SHORT COMMUNICATIONS

HEAT LOSS FROM DUCKS' FEET IMMERSED IN COLD WATER

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The feet of birds are important in the regulation of core temperature (Kahl 1963, Steen and Steen 1965, Johansen and Millard 1973) and are particularly effective in heat transfer when birds are normo- or hyperthermic (Steen and Steen 1965). Under natural conditions, they must also be sites of considerable heat loss when they are immersed in cold water or in contact with cold substrates (e.g., ice). However, the heat loss during cold stress can be substantially reduced by altering the pattern of blood flow to the feet (Grant and Bland 1931, Johansen and Millard 1973) and/or by transfer of heat from the arterial to the venous blood in vascular retes (Ederstrom and Brumleve 1964, Steen and Steen 1965).

Nevertheless, since tissues in the feet of birds presumably are maintained at or above 0°C (Irving and Krog 1955), some heat must be lost from the feet. We expected that, at temperatures below the freezing point, additional heat would be required to keep the feet from freezing, and that this amount of heat would increase with decreasing temperature. We therefore used calorimetric measurements to determine the exact amount of heat lost from the feet of Mallards (*Anas platyrhynchos*) when their feet are immersed in fluids at low and subfreezing temperatures.

MATERIALS AND METHODS

Experimental animals. The seven, adult Mallards used in these experiments were either wild-captured (three of seven) or incubator-hatched animals at least one year old. Prior to use they were kept in outdoor pens with access to water for swimming and were fed commercial bird feed. Their mean mass was 0.989 kg.

Accuracy, precision, and units. The accuracies of the various measurement processes are expressed as systematic error (bias) and imprecision as recommended by Eisenhart (1968). Systematic error of a measurement strictly speaking is unknowable; however, reasonable bounds to the magnitude of this error can be inferred from knowledge of the sensitivity of the particular measurement process to uncontrolled factors, namely, from statements of uncertainty or manufacturer's specifications. Imprecision, which measures the disagreement of repeated determinations of the same quantity by the same method, is best expressed by the standard error of that measurement (Eisenhart 1968).

The systematic error of a measurement was considered negligible if it was one tenth or less of the imprecision of measurements obtained during calibration or under experimental conditions.

When physical and derived quantities are reported in the International System of Units, equivalent values, expressed in other units, are included in parentheses.

Direct calorimetry. Heat loss from the bare portion of the ducks' feet was determined directly in a calorimeter in which the feet were immersed. A scaled cross-sectional view of the calorimeter is shown in figure 1. It consisted of two nested boxes, made from a thermostable plastic material (Textolite) and separated by low density insulation (18.2 kg m^{-3}) molded *in situ* from pre-expanded polystyrene beads (Dylite F-40T). The calorimeter was positioned within the working section of a refrigerated water bath (Forma, model 2088), which was maintained to within $\pm$ 0.5°C of the calorimeter temperature.

Calibration of the calorimeter was accomplished electrically (fig. 2). A measured voltage from a regulated power supply (Heath, model IPW-27) was applied to a coil of nichrome wire (R_2) and the rise in calorimeter temperature recorded. Voltage differentials E_1 and E_2 were determined with a Heath digital volt meter (model EU-805A). An Eppley standard cell (no. 760193) was used to check the calibration of the digital volt meter. The standard error (imprecision) of voltages recorded during calibrations was less than 0.2% of the values (0.6 v to 15.6 v). Systematic error of these measurements was negligible.

Rise in calorimeter temperature was measured with a system described elsewhere (Kilgore et al. 1973). Basically, the voltage output of a copper-constantan thermocouple was amplified, then adjusted to zero with a bucking voltage supply. Potentials beyond the bucked source (resulting from a rise in calorimeter temperature) were then recorded. Actual calorimeter temperature was measured with a Hewlett Packard quartz thermometer (model 2801A), calibrated with a mercury thermometer certified by the National Bureau of Standards. The systematic error of the absolute temperatures obtained during experiments does not exceed 0.03°C, while the imprecision does not exceed 0.05°C.

The fluid level within the calorimeter was held constant by adjusting the level in the outer water bath. The calorimeter bath volume (1600 cm^3) maintained during experiments was always within 1% of the volume during calibration. The maximum error in heat loss measurements resulting from this discrepancy was likewise less than 1%.

