW}}-T_{\text{AIR}}$) was observed across the feather coat. At flight U_{WIN} , this proportion was 80–88% across the insulation plumage (Fig. 6A,B) and 91–96% across the flight plumage (Fig. 7A,B), with the highest values obtained at low T_{AIR} and high U_{WIN} . The ΔT values responsible for the main radiative heat loss ($\Delta T_{\text{RP}}=T_{\text{SUR}}-T_{\text{ASK}}$) and for the convective heat loss ($\Delta T_{\text{CP}}=T_{\text{SUR}}-T_{\text{AIR}}$) from the external surfaces of the plumage to the environment were therefore rather small, typically 1–3°C. In starlings flying under similar conditions, the corresponding ΔT values were higher (on average, by 50%) but generally still less than 3°C, with the notable exception of those associated to the brachials, where higher values were commonly observed (fig. 5 in Ward et al., 1999).

Effects of T_{ASK} on plumage temperature

The superficial temperature of the upper-facing plumages was reduced in the presence of a radiative sink (Fig. 4), producing opposite changes on ΔT_{RP} and ΔT_{CP} . In the upper-facing insulation plumage of the wing, for example, creating a radiative temperature deficit (ΔT_{RAD}) of 20°C by lowering T_{ASK} to 5°C while keeping T_{AIR} at 25°C caused a 10- to 14-fold increase in ΔT_{RP} and a 50–55% decrease in ΔT_{CP} at flight U_{WIN} (Fig. 6C). The effect was stronger in the flight plumage where a reversal of ΔT_{CP} was observed at ΔT_{RAD} larger than 10°C (Fig. 7C). A similar reversal could also be observed across the insulation plumage, but it required a larger ΔT_{RAD} (>42°C; Fig. 4).

The distinctive effects of ΔT_{RAD} of 20°C at $T_{\text{AIR}}=25^\circ\text{C}$ on ΔT_{RP} and ΔT_{CP} resulted in marked changes in the relative contributions of radiation and convection to the loss of the heat gained from the skin by the external surface of the plumage exposed to the radiative sink (Fig. 8). The predicted values of F_{RP} for the insulation plumage then increased from less than 10% to 58% at $U_{\text{WIN}}=10 \text{ m s}^{-1}$ and to 53% at $U_{\text{WIN}}=20 \text{ m s}^{-1}$. For the flight plumage, the corresponding increase was from below 10% to above 100%, as its T_{SUR} remained below T_{AIR} when ΔT_{RAD} was larger than 10°C.

In pigeons, the predicted balance ΔT_{RAD} (at which $F_{\text{RP}}=F_{\text{CP}}$) was 16°C for the insulation plumage exposed to the radiative sink at a U_{WIN} of 10 m s^{-1} and a T_{AIR} at 25°C. Its value was relatively insensitive to the value arbitrarily chosen for reference F_{RP} (9%; see Materials and methods), changing by about 1°C when this F_{RP} was either decreased to 5% or increased to 15%. As expected, doubling U_{WIN} increased the predicted balance ΔT_{RAD} , but only by ~2°C. The predicted balance ΔT_{RAD} for the flight plumage was only 4–5°C under the same conditions.

Exposure to a ΔT_{RAD} of 20°C at a T_{AIR} of 25°C and a U_{WIN} of 10 m s^{-1} also facilitated transplumage heat flow, as ΔT_{TP} increased by 13% and 22% for the exposed insulation and flight plumages, respectively (Figs 6C, 7C, 8). The increases, however, were reduced by about 40% when T_{AIR} was lowered to 15°C at constant ΔT_{RAD} ($T_{\text{ASK}}=-5^\circ\text{C}$) but they were essentially unaffected by doubling U_{WIN} at a given T_{AIR} .

