The Condor 90:107–112

NOCTURNAL ENERGY EXPENDITURE OF DARK-EYED JUNCOS ROOSTING IN INDIANA DURING WINTER[1]

D. R. WEBB[2] AND CHRISTOPHER M. ROGERS
Department of Biology, Indiana University, Bloomington, IN 47405

Abstract. To determine the thermoregulatory significance of roosts used by Dark-eyed Juncos (*Junco hyemalis*) wintering in Indiana, we measured microclimatological variables inside and outside the roost and combined these measurements with earlier laboratory studies carried out in a wind tunnel. Air temperatures and vapor densities measured inside the roost did not differ from those outside the roost; however, the roost did afford significant shielding from winds present outside the roost, reducing wind speeds by about a factor of five. Shielding from wind was about four times as important to the birds' heat budget as was shielding from long-wave radiative exchanges. Despite the great reduction in wind speed, energetic cost of occupying the roost was 2.1 × SMR as opposed to 2.3 × SMR outside the roost. The selection of open roosts by small birds has limited advantages for energy conservation at low air temperatures. Fasting time, rather than direct thermoregulatory stress, is probably the critical factor for small birds roosting in winter.

Key words: Energetics; thermoregulation; Junco hyemalis; *winter; roost.*

INTRODUCTION

Birds wintering at temperate latitudes are faced with cold temperatures, long nights requiring fasting, and periods when food resources are covered by snow. Furthermore, air temperatures are often lowest during the nighttime period of enforced fasting. Such potential stressors suggest that the choice of the most favorable roost microclimate is particularly important in winter.

For convenience, avian roosts may be divided into three basic types (Reinertsen 1986): snow cavities or burrows, tree cavities, and perches in dense vegetation (termed open roosts herein). The advantages of open roost sites selected by birds have been the subject of several investigations (Kendeigh 1961, Calder 1974, Francis 1976, Kelty and Lustick 1977, Walsberg and King 1980, Mayer et al. 1982, Buttemer 1985, Walsberg 1986) and were recently reviewed by Walsberg (1985) and by Reinertsen (1986). However, only four previous studies have used heat exchange estimates based on wind tunnel studies incorporating the effects of wind penetration into the coat (Kelty and Lustick 1977, Mayer et al. 1982, Buttemer 1985, Walsberg 1986). Also, many studies have focused on relatively large species; only two studies have involved birds smaller than about 80 g in open roosts (Buttemer 1985, Walsberg 1986). Despite the large amount of physiological and ecological work on emberizids, no previous study has been concerned with the energetics of wintering emberizids. Finally, no previous study of which we are aware has continuously monitored climatic factors over a substantial portion of the wintering season. Instead, spot sampling techniques have been used over a period of several days to 2 weeks.

In this study, we use continuously recorded microclimatic data to:

(1) apply a previously developed model incorporating wind penetration into the plumage to the winter roosting energetics of a small roosting emberizid, the Dark-eyed Junco (*Junco hyemalis*),

(2) assess the effects of the physical structure of the roost on various components of heat exchange, and

(3) provide estimates of the net nightly energetic benefit of the roost selected by this small bird for several weeks of the winter season.

METHODS

STUDY SITE AND POPULATION

We studied a population of wintering Dark-eyed Juncos at Kent Farm in Monroe County, Indiana (39°N latitude). The site consists of old fields and several rows of evergreen shrubs surrounded by a deciduous woodland. The roosts used by the birds consisted of dense, closely growing cedar

---

[1] Received 25 February 1987. Final acceptance 8 July 1987.

[2] Present address: The Pennsylvania State University, Wilkes-Barre Campus, Lehman, PA 18627.

(*Juniperus virginiana*) and yews (*Taxus* sp.) about 2.5 m in height. We determined the roost sites used by the birds by watching them as they entered the roost at twilight and by examining branches for feces from roosting birds. During the early part of the study (January and February), we noted only juncos roosting in this area; by the end of the study (March), other birds had begun using the roost.