The calorimeter was calibrated prior to each experiment; hence, variations in heat flow across the walls of the calorimeter and in the specific heat of the calorimeter bath fluid were included in the calibration. This also applies to the aqueous solution of glycerol (36%) which was substituted for tap water at 0°C and subfreezing temperatures.

Oxygen consumption. Oxygen consumption was measured in an open-flow system. Room air was

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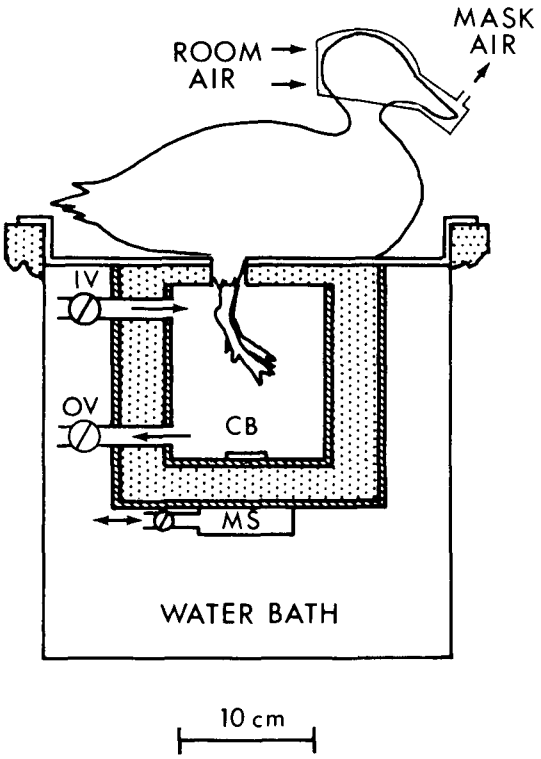

FIGURE 1. Cross-sectional view of calorimeter positioned within the refrigerated water bath. Circulation of fluid through the calorimeter bath (CB) was controlled by the inlet (IV) and outlet (OV) valves. The magnetic stirrer (MS) was air driven. Room air was drawn through the mask fitted over the duck's head.

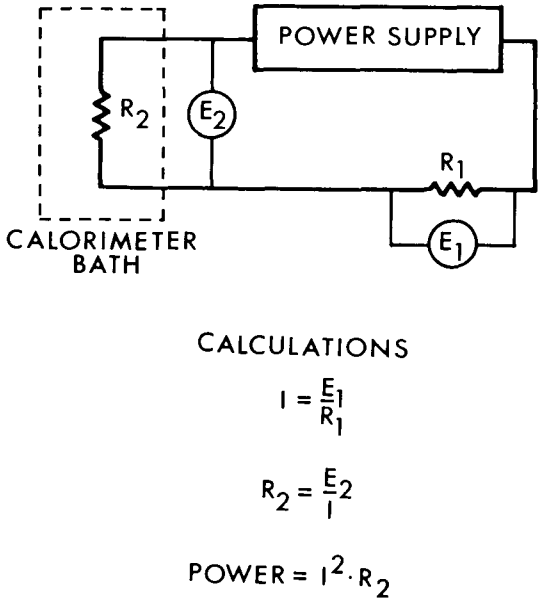

FIGURE 2. System used to calibrate the calorimeter. R_1 was a precision resistance of $10.5 \pm 0.1\Omega$, while R_2 was a coil of nichrome wire (diameter 0.25 mm). E_1 and E_2 represent the voltage drops across R_1 and R_2, respectively. For details, see text.

drawn at a constant rate through a mask fitted over the duck's head. Flow rate (V_E) varied from 88 to 94 $cm^3\ s^{-1}$ and exceeded the predicted respiratory minute volume of Mallards (Lasiewski and Calder 1971) by more than a factor of 10, ensuring that no exhaled air was lost. Flowmeters were calibrated with a VOL-U-METER (Brooks, model 1058) at pressures and temperatures identical to those maintained during experiments. The systematic error and imprecision of flow measurements obtained during flowmeter calibrations were less than 0.2% of the observed values.

