THE THERMOREGULATORY SIGNIFICANCE OF THE WINTER ROOST-SITES SELECTED BY ROBINS IN EASTERN WASHINGTON

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Selection of appropriate microclimates is generally thought to be an important component of avian behavioral thermoregulation. For many species, the winter night is perhaps the most thermally stressful part of the annual cycle, but the effect of winter roost-site selection on a bird's energy expenditure has been estimated quantitatively for only a few species, and the results are variable (e.g., Monk Parakeet [*Myopsitta monachus*], Caccamise and Weathers 1977; Jackdaw [*Corvus monedula*], Gyllin et al. 1977; Starling [*Sturnus vulgaris*], Yom-Tov et al. 1977, Kelty and Lustick 1978; House Sparrow [*Passer domesticus*], Kendeigh 1961).

Flocks of American Robins (*Turdus migratorius*) persistently roost in dense vegetation during winter nights in eastern Washington, as elsewhere in North America, although the flocks that we observed are much smaller than those reported near the center of the winter range (e.g., typically 20–40 birds/flock, compared with a group of 250,000 in Arkansas [Black 1932]). We hypothesized that roosting in dense vegetation is a habit that has evolved as a response to selection for thermoregulatory economy, and we tested this by examination of the microclimatic amelioration afforded by a dense grove of Douglas-fir (*Pseudotsuga menziesii*) that is habitually occupied by flocks of robins in winter near Pullman, Washington.

THEORY

Meteorological data may be used to estimate the power consumption of a roosting bird by application of an equivalent black-body temperature model. The model we use has been fully described and derived in earlier publications (Robinson et al. 1976, Campbell 1977) and tested by Mahoney and King (1977), and we give here only an abbreviated version.

The equivalent black-body temperature (T_e) is an integrated measure of an organism's thermal environment, representing air temperature (T_a) plus a temperature increment reflecting the effect of absorbed radiation:

$$T_e = T_a + (r_e/\rho c_p)(R_{abs} - \varepsilon\sigma T_a^4) \tag{1}$$

Here, ρc_p is a constant equal to 1200 J/m³−°C, R_{abs} represents radiation absorbed by the animal (W/m²), ε is the animal surface emissivity, and σ is the Stefan-Boltzmann constant (5.67×10^{-8} W/m² − °K⁴); r_e is the re-

sistance to heat transfer between the animal surface and the environment. It is calculated as the sum of the parallel resistances to heat transfer by radiation (r_r), and free (r_{fr}) or forced (r_{fo}) convection and thus subsumes, for example, effects due to wind. (See Walsberg and King [1978a] for equations and assumptions used to calculate r_e.) The difference between body temperature (T_b) and the equivalent black-body temperature of the environment defines the thermal gradient operating on the animal and net heat flux is proportional to this gradient divided by the thermal resistance of the system:

$$M - \lambda E = \rho c_p \cdot (T_b - T_e)/(r_b + r_e) \qquad (2)$$

Here, M is metabolic heat production, λE is evaporative heat loss, and r_b is the whole-body thermal resistance.

METHODS

Environmental measurements.—Meteorological data were recorded and averaged over 1-h periods by a Campbell Scientific Co. CR5 recorder. Duplicate measurements were made within the fir grove and 50 m away in an open field. All measurements in the open were made 2 m above the substrate (snow on 13, 14, 16, 17 Jan.; bare soil on 23, 24 Jan. and 9, 11, 12 Feb.). Within the fir grove, radiometers were placed 3–5 m above ground where robins had been roosting. Anemometers and thermocouples were placed 0.5 m below the radiometer. Downward long-wave radiation was measured with a Moll-Gorczynski sensor modified as described in Campbell et al. (1978). Upward long-wave radiation was calculated assuming that emissivity of the vegetation and substrate equaled 0.95 (Gates and Tantraporn 1952, Sellers 1965, Geiger 1965) and assuming that these surfaces were at air temperature. A total of 50 simultaneous measurements of T_a and plant and substrate surface temperature (with a Wahl HSA 120 infrared thermometer) during 5 nights revealed a maximum difference of 3°C. This maximum difference was detected only once and represents a soil surface temperature above T_a immediately after sunset. This difference would produce about a 4% error in the estimate of upward long-wave radiation at the air temperatures measured in this study. Measurements were made only after dark, when short-wave radiation was negligible. Air temperature was measured with 26 ga thermocouples, and wind velocity was measured with sensitive cup anemometers.

