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To augment their physiological and physical thermoregulatory capacity, many birds display long-term behavioral adjustments; the significance of this has been considered, yet detailed information is lacking (Dawson and Hudson 1970; Calder and King 1974). One such behavioral adjustment appears to be communal roosting in sheltered areas during winter nights. This behavior has been demonstrated in nuthatches (*Sitta* spp.) (Knorr 1957), finches (*Leucosticte* spp.) (French 1959; King and Wales 1964), eastern bluebirds (*Siala sialis*) (Frazier and Nolan 1959), red-winged blackbirds (*Agelaius phoniceus*), brown headed cowbirds (*Molothrus ater*), bronzed grackles (*Quiscalus quiscula*) (Francis 1976), and starlings (*Sturnus vulgaris*) (Francis 1976; Yom-Tov *et al*. 1977). Congregating in sheltered roost sites must alter some of those environmental factors which comprise the thermal climate space (Porter and Gates 1969) of the organism, and in doing so, confer an energetic advantage upon the inhabitants.

To further quantify the energetic advantage of the starling's nocturnal roost site selection in a dense coniferous pine woods, this study was undertaken to determine: (1) what microclimate factors distinguish areas of the pine woods selected as nocturnal roost sites from those that are not, and (2) what is the energetic advantage of roost site selection, and is this advantage dependent upon large roosting concentrations of birds.

MATERIALS AND METHODS

Study Area

To answer these questions, field data were collected during the winter 15 December - 21 March in a 1.5 km^2 pine woods (*Pinus strobus*) located 0.6 km north of Rathbone, Delaware County, Ohio. Trees within the pine woods averaged 9.3 m in height, 3.1 m apart in rows and 4.6 m apart. During the winter, this pine woods housed a large communal roosting flock, the size of which was estimated to be between 0.5 and 1.0 million birds. A detailed census of birds roosting in the pine plantation was not undertaken. From direct observations of the evening entry of birds into the woods and by mist netting operations, the species composition of the roosting flock was estimated to be 85% starlings, 5% red-winged blackbirds, and 10% other species, such as robins (*Turdus migratorius*), cowbirds, and grackles.

Roost Site Observations

Microhabitats within the pine woods selected by starlings as nocturnal roost sites were determined, by observing where individuals settled upon their evening entry and by noting amounts of excreta on trees and forest floor. To determine vertical positioning of birds, we constructed an observation shelter within the roost. Birds were viewed after dark with the aid of a flashlight, an infrared spotting scope (Varo Inc., model 9902 E[1]A), and a starlight scope.

Micrometerology

Four micrometeorological parameters were measured, and comparisons between the roost site and areas immediately outside the pine woods were made. Air temperatures were recorded with thermocouples connected to a Bailey Instruments, model Bat Four. Relative humidities were measured with an electric hygrometer (Hygordynamics Inc., model 15-3030E). Wind velocities were recorded with a hand-held,

three cup anemometer (starting speed 0.15 mps; Central Scientific Co., model 13B-1064) and a hotwire anemometer (Datametrics, model 800Vtp). Bird and environmental surface temperatures were measured with an infrared thermometer (minimum target diameter 3.8 cm; Mikron Instruments Co., model 44), the accuracy of which was verified by comparing surface temperature readings with the Bat Four thermometer.

Vertical temperature gradients within the roost were obtained by placing thermocouples at 0.0, 2.2, 3.7, 4.4, and 6.1 m above the forest floor in a centrally located tree. Temperature differences between the roost site and outside of the pine woods were obtained by additional temperature recordings at 2.2 m in field located upwind of the pine woods. Horizontal and vertical wind velocity profiles were obtained at the same sampling sites, except that vertical measurements within the roost sites were taken at 0.0, 1.5, 2.2, 4.7, 6.1 and 7.5 m above the forest floor. Measurements of relative humidities, which were subsequently converted to ambient water vapor pressures, were made at 2.2 m at the previously described sampling sites. These data were collected hourly on nights varying in both air temperature and wind velocity.