Oxygen concentration in room air (F_{IO_2}) and in the excurrent mask air (F_{EO_2}) was determined by passing an aliquot sample of air (4.2 $cm^3\ s^{-1}$) through a Beckman G2 paramagnetic oxygen analyzer. The analyzer was calibrated by varying the air pressure within the sample cell, and frequently checked with a gas of known oxygen concentration. The systematic error of oxygen-concentration measurements was negligible. The imprecision of fractional oxygen concentrations does not exceed 0.06%.

Oxygen consumption ($\dot{V}_{O_2}$) was calculated using equation 3 from Tucker (1968) and assuming a fasting respiratory quotient (RQ) of 0.7. The maximum error in the calculated values resulting from this assumption would be 6.7% if the RQ were actually unity. More likely the RQ would be no higher than 0.8, which would result in a maximum error of 2.2%. A caloric equivalent of 19.7 kJ (4.7 kcal) per liter of oxygen consumed was used to calculate metabolic heat production.

Body temperatures. Cloacal and subcutaneous temperatures were measured with welded copper-constantan thermocouples (wire diameter 0.12 mm) coated with polyvinyl (Mobil, S-986-015). These temperatures were recorded on a Leeds and Northrup (Speedomax G) recording potentiometer. The systematic error of temperatures obtained with this system does not exceed 0.03°C, while their standard error does not exceed 0.09°C.

Cloacal thermocouples were shielded in polyethylene tubing and inserted into the cloaca to a depth of 4 cm. Subcutaneous temperatures were measured beneath the lateral dorsal surface of the central front toe and the lateral surface of the tarsometatarsus of one Mallard at temperatures below 0°C.

Experimental procedures. All experiments were conducted in a temperature-controlled room that was maintained to within ± 0.5°C of the calorimeter bath temperature. Heat loss from the feet and oxygen consumption were measured at a series of temperatures, about 4°C apart, between −8°C and 24°C. The measurements at each of these temperatures were completed within a 12-hr period. Prior to its use, each duck was fasted for 24 hr and then exposed to the experimental temperature for 2 hr. These experiments were conducted in mid-summer.

A duck was positioned with its feet in the calorimeter, and when the oxygen consumption remained stable for 15 min (± 0.02% O_2 in the excurrent mask air), the inlet and outlet valves of the calorimeter were closed simultaneously (fig. 1). The rise in calorimeter bath temperature was then recorded. Simultaneous recordings of oxygen consumption and calorimeter temperature were obtained for 5–15 min. The rise in calorimeter temperature during these periods was usually less than 0.1°C, and never more than 0.3°C.

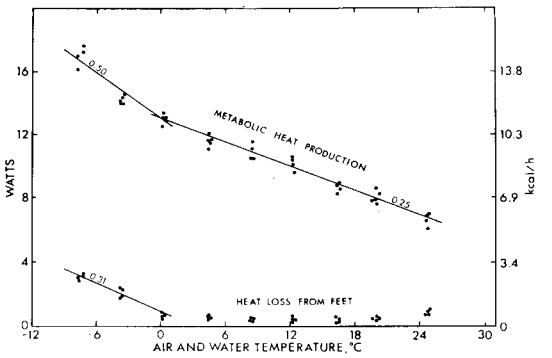

FIGURE 3. Relationship between metabolic heat production and air temperature (upper curve) and between heat loss from the feet and calorimeter temperature (lower curve). The slopes of the least-squares regression lines fitted to specific portions of the data are included in the figure, while the complete equations are included in the text.

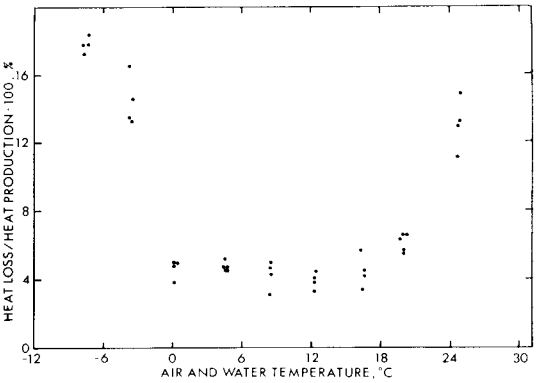

FIGURE 4. Heat loss from the feet of Mallards, expressed as a percentage of the simultaneous metabolic heat production.