Effects of the thermal environment on T_{SIW} and T_{INT}

The variability of measured T_{SIW} was relatively high with respect to that of other temperatures, mainly due to a large between-experiments component (Fig. 4). Although this led to low r^2 values in regression models (Table 1), its impact on data interpretation should be marginal in view of the low sensitivity of T_{SIW} to environmental variables. For example, predicted T_{SIW} at $T_{AIR}=25^\circ\text{C}$ and $U_{WIN}=10\text{ m s}^{-1}$ was $34\text{--}35^\circ\text{C}$, and it changed by less than 1°C from increasing U_{WIN} to 20 m s^{-1} or from decreasing T_{ASK} by 20°C .

The value of T_{SIW} was more sensitive to that of T_{AIR} , a 10°C reduction in T_{AIR} bringing a $2\text{--}3^\circ\text{C}$ decrease in T_{SIW} at $U_{WIN}=10\text{ m s}^{-1}$. But since the values of T_{SIW} were much less sensitive to T_{AIR} than that of the plumage T_{SUR} , large increases in ΔT_{TP} (74–92%) were observed when T_{AIR} was reduced by 10°C at flight U_{WIN} . Predicted values of T_{SIW} under a very low wind (0.3 m s^{-1}) were 37.0 and 33.0°C , at T_{AIR} of 25°C and 15°C , respectively.

Unlike that of other body temperatures, changes in T_{INT} were poorly correlated to environmental variables ($r^2=0.018$), but their prediction based on internal variables was significant ($r^2=0.523$), with contributions coming from P_{MW} ($r^2_p=0.517$) and M_b ($r^2_p=0.006$; results not shown).

Discussion

The main finding of this study is that exposure to a radiative sink comparable to a clear night sky can have significant effects on the thermal budget of a bird in a flying posture, particularly at warm air temperatures considered to be limiting for flapping flight. Firstly, our results indicate that radiative heat loss, which is much smaller than convective loss during a flight made in a thermally uniform environment (Ward et al., 1999), may be the dominant heat dissipation mode for the plumage surfaces exposed to a typical cloudless sky at night. Secondly, our data indicate that exposure to a radiative temperature deficit may also facilitate heat dissipation in a flying bird by reducing the temperature of its exposed surfaces. A higher heat loss from these surfaces then offers a bird the possibility to reduce its dependence on evaporative heat loss, explaining why exposure to a low T_{NSK} may extend the range of T_{AIR} over which flapping flight can be sustained. Finally, our study demonstrates that standard wind tunnels are inappropriate thermal environments to measure the capacity of animals to dissipate heat during free nocturnal flight, i.e. under conditions where many migratory flights take place.

Since lowering T_{SUR} of an object reduces its capacity to lose heat through convection and IR emission, it may at first glance appear disadvantageous to a bird threatened by hyperthermia. It must however be recalled that the main thermal input to the surface of a flying bird is the IR absorbed from the surroundings. For example, assuming a plumage area of 0.0493 m^2 , a metabolic rate of 12.7 W , a mechanical efficiency of 19% and an evaporative water loss of 0.9 W (bird 19 in Ward et al., 1999, 2001), the plumage surface of a 0.090 kg starling flying in a black wind tunnel would receive

$\sim 200\text{ W m}^{-2}$ of heat from the internal organs. At the same time, this surface would receive $\sim 450\text{ W m}^{-2}$ from tunnel walls at 25°C , but only $\sim 340\text{ W m}^{-2}$ from walls at 5°C . A surface exposed to a radiative sink thus exhibits a lower T_{SUR} because its thermal gain through radiation is reduced more than its thermal loss through convection and radiation.