Animal characteristics.—Long-wave emissivity of the bird was assumed to equal 0.98 (Hammel 1956). The characteristic dimension used in estimates of convective heat transfer was assumed to be the average horizontal diameter of the torso of 3 robins when held with the long axis of the body in a typical angle (6.5 cm). Latent heat loss (λE) is estimated using equation 56 of Calder and King (1974), and nocturnal T_b was assumed to be 40°C. Body resistance was estimated using the heat transfer coefficient (h) estimated by equation 13 of Calder and King (1974) and assuming an average body mass of 74.9 g (Stewart 1937). This equation predicts h = 1.97 W/m² - °C when the external surface area of the bird is estimated as 0.0196 m² (Walsberg and King 1978b). This heat transfer coefficient represents a total thermal resistance ($r_b + r_e$) of 611 s/m. Here, r_e is the equivalent resistance operating on a bird under metabolic chamber conditions, in which free convection presumably dominates. Using the equations for r_r and r_{fr} of Robinson et al. (1976), r_e is estimated as ranging from 104 to 118 s/m when 0° < T_a < 25°C if the bird's surface temperature under cold conditions remains approximately 13°C above air temperature, as it does in the similar sized Gray Jay

TABLE 1
METEOROLOGICAL DATA AND ESTIMATED HEAT PRODUCTION FOR ROBINS[1]

Date	Location	Air tempera- ture (°C)	Down- ward long- wave radi- ation (W/m²)	Upward long- wave radi- ation (W/m²)	Wind velocity (m/s)	T_e (°C)	r_e (s/m)	Metabolic heat production (W/m²)
13 Jan.	At roost-site:	−16.0	235	251	0.82	−16.4	48	130.1
	Outside of roost-site:	−16.1	183	250	3.62	−16.8	25	136.8
14 Jan.	At roost-site:	−13.3	241	260	0.48	−13.7	60	121.4
	Outside of roost-site:	−13.3	189	260	1.24	−14.5	40	127.7
16 Jan.	At roost-site:	−4.5	287	295	1.62	−4.6	35	105.8
	Outside of roost-site:	−4.4	256	296	6.23	−4.7	19	109.6
17 Jan.	At roost-site:	−6.6	279	289	1.33	−6.7	39	110.0
	Outside of roost-site:	−6.6	263	289	4.29	−6.8	23	113.6
23 Jan.	At roost-site:	+0.6	307	319	0.71	+0.6	50	91.6
	Outside of roost-site:	+0.6	297	319	2.59	+0.6	29	95.2
24 Jan.	At roost-site:	−3.0	283	301	0.61	−3.5	53	100.2
	Outside of roost-site:	−3.1	229	301	1.88	−4.1	33	105.4
25 Jan.	At roost-site:	+1.2	306	321	0.69	+0.7	50	91.4
	Outside of roost-site:	+1.1	250	319	2.46	+0.2	29	96.3
9 Feb.	At roost-site:	+1.7	307	325	1.12	+1.4	41	91.4
	Outside of roost-site:	+1.7	243	325	5.80	+1.0	20	96.0
11 Feb.	At roost-site:	+1.9	317	327	0.67	+1.9	51	88.6
	Outside of roost-site:	+1.9	292	327	2.47	+1.8	29	92.5
12 Feb.	At roost-site:	+2.5	312	328	0.70	+2.4	50	87.7
	Outside of roost-site:	+2.3	294	326	2.55	+2.2	29	91.6

[1] For simplicity of presentation, only average values for the entire night are given. However, all calculations were made using hourly values.