At the end of the experiments, two Mallards were given an overdose of sodium pentobarbital and sodium heparin intravenously to facilitate vascular injection. The left and right femoral arteries were cannulated and the arterial and venous systems of the hind limbs flushed with heparinized saline solution. They were then injected with silicone latex (Microfil, MV 112) and dissected after curing to determine the femoral and tibial vascular anatomy.

RESULTS

Heat loss vs. calorimeter bath temperature. Heat loss from the ducks' feet to the calorimeter bath fluid remained relatively constant at bath temperatures between 0°C and 20°C (fig. 3). The mean rate of loss was 0.48 W (0.42 kcal hr^{-1}) which represents only 3–6.6% of the simultaneous metabolic heat production of the animal ($\dot{V}_{O_2}$) as shown in figure 4. At 24°C and below 0°C, heat loss from the feet was greater. The maximum rate recorded was 3.23 W (2.78 kcal hr^{-1}) at –8°C, which represented 18.3% of the metabolic heat production.

The relationship between heat loss (HL) and calorimeter bath temperature (T_{cb}) at and below 0°C can be described by the equation:

$$HL = 0.74 - 0.31T_{cb} \quad (S_{y\cdot x} = 0.25)$$

where $S_{y\cdot x}$ is the standard error of the estimate.

Oxygen consumption vs. air temperature. Oxygen consumption ($\dot{V}_{O_2}$) was inversely related to air temperature below 24°C (fig. 3). However, the rate at which it increased with declining temperatures was not constant. Below 0°C, oxygen consumption increased by a factor of two, from 0.25 W $°C^{-1}$ (0.22 kcal hr^{-1} $°C^{-1}$) to 0.5 W $°C^{-1}$ (0.43 kcal hr^{-1} $°C^{-1}$). The change in the rate of oxygen consumption corresponded to a change in the rate of heat loss from the immersed feet of 0.31 W $°C^{-1}$ (0.27 kcal hr^{-1} $°C^{-1}$).

The equations relating rate of oxygen consumption to air temperature (T_a) below and above 0°C are:

$$(-8°C \text{ to } 0°C)\ \dot{V}_{O_2} = 12.89 - 0.5T_a \quad (S_{y\cdot x} = 0.59)$$

$$(0°C \text{ to } 24°C)\ \dot{V}_{O_2} = 12.99 - 0.25T_a \quad (S_{y\cdot x} = 0.41).$$

Cloacal temperature. Cloacal temperature remained constant during an experiment, varying less than 0.1°C. The mean cloacal temperature was 39.9°C.

DISCUSSION

Steen and Steen (1965) demonstrated that considerable amounts of heat may be lost from the water-immersed feet of birds. They exposed Great Black-backed Gulls (*Larus marinus*) and Gray Herons (*Ardea cinerea*), whose feet were immersed in cold water (4°C to 12°C), to air temperatures above 20°C and found that 60–100% of the birds' metabolic heat production was lost from their feet. At lower air temperatures less than 10% was lost. In our work, where Mallards and their water-immersed feet were exposed to the same temperature, a smaller fraction (16% or less) of the metabolic heat production was lost from the feet at temperatures above 20°C (figs. 3 and 4).

As air and water temperatures decline to 0°C the heat loss from Mallards' feet becomes minimal and remains so despite an increasing metabolic heat production. This low heat loss from the feet could be explained by a vascular heat exchanger in the upper limb, or by a reduction in blood flow to the feet. Although the arterial and venous supplies to the lower limb of Mallards are juxtaposed there is no rete mirabile present. The lack of a vascular rete makes it probable that the low rate of heat loss is due to a reduction in blood flow. In the Giant Fulmar (*Macronectes giganteus*), which also lacks a tibial rete, immersion of the feet in ice water for more than a few minutes resulted in a decline in blood flow to the feet (Johansen and Millard 1973).