Since plumage has the high insulating capacity required to keep resting birds warm under cold and windy conditions, it constitutes the main thermal resistance between the flight muscles and the environment. This is well illustrated by our results showing that in pigeons at least 80% of the total ΔT responsible for dry heat loss from skin to environment appears across the feather coat at flight U_{WIN} . A reduced T_{SUR} can then facilitate the loss of internally produced heat by increasing the transplumage ΔT . For instance, at a T_{AIR} value known to be limiting for sustained flapping flight ($\sim 25^\circ\text{C}$), exposure to a typical clear night sky, with a radiative temperature deficit of 20°C , can increase ΔT_{TP} in the exposed plumages by 13–22% according to our results. This effect is larger than that caused by increasing U_{WIN} from 10 to 20 m s^{-1} (3–7%). In flight feathers, it may lead to a reversal of the plumage-to-air temperature difference, implying that air would then heat the plumage surface (Figs 4, 8).

The use of our results to describe what happens during nocturnal migratory flight obviously depends on how well our biological model matches a flying bird and on how well our custom wind tunnel simulates the relevant radiative and convective characteristics of the atmosphere on a clear night. To address this point, we must first show in the absence of comparable data that our predicted values of F_{RP} are acceptable estimates of those that could be determined for the corresponding surfaces of flying pigeons.

The first limitation of our experimental approach arises from the fact that the convective environment to which our birds were exposed was different from that experienced during flight. On the one hand, while the posture of our bird was closer to that observed during gliding rather than flapping flight, there is no apparent reason why this could *per se* affect the thermal properties of the upper-facing surfaces of the plumage. On the other hand, the potential of the wings and adjacent surfaces for convective heat loss was certainly reduced by the absence of wing movements and underwing exposure. This potential was also likely reduced owing to the presence of a preformed boundary layer on the windward side of the wind tunnel floor, over which the wings were lying flat. For instance, U_{WIN} measured at a height of 0.5 cm above the floor was reduced by 19% with respect to freestream speed (10 m s^{-1}), indicating a 10% decrease in convective heat loss if the 0.5 exponent applies to this case. These conditions may therefore lead to an overestimate of the importance of radiative heat loss, though only to a small extent in view of the low sensitivity of the plumage temperatures to wind speed. For example, halving U_{WIN} within the flight speed range changed the temperature of the insulating plumage by about 0.5°C and the transplumage temperature difference by less than 10% (Fig. 6). This sensitivity to air speed also appears small in starlings, as

halving the flight speed resulted in changes of about 1.4°C in the plumage temperature (fig. 6 in Ward et al., 1999) and of less than 5% in the metabolic power (fig. 2 in Ward et al., 2001). It is also possible that in our setup the effect on heat exchange by the wings of the preformed boundary layer was to some extent compensated by an increase in turbulence favored by the high turbulence intensity observed in the freestream of our wind tunnel (see Materials and methods).

A second limitation of our approach that may favor overestimation of F_{RP} comes from the fact that our resting birds had less heat to dissipate than flying ones. Taking the minimal metabolic rate of flying pigeons as 100 W kg⁻¹ (Rothe et al., 1987), the mechanical efficiency of their flight muscles as 15% (Dial et al., 1997), the fraction of the heat loss taking place through non-evaporative means as 90% (Biesel and Nachtigall, 1987; Ward et al., 1999), and that the upper-facing surface of our constrained birds was 36% of the total surface exposed during flight, we estimate that flying pigeons have to dissipate about 10 W through the upper surfaces of their body. Given the thermal load imposed by our heating system and the possibility that most of the heat produced by the pigeons was lost through evaporation (as in Martineau and Larochelle, 1988), we estimate that our birds had to dissipate heat through their (dry) upper surfaces at a rate corresponding roughly to half of that during flapping flight at a T_{AIR} of 25°C. Such a difference is expected to be largely reflected in the surface temperature of the plumage; more so in areas specialized in heat dissipation during flight such as the dorsal brachials and the legs. Assuming then in the absence of relevant data that the thermal image of pigeons during flight at a T_{AIR} of 25°C is similar to that of starlings, this would imply values of ΔT_{CP} (Fig. 5) about 50% higher than those observed in our experiments under isothermal conditions ($T_{ASK}=T_{AIR}$). At a ΔT_{RAD} of 20°C ($T_{AIR}=25^\circ\text{C}$ and $U_{WIN}=10\text{ m s}^{-1}$), this would translate into increases of about 50% for P_{CP} and 5% for P_{RP} in the exposed insulation plumage. This would give a value of F_{RP} of 42% for this plumage, suggesting that our models overestimate its importance of radiative heat loss (predicted F_{RP} of 58%). However we think that the effect of higher T_{SUR} would be largely compensated by the fact that a pigeon flying in the atmosphere would be exposed to an hemispheric sink at least 140% larger than the one imposed by our experimental setup, where the view factor of the plumage towards the radiative sinks was only 0.72. Furthermore, in the flight plumage, increasing the value of ΔT_{CP} by 50% under isothermal conditions would not prevent it from becoming negative under a ΔT_{RAD} of 20°C. Its F_{RP} would thus not be lowered below 100%.