MICROCLIMATE DETERMINATIONS

We sampled air temperatures and wind speeds at six different perches within the roost and outside the roost (2 m to windward of the prevailing winds) at the same height (1 to 2 m) as the roosting birds. We used thermocouples to measure air temperatures, and a cup anemometer to measure wind speeds outside the roost. Within the roost, we used a hotwire anemometer to sample wind speeds. We also measured relative humidity with a capacitive sensor and long-wave radiative flux outside the roost with a Fritschen-type net radiometer. All instruments were monitored every minute by an electronic datalogger and readings were averaged hourly. We gathered data from late January to early March 1986, and obtained continuous records for 36 complete 24-hr periods. Fisheye photographs of overhead cover for assessment of long-wave radiative exchanges (Walsberg and King 1978) were taken in mid-February. We estimated long-wave radiation from the sky downward by equations 1.20 and 1.21 of Campbell (1981), then subtracted our net long-wave measurements to estimate radiative flux upward from the ground. We assumed that half of the bird was exposed to each radiative flux.

ESTIMATES OF NIGHTLY ENERGY EXPENDITURE

To determine the effect of weather conditions on energy budgets and thermoregulatory requirements of the birds, we used empirical measurements of the effects of air temperature and wind speed on metabolism (Murphy et al. 1986, unpubl.). The winter population of birds used in the physiological investigations occurs about 100 km from the population studied herein. These physiological measurements yield an estimate of metabolism for each combination of wind speed and temperature. Metabolic rates include the effects of latent heat of evaporation for completely dry air (Murphy et al. 1986, unpubl.).

Because vapor densities measured in the roost sometimes differed significantly from dry air, we include an assessment of the effects of evaporative water loss on the heat budget. For the assessment of the relative importance of long-wave radiation, we used the following formulations based on Robinson et al. (1976) and Campbell (1977):

$$M - E = \frac{p(T_b - T_e)}{(r_b + r_e)} \tag{1}$$

$$T_e = T_a + r_e \frac{R_{net}}{p} \tag{2}$$

$$r_e = \frac{(r_a r_r)}{(r_a + r_r)} \tag{3}$$

$$r_a = 307 \frac{(d)^{0.5}}{u} \tag{4}$$

where p is a constant used to provide unitary consistency (= 1,200 J m^{-3} K^{-1}); r_r, the radiative resistance, is estimated from table A.3 of Campbell (1977); r_b is the body resistance of the bird, estimated as the total resistance measured by Murphy et al. (1986, unpubl.) minus r_e, the effective external resistance; r_a is the boundary layer resistance afforded by the air around the animal; R_{net} is the net radiative flux (W/m^2); u is the measured wind speed; and d is the effective diameter of the bird. T_a is the measured air temperature, T_e is the operative environmental temperature (Bakken 1976, Robinson et al. 1976), and T_b is body temperature (assumed to be 39.5°C, as measured by Murphy et al. 1986, unpubl.). This formulation is identical to that used by Walsberg (1986) who also discusses the effect of alternative estimates of r_r on heat loss, and the interrelation of r_a and r_b.

RESULTS AND DISCUSSION

ROUTES OF HEAT EXCHANGE

Role of air temperature. In a nocturnal roost, no short-wave radiation is present, and conductive losses are minor due to the small amount of the bird's surface in contact with the branch. The only remaining avenues of heat loss are evaporation, convection, and long-wave radiation. Air temperatures can affect nearly all avenues of heat loss and thus constitute perhaps the single most important microclimatological variable for analyses of heat production. Air temperatures ranged from −17°C to +20°C, and averaged 0.6°C throughout the study (Fig. 1). Air temperatures within the roost averaged only 0.2°C higher than temperatures outside the roost. This small difference was not statistically significant (t-test, $P > 0.05$).

