

Surviving the Winter: The Physiology of Thermoregulation in Winter Birds

Winter is a stressful season of the year for birds of northern latitudes. Birds show many adaptations for winter survival, and some of these involve the challenge of maintaining body temperature. This article describes how birds regulate their body temperature in the cold of winter.

by Patrick T. Collins

The winter environment in arctic, subarctic, and temperate latitudes poses a number of challenges to small homeotherms. The combined factors of severe cold, lowered food availability, and shortened day length make maintenance of a high and constant body temperature much more challenging for these same animals than in the summer. There are three common strategies for dealing with the problems of winter. Mobile animals, such as birds can migrate to more hospitable climates. Less mobile animals, such as some small mammals, hibernate, and still others possess numerous adaptations which allow them to remain active in the temperate zone during winter. In this paper, I describe some of these adaptations as they relate to thermoregulation in birds. The primary focus is on physiological processes, but because both morphology and behavior are intimately tied to thermoregulation, I also will consider their importance.

HEAT PRODUCTION

There are two major methods involved in maintaining a high and constant body temperature in a cold environment, both of which are used by all birds to some degree when the temperature falls. The first one I will consider is the production of additional metabolic heat to compensate for the inevitable loss of heat to the environment.

The primary method of augmenting heat production in wintering birds is through muscular activity (Dawson and Hudson 1970). This muscular activity may be either shivering or exercise and must be fueled during the critical overnight period with stored energy in the form of either raw food items in the digestive tract or chemical stores in the body. Carey et al. (1978) found higher stores of glycogen in the pectoral muscles of winter goldfinches compared to summer individuals, and these winter

birds were able to use this glycogen and other stores of lipid for heat production when exposed to extremely low temperatures (-70°C). Summer goldfinches without these stores were unable to maintain thermal control at the same temperature. In mammals there is evidence for the production of heat which does not involve muscular activity; this takes place primarily in brown adipose tissue and has been termed non-shivering thermogenesis (Hill and Wyse 1989). This form of heat production, while it may not be completely lacking in birds (Barnett 1970), appears to be used very little.

There is little evidence that basal metabolism responds to cold by a significant increase during winter (Veghte 1964), or that arctic and temperate birds generally have a higher basal metabolism than tropical and sub-tropical birds to compensate for higher rates of heat loss (Scholander et al. 1950a). There is, however, a great deal of evidence that maintenance of thermoregulation depends on increased stores of lipid and muscle glycogen to sustain high rates of heat production (Carey et al. 1978). Schwan and Williams (1978) found that for the Common Raven in Alaska, thermoregulation depended on high rates of heat production rather than enhanced heat-conservation mechanisms.

High rates of heat production through muscular activity must be accompanied by increased food intake. This increased food intake also results in increased heat production from specific dynamic action (Brooks 1968) and may contribute significantly to the total increase in heat production required by small homeotherms.

There are relatively few studies published on unique mechanisms by which birds obtain the greater food require-

ments needed to increase heat production in an environment with lowered food abundance and fewer daylight hours in which to forage. Veghte (1964) reported that Gray Jays utilize pre-dawn and dusk hours to extend their available foraging time, and Brooks (1968) speculated that Common Redpolls may travel between overnight roosts and foraging areas in darkness to maximize the daylight hours spent searching for food. Cade (1953) has also seen redpolls feeding under the snowpack to exploit food resources which would otherwise be unavailable and speculates that the bold and inquisitive nature of these birds is an adaptation to an environment in which food must be obtained in an opportunistic manner. Whether these are common strategies for meeting the greater energy demands of winter is not yet clear, and further research needs to be done in this area.

HEAT CONSERVATION

The second major factor in maintaining a high and constant body temperature in winter is the conservation of metabolic heat. The loss of excess metabolic heat in birds during summer is accomplished to a great extent via evaporative cooling. It is intuitive, then, that minimizing evaporative heat loss is essential in conserving heat in a cold environment. A problem could arise, however, because an increase in metabolic activity to augment heat production requires an increase in oxygen consumption, and might entail an increase in evaporation in the respiratory passages. Evaporation in the respiratory passages is the primary mechanism of evaporative cooling for birds. Experimental data show, however, that evaporative water loss is constant or

decreases below the upper critical temperature for birds (Johnson 1968, Dawson and Hudson 1970, Mugaas and Templeton 1970). Mechanisms for minimizing evaporative heat loss have been speculated to be cooling of respired air via countercurrent heat exchange to lower the moisture holding capacity of the air and increasing the oxygen consumption efficiency rather than increasing the ventilation rate.

Another mechanism for conserving metabolic heat is increasing insulation. Birds have been shown to increase their insulation by adding feathers (Hutt and Ball 1938, Irving 1960, Veghte 1964, Barnett 1970, Dorst 1974), thereby increasing their tolerance to extremely low temperatures (Barnett 1970). They are able, with changes in posture, to change the surface area exposed to the environment. Birds often can be seen with one or both legs withdrawn into the plumage (Alder 1963) or with bills tucked beneath a wing or under the feathers of the back, effectively reducing conductance from these poorly insulated appendages (Veghte and Herreid 1965). Surface area can be reduced further and the boundary layer between the environment and the body interior can be increased with the erection of the feathers (Hill et al. 1980). This process makes a bird more spherical (Veghte 1964) reducing conductive and convective heat loss and trapping more air with the fluffed feathers as long as the wind speed is low. When wind speed is high, erect feathers are less effective at preventing convective heat loss than compressed feathers, and feather erection may cease to be advantageous (Veghte 1964).