(*Perisoreus canadensis*, Veghte 1964). If the surface-to-air gradient was 5° higher or lower than this, the estimated r_b value would be changed about 1%.

RESULTS

Behavior.—On 7 nights in January and February in which the number of arriving robins was counted, 24–39 ($\bar{x}$ = 28) birds occupied the fir grove. On 4 additional nights, no robins appeared. These 4 nights were not distinctive from those in which the roost was occupied, and the absence of a robin flock may be due to the use of alternative roost-sites. Birds arrived near dusk, between 16:00 and 17:00 PST, and departed at dawn, between 07:00 and 08:00 PST. Thus, the roost was occupied for 14–16 h

of a 24 h cycle. Behavior within the fir grove was observed after the birds had settled at dusk on 5 days and prior to departure at dawn on 4 days. Robins typically roosted 3–5 m above ground on a branch 1.5–2 m away from the trunk. Individuals were usually spaced 1–3 m apart and no tendency toward huddling was observed.

Meteorology.—Air temperature differed by an average of 0.1°C or less between inside and outside of the fir grove (Table 1). Wind velocity within the grove in areas typically occupied by robins averaged 28% of that outside of the grove (Table 1). Substantial differences also occurred in downward long-wave radiation. Downward radiative flux was greater within the fir grove by an average of 26% on 4 clear nights (13, 14, 24, 25 Jan. and 9 Feb.), 9% on 2 partially cloudy nights (16, 17 Jan.), and 6% on 3 overcast nights (23 Jan. and 11, 12 Feb.). Within the fir grove, downward flux averaged 5% below the calculated upward flux, thus indicating that the fir trees shielded the sensor or bird almost completely from the night sky.

Black-body equivalent temperature and equivalent resistance.—Reduction of windspeed within the fir grove produced an estimated 50–105% ($\bar{x}$ = 75%) increase in r_e compared to outside the grove (Table 1). Unexpectedly, T_e differed only slightly (0–0.8°C) between the 2 environments (Table 1). The small size of this difference may be attributed to 3 factors. (1) Air temperature is similar in the 2 environments. (2) Since T_a is similar, calculated upward long-wave flux is also similar. (3) Windspeeds are sufficiently high in both environments so that convective heat loss tends to override effects due to the radiative environment.

Power consumption.—Associated with the small differences in T_e, power consumption is estimated as being only 3–5% ($\bar{x}$ = 4.4%) higher for a bird roosting outside the fir grove rather than within it (Table 1). The general conclusion that the roost microclimate has only a slight effect on the thermoregulatory requirement is reinforced by an error analysis (Table 2). If key variables are changed 25%, the difference between the required heat production inside and outside the fir grove remains as only a few percent. Error in estimating r_b is most likely to produce a substantial error in estimates of heat production. If our estimate of r_b as 500 s/m is 100% too large (i.e., r_b = 250 s/m), then energy expenditure for birds in both environments is about 94% greater than predicted; but even in this extreme case the heat production of a robin outside the fir grove is estimated to average only 7% greater than that of a robin inside the grove. The maximum difference (about 9%) in this case occurs on 25 Jan.

Not yet considered in this analysis is the energy potentially saved by radiative exchange between robins or by reduction of wind penetration into the plumage. No net radiative heat transfer from 1 bird to another will

TABLE 2
SENSITIVITY OF ESTIMATES OF AVERAGE NOCTURNAL ENERGY EXPENDITURE TO 25% ERRORS IN KEY VARIABLES

Component of calculation	Percent change in estimated average metabolic rate		Average percent difference between metabolic rates inside and outside of roost-site[1,2]
	At roost-site	Outside of roost-site	
Characteristic dimension			
25% increase:	−0.8	−0.4	4.8
25% decrease:	+0.9	+0.5	4.0
r_r			
25% increase:	−1.1	−0.5	5.0
25% decrease:	+0.3	+0.3	4.3
r_{fo}			
25% increase:	−1.9	−1.0	5.3
25% decrease:	+2.0	+1.7	4.1
r_b			
25% increase:	−18.6	−19.2	3.7
25% decrease:	+30.0	+31.1	5.5

