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## THERMAL CONSEQUENCES OF ROOST-SITE SELECTION: THE RELATIVE IMPORTANCE OF THREE MODES OF HEAT CONSERVATION

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**ABSTRACT.**—Thermal factors potentially important in the selection of nocturnal roosts by birds include shelter from wind, local increases in air temperature, and improvement in radiation balance. I analyze the relative importance of these three factors using data describing the thermal relations of *Phainopepla nitens* and the meteorological properties of winter roost sites selected by this species. Shelter from forced convection provides approximately 5 times more thermal benefit than improvement of radiation balance. Possible metabolic heating by the bird of air within the roost site is unimportant. *Received 4 March 1985, accepted 15 August 1985.*

BASAL and thermostatic energy demands account for approximately 40–60% of the total energy expended by free-living birds (Walsberg 1983). Variation in thermostatic demands can importantly determine the fraction of an animal's energy budget that is available for allocation to elective activities such as reproduction, resource defense, and social activities (Walsberg 1983). Because thermoregulatory requirements are critically sensitive to variation in the local physical environment, microclimate selection is of central importance to thermal ecology and ecological energetics.

Birds typically restrict their foraging to daylight hours and therefore must rely on stored energy reserves to survive overnight. This period of fasting often coincides with peak thermostatic demands that may occur on relatively long and cold winter nights. It is not surprising that substantial mortality has been observed at nocturnal roosts during periods of intense cold stress (e.g. Odum and Pitelka 1939). This suggests that strong selective pressures exist to minimize thermoregulatory stresses by selection of appropriate nocturnal roost sites. Factors likely to be critical in such microsite selection are local air temperature, radiation balance, and shelter from wind and precipitation.

In this analysis, I quantify for one species at its winter roost site the relative importance of three of these factors: forced convection (wind), radiation, and local increases in air temperature likely to be caused by the presence of a bird resting in dense vegetation. Effects of precipitation were ignored due to the sporadic occurrence of rainfall in the desert habitat studied. Such a comparative analysis should allow insight into selective pressures affecting microhabitat selection.

### METHODS

The Phainopepla (*Phainopepla nitens*) is a small (about 25 g) songbird that resides in the Sonoran Desert during the winter. Individuals defend winter territories and roost solitarily. Nocturnal roost sites are usually in a particularly dense portion of a small tree (e.g. *Cercidium floridum*, *Olnya tesota*, *Prosopis juliflora*) or a mistletoe (*Phoradendron californicum*) clump infesting such a tree. Each night, an individual habitually returns to one of 2–3 such roost sites within its territory.

*Laboratory studies.*—Birds were captured during December in mist nets and maintained in an outdoor aviary at Arizona State University. They were therefore exposed to similar thermal and photoperiodic conditions as free-living birds. Birds were fed their

natural diet of mistletoe berries. All physiological measurements were made within 5 days of capture to reduce errors associated with acclimation.

Body temperature, oxygen consumption, and evaporative water loss were measured as a function of wind velocity in 5 individuals. Birds were held in a closed-circuit wind tunnel (volume = 18.3 l) similar to that of Gessaman (1972). Wind velocity could be varied from 0 to 4 m/s, as measured with a Thermo-netics HWA-101 hot-wire anemometer that had been calibrated with a laboratory standard pitot tube. Turbulence in the wind tunnel averaged 3% at 0.5 m/s and increased to 8% at 4 m/s, determined by the methods of Hinze (1959). Air temperature was held at  $10 \pm 0.2^\circ\text{C}$  by placing the wind tunnel in a Queue System environmental chamber. Oxygen consumption ( $\text{VO}_2$ ) was measured in an open-flow system utilizing an Applied Electrochemistry S3A oxygen analyzer. Flow rate of dry air was maintained by a Brooks mass flow controller at 600 cm/min.  $\text{VO}_2$  was calculated from the equation of Withers (1977). The energy equivalent of consumed oxygen was assumed to equal 20.1 kJ/l. Evaporative water loss was determined by measuring the dew point of excurrent air using an EG&G dew-point hygrometer and calculating water-vapor density using the equation of Riegel et al. (1974). Latent heat of vaporization was assumed to equal 2.4 J/mg. Body temperature was determined at the end of each experimental run by quickly removing the bird from the wind tunnel and inserting a 26-gauge thermocouple 2 cm into the cloaca for 60 s. Temperature was measured with a Wescor TC65 thermometer.