Evaporation. Evaporative water loss constitutes a significant source of heat loss for endotherms in cold environments. Evaporative losses are driven by the gradient between the water vapor density at the bird's surface and that of the environment, which varies as a function of air temperature and relative saturation (List 1951). For wintering juncos in completely dry air, heat loss due to evaporation varied from 5% to 17% of total heat loss, depending on air temperature and wind speed (Murphy et al. 1986, unpubl.). However, evaporative water loss in completely dry air would be greater than evaporative water loss for birds under the more humid field conditions of this study. This occurs because the gradient for water loss by the birds in the laboratory study was greater than that in the roost. It is possible to determine the imprecision in our field estimates of metabolism resulting from reliance on these laboratory data by examining the variation in saturation of the air that occurred during the study. We expressed this as the ratio of the actual gradient in water vapor densities measured at the roost site to the experimental gradient used by Murphy et al. (1986, unpubl.). Ratios of actual evaporative water loss gradients to the experimental gradient were highly correlated with air temperature. The relationship was curvilinear, with the actual gradient averaging 97% of the experimental gradient at −20°C, 90% at 0°C, and only 67% at 20°C. Over the course of the study, our data probably overestimate energetic demand by about 8%.

Thus, natural variation in water vapor densities can cause substantial differences in estimates of heat loss at higher air temperatures, even if the birds are not heat stressed. Although this analysis does not consider the effects of changes in organismal resistance with environmental vapor density, it is sufficient to show that future field studies would benefit from further experimental work on evaporative water loss. Additionally, water relations of wintering birds have rarely been considered. But low levels of environmental moisture at low temperatures, enhanced water loss associated with requirements for locomotion and thermostatic heat generation, and reduced availability of water because of seed diets and freezing of free water sources all combine to indicate the potential importance of water relations during winter.

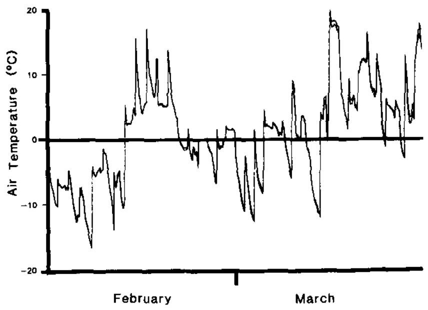

FIGURE 1. Air temperatures inside (upper trace) and immediately outside (lower trace) the roost during the study. Two lines are shown, but virtually coincide. The date axis originates at 10 February and ends at 21 March.

Convection. The roost provided substantial protection from the effects of wind (Fig. 2). Wind speeds outside the roost frequently exceeded 2 m/sec and wind speeds averaged over 1 hr sometimes exceeded 5 m/sec. By contrast, wind speeds within the roost rarely exceeded 1 m/sec and were usually about 0.3 m/sec (Fig. 2). Wind speeds within the roost were only mildly correlated with those outside the roost ($r^2 = 0.15\%$), probably because of momentary gusts and the differing responses of the different sized sensors to eddies of various sizes. On average, wind speeds within the roost were about 19% of those measured outside the roost.

Radiation. Previous studies incorporating wind penetration in heat exchange analyses of nocturnally roosting birds have noted a relatively minor role for long-wave radiation (Walsberg 1986). We compared the effects of the average differences in air temperature, the radiation environment, and wind speeds in terms of the metabolic power necessary to maintain homeothermy for birds inside and outside the roost. Because average air temperatures differed by only 0.2°C, the difference between metabolic power required inside the roost and that required outside the roost due to differences in air temperatures is less than 1%. The roost provided significant shielding (75%) from the night sky, suggesting that significant reductions in long-wave fluxes were possible. However, the difference in metabolic power based on this radiative shielding was only 3%. The difference in metabolic power based on reductions in wind speed inside the roost was 11%.

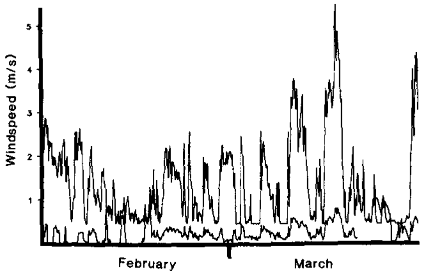

FIGURE 2. Wind speeds inside (lower trace) and immediately outside (upper trace) the roost during the study.