Huddling is an important behavioral mechanism to reduce heat loss to the environment (Brenner 1965). Huddling

may be especially important at night (Moore 1945) when energy conservation must be maximized so as not to deplete limited energy reserves before more can be obtained in the morning. Radiant energy is exchanged between the birds in a huddle, conserving much of the energy which would have been lost to the environment (Brenner 1965, Dawson and Hudson 1970). A bird completely surrounded by others benefits by receiving radiation from all sides, and losing none to the relatively greater radiation absorbers of the environment. A bird on the periphery of the group benefits less but still receives more radiant energy from its fellows than it would from most other environmental features, and may be able to exchange positions with those deeper in the huddle as the night goes on.

Comparisons of energy expended overnight by birds at a given environmental temperature in the laboratory with energy expended by birds in the wild often show significant differences (Chaplin 1974). Birds in the wild typically expend less energy overnight than do conspecifics in a metabolism chamber. One reason for this may be the use of huddling, but a more common procedure used by birds in the wild is the use of shelter or more favorable microclimates. Black-capped Chickadees and House Sparrows commonly use tree cavities for shelter in severe weather. These cavities protect the birds from effects of wind and from radiant heat loss to the night sky (Moore 1945). When environmental temperatures are -30°C , House Sparrows can conserve more than 13% of their normal overnight energy expenditure (Kendeigh 1961) by sheltering in cavities. Ruffed Grouse and Willow Ptarmigan (Irving 1960) dive into deep snow and tunnel into the snowpack so as to

use the insulating ability of the snow to their advantage, and chickadees and redpolls have been found to take shelter in the thickest parts of conifer trees at night (Odum 1949, Brooks 1968). Other features which birds may use to their advantage include thick grass, ground irregularities, and the shelter provided by a tree trunk (Moore 1945).

It is well known that birds which migrate long distances put on a large quantity of fat to sustain their energy needs on the journey. As much as 50% of their pre-migration body weight may consist of lipid (Welty 1982). Birds which remain in the temperate zone also may put on additional stores of lipid (White and West 1977, Carey et al. 1978). These stores may be more than 12% of the body weight (Chaplin 1974). Part of the need for this apparent surplus is in maintaining a heightened level of metabolism during the longer, colder winter nights but subcutaneous fat tissue also may function in increasing insulation in birds (Veghte 1964) as it does for many mammals, including humans (Cannon and Keatinge 1960). King and Farnner (1966) found a significant negative correlation between subcutaneous fat and temperature below 3°C, indicating a response to cold of adding insulative fat tissue.

Heat loss is relative to the heat gradient between the bird's body and the environment. To reduce this gradient for appendages which cannot be adequately insulated (the legs, for example), homeothermy is relaxed for a region of the body in some birds. The legs of a Herring Gull standing in cold air may be near 0°C (Chatfield et al. 1953) but are still under thermal control. The mechanism which allows this is termed countercurrent heat exchange. In this process, the arteries carrying blood to

the periphery lie in close proximity to the veins returning blood to the core. Heat from the warm outgoing blood diffuses into the cooler returning blood via the thermal gradient established in the periphery. In this way, heat is "spent" on warming the returning blood rather than on attempting to keep the periphery at the core body temperature where more of it would be lost to the environment (Chatfield et al. 1953). There are three obvious benefits in this system. First and foremost is the conservation of heat, second is the prevention of shock to the body core by cold blood which would need to be rewarmed and could lower the core temperature. Third is the benefit of keeping the periphery under thermoregulation, which prevents freezing which could occur if there were a simple reduction in blood flow as there is in many animal appendages such as in human fingers and toes.

Some birds may undergo controlled hypothermia (lowering of body temperature) to reduce the thermal gradient between their body and the environment. Black-capped Chickadees have been found to allow their body temperature to fall 10–15°C from a normal of 42°C (Chaplin 1974, 1976). This is essential for these small birds to conserve enough energy to survive the night. Chickadees are primarily insectivores which are unable, with this relatively low-calorie diet, to consume and store enough food energy to survive the night without lowering their body temperature to conserve energy (Chaplin 1974, 1976). Reduction in body temperature of this magnitude results in an energy savings of 23% per hour (Chaplin 1974). Redpolls, by comparison, feed on a higher-calorie diet of birch seeds and are able to consume and store a larger amount of energy. Redpolls can store

enough energy to maintain their temperature at the daytime level and so do not need to employ controlled hypothermia (Brooks 1968). This also appears to be the case of the Gray Jay which with its larger body size and behavioral adaptations (see above), can store enough energy to sustain significant heat loss overnight (Veghte 1964).

SUMMARY

Many species of birds appear to be well adapted physiologically, morphologically, and behaviorally to the special conditions of the winter environment. Mechanisms for increasing heat production include shivering thermogenesis, exercise, specific dynamic action and may include non-shivering thermogenesis. Mechanisms for heat conservation include minimizing evaporative cooling, increasing insulation, specialized overnight behaviors such as huddling and seeking shelter, winter fattening, regional heterothermy, and controlled hypothermia. While each of these mechanisms is effective for helping to maintain thermal balance for winter birds, few if any birds rely solely on one. Many of these mechanisms are used as components in the overall, integrated strategy that a bird employs to survive the winter.

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