*Calculation of body resistance.*—Thermal resistance of the animal's body ( $r_b$ ) was determined from the relation

$$M - E = \rho C_p (T_b - T_e) / (r_b + r_e) \quad (1)$$

(Robinson et al. 1976). Here,  $\rho C_p$  is a constant ( $1,200 \text{ J} \cdot \text{m}^{-3} \cdot ^\circ\text{C}^{-1}$ ),  $T_e$  is operative temperature ( $^\circ\text{C}$ ),  $M$  is metabolic heat production ( $\text{W}/\text{m}^2$ ),  $E$  is latent heat loss ( $\text{W}/\text{m}^2$ ), and  $r_e$  is the total thermal resistance between the animal surface and the environment ( $\text{s}/\text{m}$ ). External plumage surface area was calculated as a function of body mass using Walsberg and King's (1978a) equation. During laboratory measurements the only thermally significant source of radiation was the chamber walls, and because these walls had a thermal emissivity greater than 0.9 and remained within  $1^\circ\text{C}$  of air temperature ( $T_{\text{air}}$ ),  $T_e = T_{\text{air}}$  (Bakken 1976, Robinson et al. 1976). Except under still air conditions,  $r_e$  was calculated using the equations of Robinson et al. (1976) and represents the parallel equivalent resistance to convective heat flow ( $r_a$ ) and an apparent radiative resistance ( $r_r$ ):  $r_e = (r_a r_r) / (r_a + r_r)$ . The equation for  $r_r$  is

$$r_r = \rho C_p / 4\sigma \epsilon T_{\text{air}}^3, \quad (2)$$

where  $\epsilon$  is thermal emissivity (assumed to equal 0.98)

and  $\sigma$  is the Stefan-Boltzmann constant ( $5.67 \times 10^{-8} \text{ W} \cdot \text{m}^{-2} \cdot \text{K}^{-4}$ ). The equation for  $r_a$  is

$$r_a = k(d/u)^{0.5}, \quad (3)$$

where  $u$  is wind velocity (m/s) and  $d$  is the characteristic dimension of the animal (m). The constant  $k$  is assumed to equal 307 (Robinson et al. 1976). The characteristic dimension is taken as 0.031 m, the typical midtorso diameter of Phainopeplas. The equation for  $r_r$  is one of several available (e.g. Bakken 1976); however, variation in this estimate is unlikely to have a significant effect upon estimates of  $r_e$  and  $r_b$ . For example, the largest contribution of  $r_r$  occurs at low wind velocities. At 0.5 m/s and  $T_{\text{air}} = 10^\circ\text{C}$ , these equations predict  $r_a = 81 \text{ s}/\text{m}$  and  $r_r = 953 \text{ s}/\text{m}$ . Thus,  $r_e = 75 \text{ s}/\text{m}$ . A 25% change in the estimate of  $r_r$  produces only a 2-3% error in  $r_e$  ( $r_e = 76 \text{ s}/\text{m}$  when  $r_r = 1,191$  and  $r_e = 73 \text{ s}/\text{m}$  when  $r_r = 715 \text{ s}/\text{m}$ ). Under still air conditions,  $r_e$  was estimated as 100 s/m (Robinson et al. 1976).

*Field studies.*—Phainopepla roosts were studied between 15 December 1982 and 30 January 1983 in the Sonoran Desert 48 km east of Gila Bend, Arizona along Vekol Wash at an elevation of about 935 m. Phainopeplas largely restrict their activity to a small territory ( $\bar{x} = 0.38 \text{ ha}$ ; Walsberg 1977). Roost sites were located by observing the birds as they moved to these sites approximately 15-30 min before sunset. Each of the 5 roosts analyzed was used by a different individual. In all cases, close approach stimulated the bird to leave the roost site, and data are thus for unoccupied roosts.