To establish radiant environment, surface temperatures of sky, trees, and ground were measured. In addition, surface temperatures of five starlings (tethered to hardware cloth platform on tree branches and allowed to settle for at least 30 minutes) were measured. Birds were placed in precisely the location in which individuals had roosted during clear, cold nights. Tethering prohibited flight but allowed for postural changes. Simultaneous to measuring the surface temperatures, cloacal temperatures of one of the birds was telemetrically monitored with a temperature sensitive radio transmitter (Mini-Mitter Co., Inc., model L-PM) in conjunction with a portable receiver (Lafayetter Radio Electronics Corps., model HA-420). In a similar manner, microclimatic data and surface and cloacal temperatures of tethered starlings were recorded in an adjacent open field.

To calculate radiation exchange, estimates of that percentage of a bird's surface exposed to the night sky and that percentage exposed to the coniferous microhabitat were necessary. To this end, measurements of the vegetation cover by use of a hemispherical fish-eye lens were made. Hemispherical photographs were taken by pointing the camera in an upward direction at different heights above the ground. Percent cover is then obtained by superimposing a standard grid on the photographs as described by Anderson (1964).

Through hemispherical photography, it was estimated that the coniferous trees shielded 75% of the bird's dorsal surface from the night sky. Incident nocturnal long wave radiation was measured with a net radiometer with a unidirectional attachment (Swissteco Pyt. Ltd., type S-1).

Experimental Animals

Thirty starlings were mist netted during January and February at the roost site. Animals were housed in individual cages in a walk-in environmental chamber (Scheer-Gillet, model 810). Birds were kept at ambient temperatures ranging from 5.0 to -10.0 C on natural photoperiods and were provided turkey pellets (Ralston Purina Co.) and water *ad libitum*. Birds were in the laboratory for at least 1 week prior to any metabolic rate determinations.

Oxygen Consumption

Metabolic rates (oxygen consumption) of 30 starlings were measured at three temperatures (-10.0, 0.0, 5.0 C) and at four wind velocities (0.0, 2.9, 7.3, 15 km h^{-1}). Oxygen consumption was measured in an open circuit system connected to an oxygen analyzer (Beckman Instruments Inc., model F-3) in conjunction with a potentiometric recorder (Heath Corp., model EUW-20A). A plexiglass tunnel equipped with a fan connected to a variable speed transformer, described by Neal (1976), was the respiration chamber. Desired chamber temperatures (± 1.0 C) were maintained by placing the apparatus in the walk-in environmental chamber. Water vapor pressure within the respiration chamber was not controlled during metabolic rate determinations.

Oxygen consumption was measured in darkness during 1800-2400 h on birds that had been fasted at least 2 h. Values were taken only after birds had maintained a steady state for 20-30 min. Having recorded the steady state value, I dimly lit the environmental chamber to observe behavioral reactions of birds to wind. After each oxygen consumption determination, except at the 5.0 C test temperature, the cloacal temperature of the bird was measured with a telethermometer (Yellow Springs Instruments, model 428C).

Statistics

Paired t-tests were used to compare temporally comparable microclimate data. Non-paired data were tested with the Student's t-test. The Jonckheere test was used with ordered alternatives when data fitted the one-way layout construct (Hollander and Wolfe 1973). A test devised by Skillings and Wolfe (1976) was used to test for ordered alternatives in block design experiments. Kendall's test was used to calculate correlations of microclimate data. Regression and correlation analyses of metabolism data were also used. All statistical analyses were performed at the 0.05 significance level.

RESULTS

Roost Site Observations

Differential use of certain areas in the pine woods for nocturnal roosting sites was displayed by starlings throughout winter. Initially (Dec. 1-9), roosting was vertically and horizontally homogeneous throughout the pine woods. By mid-December, however, roost site selection, which would last the duration of the winter, shifted from the periphery to the center of the woods. Roost site selection was refined as birds generally roosted between 1 and 4 m above the ground on windy and/or clear nights, and between 1 and 9 m on cloudy, windless nights. At all times birds roosted beyond bodily contact distance from each other.