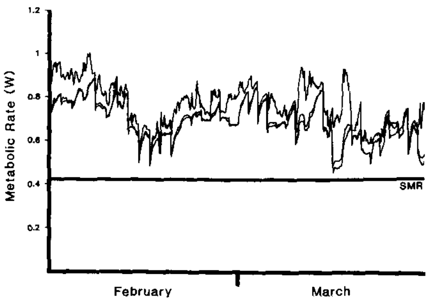

FIGURE 3. Required metabolic rate to achieve homeothermy estimated for conditions of free convection (bottom trace), inside the roost (middle trace), and outside the roost (top trace). Standard metabolic rate (SMR) from measurements of winter juncos (Murphy et al. 1986, unpubl.).

Thus the effects of the roost on ameliorating wind are "worth" about 3.7 times as much as the reduction in long-wave radiative losses. These results are similar to the factor of 5.3 thermal benefit in favor of wind shielding found by Walsberg (1986) and support his conclusion that reduction of long-wave radiative losses in open nocturnal roosts is relatively unimportant compared to reductions in convective heat loss.

EFFECTS OF THE ROOST ON METABOLIC POWER REQUIREMENTS

The effect of amelioration of wind in the roost is shown by the differences in the three curves for the required metabolic rate to achieve homeothermy (Fig. 3). The top curve represents conditions outside the roost, and the bottom curve represents conditions in a completely protected environment with no wind speed (free convection). The middle curve represents conditions within the roost. The curves for the roost and for nil wind-speed conditions nearly coincide, showing that even these open (noncavity) roosts are able to provide nearly complete shielding from wind. On average, metabolic power requirements in the roost differed from those of free convection conditions by less than 5%, which is less than the imprecision in most biophysical heat transfer models. Although we did not specifically assess whether birds chose the thermally best perches within the roost (Walsberg and King 1980), it is clear from this graph that little improvement in wind shielding is possible.

However, the major factor affecting the bird's heat budget, air temperature, cannot be ameliorated at all by birds roosting without the aid of cavities (Walsberg and King 1980, Buttemer 1985, Reinertsen 1986, Walsberg 1986). Thus, the required metabolism for homeothermy was substantially elevated above the basal metabolic rate and birds never achieved a thermoneutral condition (Fig. 3). Although we are unaware of any studies which specifically measured the metabolic scope of juncos, studies with other small passerines have demonstrated metabolic capabilities far in excess of the approximately 3 × SMR requirements shown in Figure 3 (Dawson and Carey 1976). In fact, the levels of metabolism shown in Figure 3 can be sustained by White-crowned Sparrows, *Zonotrichia leucophrys,* while they are asleep (S. McGuire and J. R. King, unpubl. data).

EFFECTS OF THE ROOST ON ENERGY EXPENDITURE

For the sake of simplicity, we may divide effects of heat loss on the birds into two problems: (1) thermoregulatory problems, in which it is sufficiently cold that the birds cannot physiologically produce enough heat to maintain their body temperature, and (2) energetic problems, in which the birds run out of food stores or are unable to mobilize food stores with which to generate heat (Marsh 1986). It is unlikely that healthy, well-fed, and well-watered juncos experience significant thermoregulatory problems during their time in the roost. In fact, Figure 3 makes it clear that such birds can easily survive outside the roost given sufficient energy stores. However, birds may well experience energetic problems in that they may run out of food stores during the night (Buttemer 1985) or be unable to gather adequate food stores during the day.

Figure 4 shows the nightly energy expenditure for juncos inside and outside the roost for each day of the study period. As in other such studies, our estimates assume that thermostatic requirements add to basal requirements and that activity costs are nil. The latter is likely a good assumption because birds are quiescent during the dark hours. A more tenuous assumption is that birds do not reduce their body temperature during the night. Although some studies have documented reduced body temperatures at night (Chaplin 1974, Reinertsen 1983), no studies of roost microclimates have yet determined the extent to which roosting birds engage in nocturnal hypothermia. Murphy et al. (1986, unpubl.) found no significant differences in body temperatures in their well-fed, wild-captured birds. Juncos fasted for 2 days showed slight hypothermia averaging 1.3°C (Stuebe and Ketterson 1982). This suggests that if nocturnal hypothermia is present in roosting juncos, it may be limited to birds that failed to fulfill their requirements for food during the day.