Data for a particular nest were collected during only one night and only during periods in which wind velocity was 0-4 m/s and air temperature was  $7-13^\circ\text{C}$ , to approximately parallel laboratory conditions. Data were collected only on clear nights, to maximize effects of roost-site selection on the bird's radiative environment. Density of cover over the roost was quantified by analyzing hemispherical photographs taken from each roost site with the camera axis placed vertically (Walsberg and King 1978b). The fraction of the upper radiative hemisphere occluded by vegetation was calculated from each photograph using the method of Walsberg and King (1978b). A Fritschen radiometer, modified as described by Idso (1971), was used to measure all-wave radiation. In this case, radiation consists almost entirely of long-wave radiation. Preliminary measurements of short-wave radiation (starlight and moonlight) using an Eppley pyranometer revealed this component to be negligible (i.e.  $<20 \text{ W}/\text{m}^2$ ). Air temperature was measured with a shielded 26-gauge thermocouple and wind velocity determined using the HWA-101 hot-wire anemometer. Instrument output was recorded on a Campbell CR5 data logger. Mean wind velocity for a 30-min period was determined by averaging instantaneous values recorded at 5-min intervals. Operative temperature was measured using taxo-

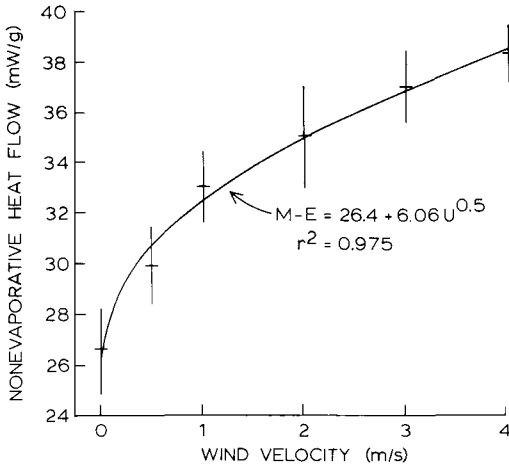


Fig. 1. Nonevaporative heat loss as a function of wind velocity in the Phainopepla. Values are  $\bar{x} \pm SE$ ,  $n = 5$ . Line fitted by least-squares regression using square-root transformation of wind-velocity data.

dermic mounts (Bakken and Gates 1975). These mounts consisted of a hollow copper cast of the bird's body covered by the animal's integument [see Walsberg (1982) for details of construction]. These devices closely resembled live Phainopeplas perching in normal posture. When allowed to thermally equilibrate with a microclimate, internal mount temperature equals  $T_e$  (Bakken and Gates 1975, Bakken 1976). After a 30-min equilibration period, mount temperature was measured using implanted thermocouples and the CR5 data logger.

Both  $T_e$  and meteorological variables were measured simultaneously inside and outside of roost sites. Measurements outside of roost sites were made in the open at a height above ground matching that of the roost.  $T_e$  was taken as the average temperature of 4 mounts in each site.

*Calculation of standard operative temperature.*—Standard operative temperature ( $T_{so}$ ) is a thermal index that allows direct comparison of widely varying microclimates (Bakken 1976). It represents the air temperature within a standard metabolic chamber that produces a degree of thermal stress equivalent to that produced by a natural microclimate. Here, standard conditions consist of still air within a black-body radiative environment (i.e. conditions produced in laboratory studies of Phainopeplas). Thus, this system of analysis allows one to equate variable effects of wind and radiation to equivalent changes in thermal balance that would be produced by air temperature variation. Modifying the formula of Bakken (1976) to incorporate thermal resistances rather than thermal conductances yields the equation

$$T_{so} = T_b - (r_w/r_t)(T_b - T_e). \quad (4)$$

Here,  $T_b$  is assumed to equal 39.6°C (the mean value observed in wind-tunnel studies),  $r_t$  is the sum of  $r_b$  and  $r_e$  under natural conditions, and  $r_{so}$  is the sum of  $r_b$  and  $r_e$  in standard metabolic chamber conditions. For estimates of  $r_w$ ,  $r_b$  was derived from wind-tunnel analyses and  $r_e$  was estimated using the equations of Robinson et al. (1976) for  $r_a$  and  $r_c$ . Equation 4 cannot be solved directly for  $T_{so}$  and was therefore solved numerically using the Marquardt iterative algorithm.