A further limitation of our experimental approach concerns the source of the heat dissipated by the plumage, as heat was supplied to our experimental birds by microwave irradiation rather than by muscular activity. The heat distribution within the body of our birds as well as the way thermoreceptors and thermoregulatory controls operate are likely to differ from that observed during flight. We consider these effects are largely irrelevant to our predictions as long as direct microwave

heating of the upper facing skin and feathers is negligible. This was shown to be the case, as close examination of graphs such as Fig. 4 revealed that the variations in T_{PIW} and T_{PFW} induced by discrete changes in microwave power level were slow and did not follow those observed in core temperature. Comparison of our T_{SIW} with the rare relevant values found in the literature also indicate that they are representative of those obtained in flying birds. The wing skin temperatures measured by Eliassen (1962) in seagulls held in a gliding posture in a wind tunnel at a U_{WIN} of 12 m s⁻¹ and T_{AIR} of 15–19°C are quite similar to those predicted for our pigeons under the same conditions (31.5–32.6°C vs 32.2–33.3°C). The breast skin temperatures reported by Hirth et al. (fig. 2B in Hirth et al., 1987) in pigeons during flapping flight in a wind tunnel at $T_{AIR}=16.1^\circ\text{C}$ and $U_{WIN}=12\text{--}18\text{ m s}^{-1}$ are also close to our predictions for wing skin under the same conditions (30.8–32.7°C vs 32.2–32.5°C).

Given these considerations, we feel confident that our F_{RP} values for the insulation (58%) and flight (100%) plumages constitute valuable starting points to estimate the overall contribution of the radiative heat loss to the thermal budget of a bird engaged in a flight under a typical cloudless sky ($\Delta T_{RAD}=20^\circ\text{C}$) during a warm night ($T_{AIR}=25^\circ\text{C}$). To obtain a whole-body value for F_{RP} , we must first combine the values for both plumage types according to their relative contributions to dry heat loss. Estimating the contribution of flight plumage at 10%, a conservative value when compared to that (>30%) suggested by the data of Ward et al. (table 6 in Ward et al., 1999), we obtain $F_{RP}=62\%$ for the total plumage surface exposed to the radiative sink (36% of total body surface). Assuming that the rest of the body surface is exposed to surfaces having a radiative temperature equal to T_{AIR} would give a value for whole body $F_{RP}=28\%$.

While a value of 28% is much higher than that of 9% obtained in the absence of a radiative temperature deficit, we think that larger values may be obtained by avian migrants by choosing when and where they will fly. Since water vapour is the major contributor to the downward radiation flux from the sky (Monteith and Unsworth, 1990), ΔT_{RAD} increases with air dryness. For example, as calculated using Brunt's formula (Hatfield et al., 1983), at $T_{AIR}=25^\circ\text{C}$, ΔT_{RAD} at a relative humidity of 20% is 9°C greater than at a relative humidity of 50%. As water vapour is more concentrated in the bottom part of the atmosphere, ΔT_{RAD} is expected to increase with height. Flight at high altitude should also increase the relative importance of radiative heat loss because convective loss is then reduced (8–9% km⁻¹) owing to the proportionality between the thermal conductivity of air and its specific gravity (Holman, 1990). Finally, subjected to radiative cooling like any other body exposed to the atmosphere at night, the ground may act as secondary radiative sink and increase the value of F_{RP} for the downward surface of a flying bird.

