

Heat Loss from Avian Integument: Effects of Posture and the Plumage

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Introduction

Heat loss from the body surface of birds is reduced through physiological adjustments of heat flow to the skin surface and by the presence of an insulating feather coat. Maintenance of a high and stable body core temperature is made possible by high avian metabolic rates coupled with behavioral, physiological, and morphological adaptations to reduce heat loss in the cold and to increase heat dissipation when air temperature is high. Previous studies of avian thermoregulation have provided a strong theoretical and empirical framework for studies of energy expenditure in birds, but relatively few investigators have focused on the role of the plumage in impeding heat loss through the integument (5).

The fibrous coat of mammals and birds, like human clothing, provides a barrier to heat flux by trapping a layer of still air next to the skin. The effectiveness of the insulating coat can be reduced by wind penetration or by free convection due to temperature gradients within the coat (4). Cutaneous tissue beneath the coat also provides some insulation, depending on the amount of bloodflow (hence heat flux) to different body regions. The relative importance of these and other factors in heat transfer relations of birds can be evaluated using relatively simple biophysical models that incorporate measurements of animal and environmental variables (3, 5, 9).

Sensible heat flux at the surface of an animal may be treated, as a first approximation, as a linear diffusion process in which radiative and convective heat losses occur across a thermal resistance and down a temperature gradient. Thermal resistance for a whole animal is given by:

$$r_{hb} = [\rho C_p (T_b - T_a)] / (M - \lambda E), \quad (1)$$

where r_{rh} is in s/m, ρC_p is the volumetric heat capacity of air ($1200 \text{ J m}^{-3} \text{ K}^{-1}$), T_b is the body core temperature (C), T_a is air temperature (C), M is metabolic rate in W/m^2 , and λE is the total evaporative heat flux (W/m^2) [3, 5, 8, 9].

The whole-body thermal resistance (Eq. 1) can be illustrated and partitioned into tissue, coat, and boundary layer components using electrical circuit analogues (8, 9). Temperature differences between points in the animal-environment interface are treated as voltages and heat fluxes across the interface as current sources. The plumage, boundary layer, and subcutaneous tissues form three series resistances to heat flow, which can be quantified using equivalent circuit analysis (3, 8, 9).

Materials and Methods

Five male and five female pigeons ($472.9 \pm 12.4 \text{ g}$ body weight) were obtained from a local breeder and acclimated to standard environmental conditions prior to experimentation. The birds were maintained under a 12:12 light-dark cycle, at 20C and 40-50% relative humidity, and were fed and watered ad lib. Pigeons were selected for docility and acceptance of training to tolerate experimental restraint.

To separate cutaneous from respiratory evaporative water loss I used a two compartment metabolic chamber constructed of plexiglass and placed in a temperature-controlled cabinet. Air dried to less than 0.3 g/m^3 water vapor density by columns of Drierite was pumped into each compartment at 1.5-1.8 l/min, and led to a dew-point hygrometer (EG&G 660) for humidity determination and to an oxygen analyzer (Electrochem N-3) for measurement of oxygen consumption. Skin temperatures were measured with fine wire Cu-Cn thermocouples closely affixed to the skin and glued (methyl-cyanoacrylate adhesive) to the base of a contour feather to hold them in place. Temperature transmitters (Minimitter Model M) surgically implanted in the birds allowed continuous monitoring of intraperitoneal body temperature. Humidity in the chamber was determined with a Weathertronics 5118 electrical hygrometer, and compartment temperatures were measured with thermocouples and controlled to within $\pm 0.2 \text{ C}$. Further details of the experimental apparatus are provided in (12).

Each of the pigeons used in this study was trained (for 20-25 h) to stand quietly in the chamber, with its head protruding through a latex collar into the head compartment and supported by a plexiglass pillory. Each experiment was conducted in darkness, during the subjective night of the birds, on resting and postabsorptive animals. No measurements were taken until the 95% equilibration time for body compartment water vapor had expired (1 1/2 hrs.), and efflux air oxygen content and body temperature remained stable for a minimum of five min before a measurement was taken. Data from runs in which fecal water contaminated the chamber air were discarded.