*Manipulation of  $T_{air}$  in the field.*—It is possible that the metabolic heat production of a cold-stressed bird locally heats air trapped within the dense vegetation surrounding the nocturnal roost (Buttemer 1981). To test for this, a resistance heater of the approximate size and heat output of a Phainopepla was placed in the roost. This heater consisted of a coil of nichrome wire placed within a 3.5 × 10-cm glass vial, which was painted flat black. The resistance wire was heated by applying approximately 12 V from a battery and power consumption determined from measurement of voltage and current flow. Because local heating of air in the roost site is most likely to be important under still air conditions, heat output was adjusted to 0.67 W, to mimic the average metabolic heat production of a Phainopepla in still air at 10°C. Measurements were made at each roost site once on each of 6 nights, but only during periods in which wind velocity was <0.4 m/s. As an additional test, heater output was increased to twice normal levels, 1.34 W. The effect of  $T_{air}$  within the roost site was examined using a shielded 26-gauge thermocouple connected to a Wescor TC-65 thermometer and mounted on a 40-cm long, 5-mm diameter plastic probe. This allowed  $T_{air}$  to be measured without disturbing the thermal conditions of the roost. Roost temperature was determined at 4 sites, each located 3 cm from the heater. The sites were (1) directly above the heater, (2) below the heater, (3) lateral to the windward side of the heater, and (4) lateral to the leeward side. Average roost temperature was compared with air temperature measured outside the roost, determined using the same probe and at the same height above ground.

## RESULTS

*Sensitivity of metabolic variables to wind velocity.*—As found in several previous analyses (e.g. Gessaman 1972, Robinson et al. 1976), nonevaporative heat flow was closely correlated with the square root of wind velocity ( $r^2 = 0.975$ ; Fig. 1). In this case, square-root transformation was preferable to logarithmic transformation because the entire data base could be used [data at  $u = 0$  cannot be used because  $\ln(0)$  is undefined] and because a larger fraction of the variance was explained using square-root

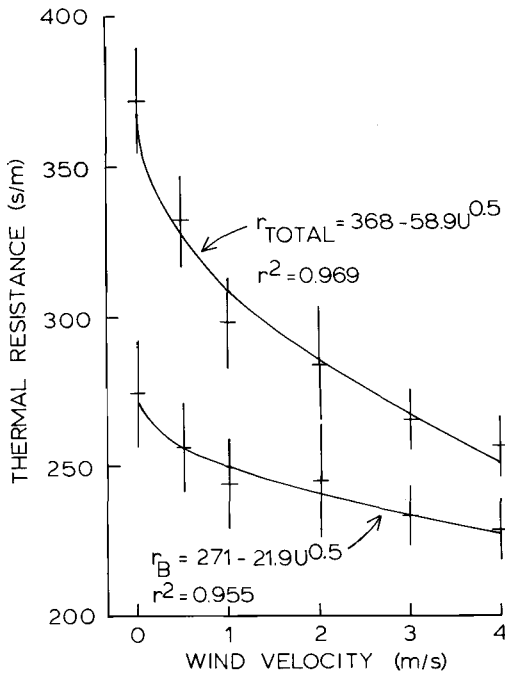


Fig. 2. Total thermal resistance ( $r_b + r_e$ ) and body thermal resistance ( $r_b$ ) of Phainopeplas as a function of wind velocity. Values plotted are  $\bar{x} \pm SE$ ,  $n = 5$ . Line fitted by least-squares regression using square-root transformation of wind-velocity data.

transformation [e.g. analysis of logarithmically transformed data indicates  $M - E = 32.3 + 3.77 \ln(u)$ ,  $r^2 = 0.873$ ; units as in Fig. 1]. Mean  $T_b$  did not vary significantly among different wind velocities (ANOVA,  $P > 0.05$ ); analysis of data

for all treatments yielded  $T_b = 39.6 \pm 0.318^\circ\text{C}$  ( $\bar{x} \pm SD$ ;  $n = 30$ ).

Similar to nonevaporative heat flow, total thermal resistance ( $r_b + r_e$ ) and body resistance ( $r_b$ ) were closely correlated with the square root of wind velocity (e.g.  $r^2 = 0.969$  for  $r_b + r_e$  and  $r^2 = 0.955$  for  $r_b$ ; Fig. 2). The decline in  $r_b$  probably reflects penetration of wind into the plumage and consequent disruption of the insulation. Such a decline as a function of  $u^{0.5}$  has been described in a variety of species (e.g. Gessaman 1972, Robinson et al. 1976).