Conclusion

It can now be considered highly probable that radiation plays a much greater role than previously thought in the heat

dissipation of birds during nocturnal flight in warm weather under clear skies. In spite of the limitations imposed by our experimental approach, there is no reason to believe that the main physical phenomena responsible for heat removal from the plumage surface in our setup are different from those occurring in the atmosphere.

All other variables being constant, an increase in radiative heat loss due to exposure to a radiative sink will necessarily be accompanied in a bird by a decrease in surface temperature and an increase in transplumage heat flow. However, because of the experimental limitations of our approach, a precise determination of the extent to which natural radiative sinks can increase the range of T_{AIR} over which prolonged flight is possible will await future study. Chances are that radiative cooling will be found most useful for birds needing it most, i.e. for those having to cross desert areas where air is warm but dry.

The radiative interface offered to nocturnal migrants can thus be more complicated than previously thought, and this can make the decision to engage in a prolonged flight more complex. Humbly said, this interface may deserve to be recognized as a 'neglected interface', *sensu* Schmidt-Nielsen (1969).

List of symbols

c_p	heat capacity ($\text{J g}^{-1} \text{K}^{-1}$)
F_{CP}	ratio of the convective heat loss by the plumage surface to the transplumage heat flow (%)
F_{RP}	ratio of the main radiative heat loss (to the artificial sky) by the plumage surface to the transplumage heat flow (%)
G	thermal conductance (W K^{-1})
G_{CP}	thermal conductance of the air boundary layer at the external plumage surface (W K^{-1})
G_{TP}	plumage thermal conductance (W K^{-1})
IR	infrared radiation
K_{CT}	ratio between the boundary layer and the transplumage thermal conductances
M_b	body mass (kg)
MW	microwave
P	power or rate of heat flow (W) or statistical probability of error
P_{CP}	absolute rate of convective heat loss by the plumage surface (W)
P_{MW}	microwave heat load in birds (W)
P_{TP}	rate of transplumage heat flow (W)
r^2	model coefficient of determination
r^2_p	partial coefficient of determination
T_{AIR}	air temperature ($^{\circ}\text{C}$ or K)
T_{ASK}	artificial sky temperature ($^{\circ}\text{C}$ or K)
T_{INT}	body core temperature ($^{\circ}\text{C}$ or K)
T_{NSK}	natural sky temperature ($^{\circ}\text{C}$ or K)
T_{PFW}	upper surface temperature of flight plumage of the wings ($^{\circ}\text{C}$ or K)
T_{PIB}	upper surface temperature of insulation plumage of the back ($^{\circ}\text{C}$ or K)

T_{PIW}	upper surface temperature of insulation plumage of the wings ($^{\circ}\text{C}$ or K)
T_{SIW}	skin temperature under insulation plumage of the upper wing ($^{\circ}\text{C}$ or K)
T_{SUR}	surface temperature ($^{\circ}\text{C}$ or K)
U_{WIN}	wind velocity (m s^{-1})
Δt	unit time (s)
ΔT	temperature difference ($^{\circ}\text{C}$ or K)
ΔT_{CP}	temperature difference across the air boundary layer at the external plumage surface, responsible for convective heat exchange with air ($^{\circ}\text{C}$ or K)
ΔT_{RAD}	radiative temperature deficit, equal to the temperature difference between air and an ambient radiative sink ($^{\circ}\text{C}$ or K)
ΔT_{RP}	temperature difference responsible for radiative heat exchange between a plumage surface and an ambient radiative sink ($^{\circ}\text{C}$ or K)
ΔT_{TP}	transplumage temperature difference ($^{\circ}\text{C}$ or K)

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