Determinations were performed at six temperatures over the range of 0 C to 40 C . Each bird was used at each air temperature, and the number of replicates ranged from 23 to 36 measurements at each chamber temperature. Statistical analyses relied on stepwise comparisons between temperature groups using analysis of variance.

Thermal resistances to heat loss were computed using the methods of (9). Boundary layer resistance was taken as the sum of free and forced convective resistances, since windspeed in the chamber was low and constant ($0.1\text{-}0.15 \text{ m/s}$) at all air temperatures (13). For computing boundary layer resistance, the characteristic dimension of the birds was estimated as 10 cm , the approximate diameter of the pigeons sitting parallel to chamber airflow.

Results

Body temperature remained approximately stable with increasing air temperature, averaging $40.6 \pm 0.1 \text{ C}$ at 0 , 10 , and 20 C , but increased significantly (ANOVA, $p < 0.05$) at 35 C air temperature, to $41.0 \pm 0.1 \text{ C}$, and at 40 C increased ($p < 0.05$) to $41.6 \pm 0.15 \text{ C}$. Skin temperature was linearly related to chamber air temperature, increasing from $22.6 \pm 0.5 \text{ C}$ at 0 C by $4.2 \pm 0.5 \text{ C}$ each 10 C increment until reaching values near core temperature. At 40 C , skin temperature ($40.9 \pm 0.2 \text{ C}$) was not significantly different from body temperature (12, 13).

Whole-body thermal resistance (r_{hb}) was constant between 0 and 35 C air temperature at $335 \pm 30 \text{ s/m}$ (Figure 1). At 40 C , r_{hb} was reduced to $192 \pm 22 \text{ s/m}$ ($p < 0.05$). Comparison of these estimates to pigeon whole-body resistances computed from available data (3) reveals that my restrained pigeons were able to increase r_{hb} to levels that were only 50-60% of those measured in unrestrained pigeons at 0 to 10 C .

Tissue thermal resistance was $140 \pm 14 \text{ s/m}$ at 0 , 10 and 20 C , but declined significantly to $105 \pm 3.2 \text{ s/m}$ at 30 and 35 C , and dropped to $76.5 \pm 1.8 \text{ s/m}$ at 40 C (Figure 2). Feather coat thermal resistance did not change significantly from $0\text{-}35 \text{ C}$, and averaged $139 \pm 25 \text{ s/m}$ over that temperature range. At 40 C , however, a sharp decrease in plumage thermal resistance was noted, to $30.5 \pm$