*Physical environment of the roost.*—Roost sites were characterized by nearly complete overhead cover; analysis of hemispherical photographs revealed that a mean of 88% (SE = 10%,  $n = 5$ ) of the upper hemisphere over roost sites was composed of vegetation. Associated with this dense cover, downward long-wave radiation averaged 17–23% greater inside the roost site than outside; the difference was statistically significant at each of the 5 sites (Table 1). Wind velocity was significantly lower inside the roost site, averaging 18–30% of the velocity outside the roost (Table 1). Air temperature, however, differed slightly between the inside and the outside of roost sites. Statistically significant differences were observed in only 3 of the 5 sites, with  $T_{\text{air}}$  averaging lower within the roost in 2 cases and higher within the roost in 1 other case (Table 1). Note that roost sites were not occupied during measurements; thus, possible effects of metabolic heating on roost temperature are not subsumed in these data.

*Thermal consequences of roost-site selection.*—

TABLE 1. Meteorological conditions at, and adjacent to, Phainopepla nocturnal roosts.<sup>a,b</sup>

Site	$T_{\text{air}}$ ( $^\circ\text{C}$ )		Downward radiation ( $\text{W}/\text{m}^2$ )			Wind velocity ( $\text{m}/\text{s}$ )		
	In roost	Out of roost	In roost	Out of roost	Ratio <sup>c</sup>	In roost	Out of roost	Ratio <sup>c</sup>
A	9.0 (0.16)	< 9.6 (0.13)	327 (9.5)	> 278 (12.5)	1.18	0.36 (0.18)	< 2.02 (1.15)	0.18
B	10.4 (0.24)	10.4 (0.18)	339 (12.6)	> 283 (12.9)	1.20	0.86 (0.66)	< 2.38 (1.04)	0.30
C	11.1 (0.06)	< 11.6 (0.08)	347 (11.4)	> 286 (12.8)	1.21	0.68 (0.43)	< 2.76 (1.25)	0.25
D	11.0 (0.10)	> 10.8 (0.14)	340 (11.1)	> 290 (10.4)	1.17	0.68 (0.63)	< 3.11 (1.18)	0.22
E	8.8 (0.15)	8.7 (0.16)	335 (22.2)	> 271 (13.6)	1.24	0.60 (0.51)	< 2.53 (1.28)	0.24

<sup>a</sup> Values given are means, with standard errors in parentheses.  $n = 10$  for each case.

<sup>b</sup> ">" or "<" indicates that values are significantly different (paired sample  $t$ -test;  $P < 0.05$ ).

<sup>c</sup> Calculated as value in roost divided by that outside of roost.

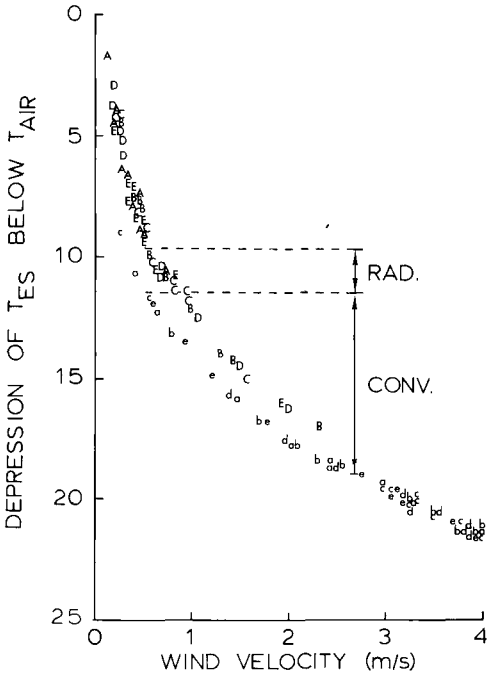


Fig. 3. Depression of standard operative temperature ( $T_{es}$ ) below air temperature ( $T_{air}$ ) as a function of wind velocity. Wind speed is either that inside or outside the roost, as appropriate for the datum. All data were collected when  $T_{air} = 7-13^{\circ}\text{C}$ . Letters identify sites. Upper-case letters represent data collected inside the roost; lower-case letters represent data collected outside the roost. Arrow labeled CONV represents average elevation in  $T_{es}$  produced by reduction of convective cooling within the roost. Arrow labeled RAD represents average increase in  $T_{es}$  produced by more favorable radiative environment of roost site. Dashed lines indicate location of average values over the data taken; see text for discussion.