The roost provides a reduction in energy demand per night, averaging 10% over the course of the study (Fig. 4). Although the effect of the roost in reducing energetic demand per night is substantial, it is clear that this represents only a small portion of the total energetic demand imposed by climatic factors. For example, the roost reduces the average metabolic requirement from 2.3 × SMR to 2.1 × SMR. This reduction is relatively small (10%) because two major factors affecting energetic demand per night are unaffected by the roost microclimate: air temperatures and the length of time the birds must spend in the roost. Air temperature is the most important of these two factors, explaining 72% ($r = -0.85$, $P < 0.001$, multiple regression) of the seasonal variation in nightly energy expenditure in the roost. Night length explained only an additional 6% of the variation ($r = 0.72$, $P = 0.004$).

EFFECTS ON POTENTIAL FASTING TIME

We translated the reduction in nightly energy expenditure due to occupation of the roost into the number of hours a bird could fast at nightly metabolic rate inside the roost. Fasting hours were determined for each night with the following equation:

$$\text{fasting hours} = (E_{out} - E_{in}) \times \frac{\text{night length (hr)}}{E_{in}} \quad (5)$$

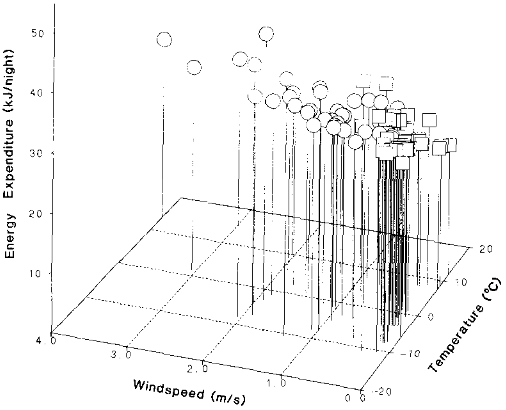

FIGURE 4. Effects of the roost on amelioration of wind speeds, but not air temperatures. The required energy expenditure to maintain homeothermy is plotted as a response surface on air temperature and wind speed. Circles: outside the roost; boxes: inside the roost.

where E_{out} and E_{in} refer to nightly energy expenditure outside the roost and inside the roost in units of kJ, respectively. Nightly metabolic rate was estimated by dividing nightlength into energy consumed inside the roost. Additional fasting time due to roost occupation ranged from 0.1 to 4.7 hr ($\bar{x} = 1.3$, SE = 0.14, $n = 36$ nights). As expected, this quantity was positively correlated with nightly wind speed measured outside the roost (Pearson's simple $r = 0.97$, $P < 0.001$). Because wind speed was usually not high at night (Fig. 2), roost occupation rarely added a substantial increment to potential fasting time of juncos. The additional fasting time provided by the roost is thus probably important only during episodic periods of heavy snowfall which limit foraging.

CONCLUSIONS

Our analysis agrees with most previous studies in that the open roost functions primarily to ameliorate convective rather than radiative heat loss. Although reduction in convective heat loss was the major advantage of roost occupation, the overall reduction in nightly energy expenditure was relatively small. This occurred because air temperature, the most important factor affecting metabolic rate, differed little between the roost and outside. Because the birds are evidently not in danger of exceeding physiological limits of heat production (termed thermal problems herein), the rate of heat loss itself is but one effect on the birds' energetic state. The ability to accumulate sufficient energy stores before entering the nightly fast may be of primary importance. We suggest that the provision of food stores for the night, particularly fluctuations in available resources caused by snowfall, and the extent of nocturnal hypothermia may ultimately prove of greater significance to individual survival than selection of any particular open roost.