[1] Calculated as $100 \times (1 - [M^{outside\ of\ roost\text{-}site}/M^{at\ roost\text{-}site}])$.
[2] Average difference is 4.4% using values described in Methods section.

occur if both maintain the same surface temperature. The significance of this effect is directly proportional, however, to the fraction of an individual's radiative environment that is composed of other robins. This fraction is undoubtedly small. Robins rarely roosted less than 1 m apart. The projected surface area of 1 robin viewed by another must be less than ½ of the bird's total surface area, or less than about 0.0098 m² (Walsberg and King 1978b). Thus, if all individuals in the largest observed flock (39 birds) remained at a 1-m radius and oriented themselves so that a maximum proportion of each bird's surface area was viewed by a single, central individual, less than 3% of the central bird's radiative environment would be composed of other robins.

It is not currently possible to estimate reliably heat loss from wind penetrating and disrupting the plumage, as contrasted with convective cooling at the plumage surface. Some investigations have analyzed the effects of wind penetration on swatches of fur (e.g., Lentz and Hart 1960), but little is known about the effect of live birds. Robinson et al. (1976) observed progressive decreases of the r_b of White-crowned Sparrows (*Zonotrichia leucophrys*) associated with increases of windspeed. This suggests penetration of wind into the coat with a consequent decrease of plumage thermal resistance. Values of r_b estimated from the average wind-

speeds in this investigation and the regression equation of Robinson et al. (1976) for r_b as a function of windspeed at $T_a = 1°C$ are 6–14% less for birds roosting outside the grove rather than within it ($\bar{x} = 9\%$). This would reduce the power consumption of robins inside the grove by an average of about 7% (range, 4–12%) compared with robins outside the grove.

DISCUSSION

The small effect upon power consumption that we estimate is produced by nocturnal roosting in the Douglas-fir grove indicates either that climatic effects not accounted for in conventional heat-budget modeling are of major importance or that our hypothesis is wrong and that factors such as protection from predators may be of greater significance than thermoregulatory economy. The latter seems particularly likely since robins conspicuously did not use what was apparently the thermally most favorable microhabitat available within the fir grove, against the tree trunk. Measurements with a Hastings air meter equipped with an omnidirectional probe revealed that potential roost-sites at the junction of a branch with the leeward side of a tree trunk were generally characterized by windspeeds (0–0.1 m/s) much lower than those at sites occupied by robins. Roosting close to the trunk could thus produce nearly total protection from forced convection. If heat loss under free convection conditions is estimated as described previously, the power consumption of a robin next to a tree trunk is estimated as 20% below that which would be required outside of the grove or about 5 times the reduction that probably is actually achieved. However, the potential advantage of this wind-free site may be offset by increased predation. A bird roosting on a branch 1–2 m from the trunk would be more likely to detect and escape a predator moving up the trunk than would a robin roosting nearer the trunk. Thus, our inability to associate nocturnal roost-site selection with substantial energy conservation refocuses attention on other modes of selection favoring shelter-seeking in birds, and may serve as a caution that either as yet unquantified meteorological effects may be of major importance or that the thermal significance attributed to the nocturnal microclimate in other studies (e.g., Kendeigh 1961, Calder 1973, Kelty and Lustick 1977) may not be transferable to other species and settings.

SUMMARY

Flocks of American Robins habitually roost in dense vegetation during winter nights in eastern Washington. A microclimatic analysis indicates that this behavior produces only a slight thermoregulatory benefit. It thus appears that either nonthermal factors (such as protection from predators) or thermal effects too poorly known to quantify may be of major importance.

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