Data describing depression of standard operative temperature below air temperature both inside and outside of the roost site were adequately described by linear regression with logarithmic transformation of wind-velocity data (Fig. 3, Table 1). Unlike analyses of laboratory measurements, data were logarithmically transformed because the entire data base could be used (i.e. no data were collected at  $u = 0$ ) and because logarithmic transformation explained a larger fraction of the variance than did square-root transformation. For example, when analyzing pooled data collected inside the roost, logarithmic transformation yielded  $r^2 = 0.897$  (Table 2) and square-root transfor-

TABLE 2. Relation of the depression of  $T_{es}$  below  $T_{air}$  to the logarithm of wind velocity.<sup>a</sup>

Site	a (SE)	b (SE)	r <sup>2</sup>
<b>Inside roost<sup>b</sup></b>			
A	12.2 (0.332)	4.68 (0.258)	0.976
B	12.6 (0.061)	4.93 (0.073)	0.998
C	12.3 (0.171)	4.41 (0.180)	0.986
D	12.4 (0.369)	5.03 (0.319)	0.962
E	12.6 (0.143)	5.13 (0.156)	0.992
Pooled data <sup>c</sup>	13.2 (0.278)	5.18 (0.005)	0.897
<b>Outside roost<sup>b</sup></b>			
A	14.0 (0.111)	5.01 (0.131)	0.994
B	13.6 (0.156)	5.43 (0.148)	0.994
C	13.3 (0.166)	5.23 (0.140)	0.943
D	14.4 (0.113)	4.86 (0.086)	0.987
E	14.0 (0.099)	5.19 (0.100)	0.997
Pooled data <sup>c</sup>	14.9 (0.295)	4.32 (0.005)	0.859

<sup>a</sup> Equations are in the form  $y = a + bx$ , where  $y = T_{air} - T_{es}$  and  $x = \ln(\text{wind velocity})$ . Units of temperature and wind velocity are  $^{\circ}\text{C}$  and  $\text{m/s}$ , respectively.  $n = 10$  for each site and 50 for pooled data.

<sup>b</sup> Analysis of covariance indicated no statistically significant differences ( $P > 0.05$ ) when comparing the equations describing  $T_{air} - T_{es}$  as a function of wind velocity outside the roosts or when comparing equations describing this relation inside of roost sites.

<sup>c</sup> Analysis of pooled data revealed that the constant  $a$  differed significantly among the regression lines describing conditions inside and outside the roost site [ $t$ -test following procedure of Zar (1974);  $P < 0.05$ ].

mation yielded  $r^2 = 0.830$ . When analyzing pooled data collected outside the roost, logarithmic transformation yielded  $r^2 = 0.859$  (Table 2) and square-root transformation yielded  $r^2 = 0.819$ . For data describing conditions inside roost sites, regression lines describing  $T_{es}$  as a function of wind velocity were not statistically distinguishable between different roost sites. Similarly, for data describing conditions outside the roost site, regression lines describing  $T_{es}$  as a function of wind velocity were not distinguishable (Table 2). Thus, for ease of presentation all data from separate sites were combined in Fig. 3. Analysis of the pooled data revealed a statistically significant difference between  $T_{es}$  as a function of wind velocity between conditions inside and outside the roost (Table 2). Use of these relations allowed an estimate of the relative importance of shielding from convection and radiative loss by the roost site (Fig. 3). Wind velocity was reduced from an average of 2.4  $\text{m/s}$  outside the roost site to 0.4  $\text{m/s}$  inside the roost. If radiative conditions remain constant and equal to those outside the

TABLE 3. Effect of simulated metabolic heat production on roost air temperature.<sup>a,b</sup>

Site	Heat input			
	0.67 W		1.34 W	
	$\bar{x}$	SE	$\bar{x}$	SE
A	-0.21	0.26	0.62	0.53
B	0.42	0.51	*0.71	0.27
C	0.36	0.27	0.41	0.62
D	0.51	0.62	*0.62	0.24
E	0.42	0.41	*0.70	0.30

<sup>a</sup> Values are elevation of roost air temperature over air temperature measured outside the roost.  $n = 8$  in all cases.