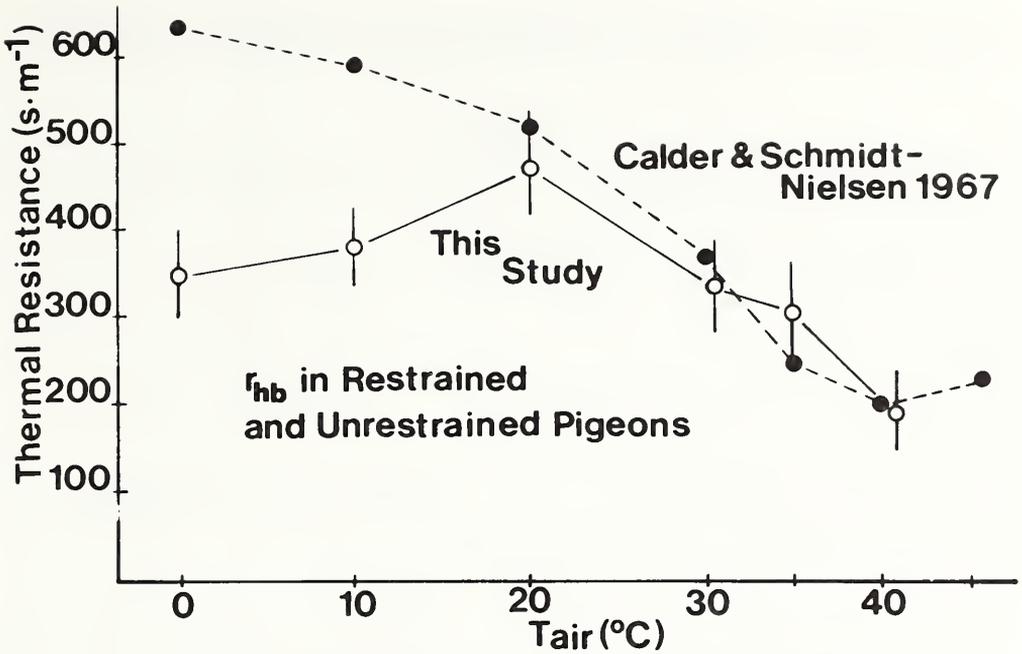


FIGURE 1. Whole body thermal resistance (mean \pm SE) of restrained and unrestrained pigeons as a function of chamber air temperatures. Data for the lower points were obtained in this study; the upper curve was calculated from data reported in (2).

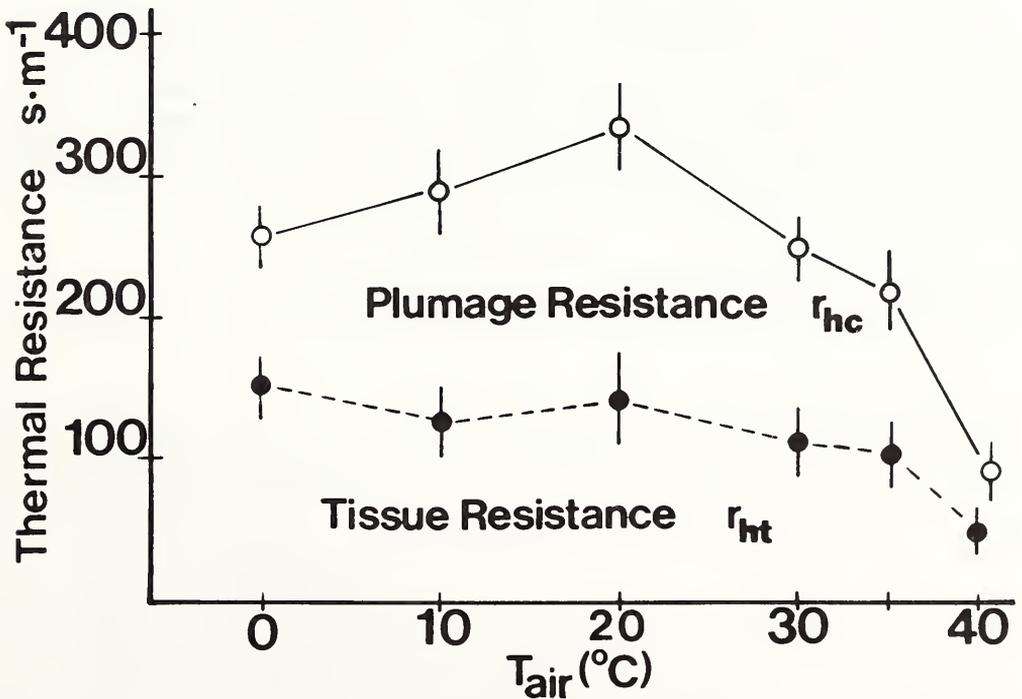


FIGURE 2. Tissue (r_{ht}) and plumage (r_{hc}) thermal resistance (mean \pm SE) in pigeons at different chamber air temperatures. No significant differences were detected between 0 and 20 C. Tissue thermal resistance decreased significantly at 30 and 35 C ($p < 0.05$, ANOVA) and both tissue and plumage resistance decreased significantly ($p < 0.05$) at 40 C.

5.3 s/m. Over the entire range of temperatures used, boundary layer thermal resistance was 90 s/m.