Below the freezing point of the tissues in the foot, additional heat flow to the feet may be necessary to prevent freezing damage to the tissues (fig. 3). Subcutaneous temperatures in the feet remained several degrees above 0°C, even when the feet were immersed in fluid at –8°C. This increased heat loss from the feet is accompanied by an increase, of similar magnitude, in the rate of heat production. The change in rate of heat production was 0.25 W $°C^{-1}$ (0.22 kcal hr^{-1} $°C^{-1}$), while the heat loss from the feet changed by 0.31 W $°C^{-1}$ (0.27 kcal hr^{-1} $°C^{-1}$).

It is apparent that when the feet of swimming and wading birds are exposed to subfreezing temperatures, freezing can be prevented by an increased blood flow, but at the expense of a substantially increased amount of heat lost from their feet. This increased heat loss

is directly compensated for by an increase in overall heat production.

SUMMARY

At temperatures between 0°C and 20°C, heat loss from the feet of Mallards was minimal (0.42 kcal hr^{-1}). In this temperature range, the metabolic heat production increased with declining temperature by 0.22 kcal hr^{-1} $°C^{-1}$. Below 0°C, however, heat loss from the feet and metabolic heat production both increased substantially. The further increase in heat production (0.22 kcal hr^{-1} $°C^{-1}$) was approximately equal to the increase in heat loss from the feet (0.27 kcal hr^{-1} $°C^{-1}$).

The observed increase in blood flow to the feet apparently serves to keep their temperatures above freezing and to prevent freezing damage to the tissues.

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INVERTED FLIGHT IN CANADA GEESE

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Canada Geese (*Branta canadensis*) are not usually associated with aerobatic flight, but during the filming of a large flock of geese (*B. c. canadensis*) landing on a field near the Bombay Hook National Wildlife Refuge, Delaware, in the winter of 1973, we recorded a series of spectacular flight maneuvers, some of which resulted in the birds flapping their wings while flying upside down. We filmed the same behavior on other occasions, and under different circumstances, and here report the results of an analysis of some properties of the behavior.

Films were taken on three separate occasions in 1973, using both Super-8 and 16mm cine equipment, and taken at various frame rates from 18 frames/second to 48 frames/second.

The first films were fortuitous. We were taking pictures of geese flying in Vee formation in connection with studies of formation flight (Gould and Heppner, Auk 91:494–506, 1974), and had a few feet of film left on a roll. We decided to shoot the rest of the roll on a flock of birds coming in for a landing, to clear the camera for a fresh roll of film. In landing, the birds flew as described below, in a way we had not seen on three previous field trips to Delaware (a reviewer has informed us that the behavior is common in geese in the midwest, but we have seen it in no more than 10% of the landing flocks we have seen in Delaware and Rhode Island). We subsequently filmed more landing flocks to obtain additional pictures of the maneuvers from different viewpoints. The geese were filmed from directly below, as they came toward the camera, as they flew away from the camera, and from the side. The only consistent meteorological variable on the days we filmed the behavior was gusty winds, although we have since seen the behavior on still days.

As working nomenclature, we have called the behavior "dumping," because it gives the visual impression that the birds are dumping, or spilling air from their wings, as a parachutist pulls his shrouds to change direction, or increase his rate of altitude loss.

Processed films were analyzed by projecting one frame at a time on a graph paper screen. Counts were taken of: 1) the number of birds in a landing flock, 2) the fraction of birds "dumping" ("dumping" defined as a 90° or greater bank) in a flock, 3) the duration in seconds of the "dumping" behavior, calculated from a wings-level position to return to wings level, 4) the fraction of "dumping" maneuvers involving some period of completely inverted flight, 5) the duration of inverted flight, 6) the number of maneuvers showing a 360° roll, and 7) the number of "dumping" maneuvers that showed a flap of the wings.

Measurements were also made of 8) the fraction of "dumping" maneuvers filmed in which a neighboring bird could also be seen displaying "dumping" behavior, 9) the mean number of birds that could be seen displaying a "dumping" maneuver at any one time, 10) the mean gain or loss in altitude of a maneuvering bird relative to the nearest neighbor in a normal attitude, measured in 1 mm "squares" on the graph paper screen, and 11) the mean period in seconds between the time the first and the last bird displaying "dumping" behavior could be seen in a landing flock.