<sup>b</sup> \* indicates that roost air-temperature elevation is statistically significant (paired sample  $t$ -test;  $P < 0.05$ ).

roost site, such a decrease in wind velocity would elevate  $T_{es}$  8.0°C (Fig. 3). At this low average wind velocity characteristic of the roost site, the shift from outside to inside the roost reflects the change in  $T_{es}$  produced by variation in the radiative environment when wind velocity is held constant. The increase in  $T_{es}$  associated with the greater radiative input provided by the roost site was 1.5°C. Thus, the thermal benefit accrued from wind shielding (8.0°C) averaged 5.3 times that arising from shielding from excess radiation loss.

*Effects of local heating by a roosting bird.*—The possibility that a roosting bird locally heats air trapped within dense vegetation was tested by supplying heat with an electrical resistance heater. At a heat-production rate typical of a roosting bird (0.67 W), there was no significant increase in  $T_{air}$  within the roost (Table 3). When heat input was doubled (1.34 W), there was a statistically significant increase in  $T_{air}$  within 3 of the 5 roosts that averaged 0.5–0.7°C (Table 3).

#### DISCUSSION

In contrast to some previous studies (e.g. Walsberg and King 1980), this analysis indicates that a major thermal benefit results from use of nocturnal roost sites. Under typical conditions, standard operative environmental temperature is increased about 9.5°C. The data of Walsberg (1977) indicate that this change would produce an important reduction in resting energy expenditure (approximately 20% at 10°C). In spite of the nearly complete (88%) shielding from radiation loss to the night sky

provided by the roost site, these results clearly demonstrate that shielding from wind, not from radiation loss, is the major thermal benefit of nocturnal roost use. Such wind shielding produces approximately 5 times the thermal benefit associated with decreased radiation loss, and small changes in wind velocity can produce major effects on the animal's heat balance. This contrasts with the emphasis placed in previous analyses on radiation balance (e.g. Calder 1973, 1974). Finally, local increases in air temperature due to heat production equivalent to that generated by a roosting bird are insignificant compared with either radiative or convective effects. Indeed, such heating of the roost site could not be demonstrated to exist at typical levels of heat generation. At least in this species and setting, therefore, prevention of convective heat loss apparently is the primary thermal benefit driving selection of sheltered nocturnal roost sites.

It is important to note that the thermal effect of wind on an animal with a fur or feather coat can be attributed to two effects: convective cooling that occurs at the coat surface due to disruption of the adherent boundary layer, and disruption of coat insulation due to wind penetrating below the coat surface (Davis and Birkebak 1975). Traditional heat-budget analyses usually account for only the former effects. Few data are available with which to estimate effects of wind penetration into plumage insulation, which would be reflected by a decrease in body thermal resistance. Body resistance in *Phainopepla* declines as a function of the square root of wind velocity. This decline is substantial; with an increase in wind velocity from 0 to 4 m/s, 40% of the decline in the total thermal resistance experienced by the animal ( $r_b + r_e$ ) apparently is due to a decrease in  $r_b$  (Fig. 2). The apportionment of changes in total thermal resistance to changes in  $r_b$  depends, of course, on the accuracy with which  $r_e$  is estimated. This, in turn, depends on a set of assumptions regarding factors such as turbulent enhancement of convection. Therefore, the estimated change in  $r_b$  is only an approximation. It is notable, however, that similarly large declines in  $r_b$  with increased wind velocity have been observed in other bird species (e.g. *Zonotrichia leucophrys*, Robinson et al. 1976; *Calidris* spp., Chappell 1980). For example, my analyses (Walsberg 1985) of the data of Robinson

et al. (1976) for *Zonotrichia* suggest that at a wind velocity of 4 m/s, penetration of wind into the plumage produces increased heat loss equivalent to a 13°C decrease in  $T_{\text{sk}}$ . The magnitude of such effects indicates that adaptations acting to reduce wind penetration into plumages should be a subject of strong selection pressures. Behavioral responses such as site selection and postural adjustments are well documented (e.g. Lustick et al. 1978). However, possible morphological adaptations in plumage structure are as yet unexplored, although the results of this analysis clearly indicate that modifications affecting rates of convective cooling may be of major importance to the thermal balance of free-living birds.

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