Discussion

Comparison of my results on the temperature dependence of whole-body thermal resistance of experimentally restrained pigeons to those of Calder and Schmidt-Nielson (2) in unrestrained pigeons indicates that in pigeons free to adjust their posture in the cold, a progressive increase in body insulation to twice that of thermoneutral levels is possible. Because these two data sets were collected under experimental conditions similar in all respects except restraint of the animal, differences in body resistance at 0 and 10 C most probably result from the inability of restrained pigeons to alter their exposed surface area by changing posture. If so, pigeons are evidently able to reduce their effective surface area to about 50% of thermoneutral zone levels by tucking the head, withdrawing the feet, fluffing the plumage, and bringing the wings in close to the body. The hypothesis that postural adjustments are an important means of increasing thermal resistance is sound, but further experimental testing is needed before these results can be confirmed.

Thermal resistances of the subcutaneous tissues and the feather coat in pigeons are approximately equal from 0-35 C under the experimental conditions of this study (Figure 2). My estimates of tissue heat loss resistance are slightly higher than those summarized by Campbell (3) for mammals, but a marked decrease in tissue thermal resistance at high air temperatures is apparently common to mammals and birds and almost certainly results from increased cutaneous bloodflow.

Estimates of avian plumage thermal insulation have been made for excised patches of feathers using heat flux plates (11), on live birds by measuring plumage surface temperatures with radiometers (6, 10), by removing the feathers and measuring changes in metabolic rate (1), and by measuring or estimating important animal and environmental variables to solve heat balance equations as in this study and (9). Excised plumage measurements may not accurately estimate coat thermal resistance in nature, although such data can be useful for comparison of the insulative value of different animal coats. Whole body measurements like those reported here reflect differences in coat thickness over the body and incorporate heat loss from unfeathered regions.

Feather coat resistances of several species of birds are given in Table 1. For comparison, the thermal resistance of a 1 cm thick layer of still air is 480 s/m (3), and the resistance of heavy winter coats worn by humans is about 400 s/m (5). Estimates

TABLE 1. Thermal resistance of avian plumages. Resistances in the third column are whole-body estimates; those in the fourth column are excised plumage measurements or whole-body data divided by estimated average coat depth.

Species	T _{air} (C)	Coat Resistance (s/m)	Coat Resistance per cm depth (s/m)	Source
Goose (down)	—	—	227	(5)
California Quail	20	282	—	(1)
Pigeon	—	—	176	(11)
Gray Jay	-8	465	232	(10)
Black-capped Chickadee	10	427	214	(6)
White-crowned Sparrow	20	400	240	(9)

of the thermal resistance of avian plumage per cm depth range from 176 s/m for pigeon breast plumage (11) to 240 s/m in the White-crowned Sparrow (9). Feather coats are evidently only 37-50% as effective as still air in impeding the loss of heat by convection and radiation from the skin surface. All available data indicate that avian plumages and mammalian pelage have thermal resistance values that are approximately half those of an equivalent depth of still air (5).

The sharp reduction of coat resistance in pigeons at high air temperatures apparent in Figure 2 may result from sleeking of the plumage, from alternate erection and depression of the plumage improving convective heat loss, or from free convection currents arising in the feathers due to the high temperature of the skin surface (4, 14). Such a reduction in coat resistance coupled with lower tissue thermal resistance could play an important role in increasing heat dissipation in heat stressed birds.

Conclusions

- 1) Whole-body thermal resistances at 0 and 10°C of the restrained pigeons used in this study differed significantly from those measured in unrestrained pigeons under identical conditions (2). These differences may reflect the inability of restrained birds to adjust their posture and thus reduce exposed surface area. Postural adjustments may therefore account for 40-50% of the increased thermal resistance of birds in cold versus thermoneutral air temperatures.
- 2) Thermal resistances of the tissue and the plumage coat in pigeons are reduced during mild heat stress, probably due to cutaneous vasodilation and ptilomotor adjustments coupled with increased free convection within the plumage.

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