ACKNOWLEDGMENTS

Portions of this research were funded by the Department of Biology, Indiana University, through a faculty development grant to Ellen Ketterson, who provided the datalogger and instrumentation. George Bakken provided the net radiometer. Mike Murphy and George Bakken graciously allowed access to unpublished data. Jan Eveleth assisted with portions of the fieldwork. Mike Murphy commented on the manuscript, and Ellen Ketterson provided fruitful discussions.

LITERATURE CITED

BAKKEN, G. S. 1976. A heat transfer analysis of animals: unifying concepts and the application of metabolism chamber data to field ecology. J. Theor. Biol. 60:337–384.

BUTTEMER, W. A. 1985. Energy relations of winter roost-site utilization by American Goldfinches (*Carduelis tristis*). Oecologia 68:126–132.

CALDER, W. A. 1974. The thermal and radiant environment of a winter hummingbird nest. Condor 76:268–273.

CAMPBELL, G. S. 1977. An introduction to environmental biophysics. Springer-Verlag, New York.

CAMPBELL, G. S. 1981. Fundamentals of radiation and temperature relations. Encycl. Plant Physiol. 12A:11–40.

CHAPLIN, S. B. 1974. Daily energetics of the Black-capped Chickadee, *Parus atricapillus*, in winter. J. Comp. Physiol. 89:321–330.

DAWSON, W. R., AND C. CAREY. 1976. Seasonal acclimatization to temperature in cardueline finches I. Insulative and metabolic adjustments. J. Comp. Physiol. 112:317–333.

FRANCIS, W. J. 1976. Micrometeorology of a blackbird roost. J. Wild. Manage. 40:132–136.

KELTY, M. P., AND S. I. LUSTICK. 1977. Energetics of the Starling (*Sturnus vulgaris*) in a pine woods. Ecology 58:1181–1185.

KENDEIGH, S. C. 1961. Energy of birds conserved by roosting in cavities. Wilson Bull. 73:140–147.

LIST, R. J. 1951. Smithsonian meteorological tables. 6th ed. Smithsonian Institution, Washington, DC.

MARSH, R. In press. Role of metabolic adjustments in surviving cold winters. Proc. XIX Int. Ornithol. Congr. (1986).

MAYER, L., S. LUSTICK, AND B. BATTERSBY. 1982. The importance of cavity roosting and hypothermia to the energy balance of the winter acclimatized Carolina chickadee. Int. Biometeorol. 26:231–238.

MURPHY, M. T., G. S. BAKKEN, AND D. J. ERKSINE. 1986. Metabolic responses of Dark-eyed Juncos (*Junco hyemalis*: Aves) to temperature and wind. Am. Zool. 26:112.

REINERTSEN, R. E. 1983. Nocturnal hypothermia and its energetic significance for small birds living in the arctic and subarctic regions. A review. Polar Res. 1:269–284.

REINERTSEN, R. E. In press. Behavioral thermoregulation in the cold: the energetic significance of microclimate selection. Proc. XIX Int. Ornithol. Congr. (1986).

ROBINSON, D. E., G. S. CAMPBELL, AND J. R. KING. 1976. An evaluation of heat exchange in small birds. J. Comp. Physiol. 105:153–166.

STUEBE, M. M., AND E. D. KETTERSON. 1982. A study of fasting in tree sparrows (*Spizella arborea*) and dark-eyed juncos (*Junco hyemalis*): ecological implications. Auk 99:299–308.

WALSBERG, G. E. 1985. Physiological consequences of microhabitat selection, p. 389–413. *In* M. L. Cody [ed.], Habitat selection in birds. Academic Press, New York.

WALSBERG, G. E. 1986. Thermal consequences of roost-site selection: the relative importance of three modes of heat conservation. Auk 103:1–7.

WALSBERG, G. E., AND J. R. KING. 1978. The heat budget of incubating mountain white-crowned sparrows (*Zonotrichia leucophrys oriantha*) in Oregon. Physiol. Zool. 51:92–103.

WALSBERG, G. E., AND J. R. KING. 1980. The thermoregulatory significance of the winter roost-sites selected by robins in eastern Washington. Wilson Bull. 92:33–39.