Micrometeorological

Micrometeorological data, recorded during winter months (Table 1) and analyzed with paired t-tests, revealed that nocturnal air temperatures recorded at 2.2 m adjacent to the pine woods were not different from those taken at 0.0, 2.2, and 3.7 m within the roost. Temperatures high in the trees (4.9 and 6.1 m) were lower than those taken adjacent to the roost. Within the roost, an inverse correlation existed between measurement height and temperature (Kendall's Test). Wind velocities at the periphery, exposed to the prevailing northwesterly winds, exceeded those measured at 2.2 m within the roost, where they were almost always zero. Throughout the woods, height above forest floor and wind velocity were positively correlated (Kendall's test). Ambient water vapor pressures did not vary between roost and periphery recordings.

Micrometeorological data, recording during winter (radiation exchange study), (Table 2) and analyzed with student's t-test, revealed that air temperature, wind, velocity, and ambient water vapor pressure recorded at 1.8 m within the roost did not differ from recordings at 0.9 m at the periphery. Similarly, sky temperature and ground surface temperature did not differ between the same recording sites. Within the roost site, ground surface temperature, tree surface temperature, and air temperature were not different. Cloacal temperatures of birds inside the roost and at the periphery of the woods were similar (Table 2). Bird surface temperatures exceeded ambient temperatures to a greater degree within the roost site than at the periphery (Fig. 1).

As pointed out earlier the pine roost supplied at least 75% cover with some measurements as high as 96% cover.

Oxygen Consumption

Metabolic response to wind velocity (Fig. 2), which was analyzed with the Skillings-Wolfe test, revealed that increasing wind velocity (0.0 to 15.1 km h^{-1}) caused a concomitant increase in metabolic rates at -10.0, 0.0, and 5.0 C. Metabolic rates at 0.0 and 5.0 C were not different and were combined. At these temperatures, metabolism increased linearly with the square root of wind velocity, and the empirically weighted regression equation describing the data is;

$$MR = 13.68 + 2.68X; r = 0.98$$

$$\text{where: } MR = \text{metabolic rate (mW g}^{-1})$$

$$X = \text{wind velocity (km h}^{-1\frac{1}{2}})$$

Metabolic rates at -10.0 C increased linearly from 0.0 to 7.3 km h^{-1} and regression equation describing these data is:

$$MR = 16.80 + 3.01X; r = 0.70$$

At -10.0 C, subjecting birds to 15.1 km h^{-1} wind velocity caused metabolic rates to increase nonlinearly.

To estimate total heat flow, heat transfer coefficients were calculated according to Calder and King (1974). Heat flow is related to metabolism and temperature by the following equation:

$$h = H/T_b - T_a$$

where:
h = heat transfer coefficient (mW g^{-1} C^{-1})

H = heat loss (mWg^{-1}) which equals metabolic rate since cloacal temperature remained constant (Table 3; Skillings-Wolfe test)

T_b = cloacal temperature (C)

T_a = ambient temperature (C)

Increasing wind velocity generally caused corresponding increased heat transfer coefficients (Table 3; Skillings-Wolfe test) at -10.0 and 0.0 C.

Birds faced the convective current at all temperatures. At lower temperatures (-10.0 and 0.0 C), we observed marked piloerection and beak tucking. These behavioral patterns subsided when the wind velocity was returned to zero.

DISCUSSION

Evidence presented suggest that starlings select as nocturnal roost sites microclimates within the pine woods where air temperature, wind velocity, and radiant enviroment are altered to form thermally tolerable environments.

Air Temperature and Wind Velocity

Nocturnal air temperature varied spatially and temporally, and roosting behavior varied accordingly. Cold air temperatures in conjunction with wind caused roost site selection to be central, rather than peripheral, and low in the canopy, rather than high. Although air temperatures and cooling rates did not differ between roosting areas and adjacent fields, Francis (1976) and Yom-Tov et al. (1977) suggest that metabolic heat production of large numbers of birds elevates roost temperature. This discrepancy may reflect size differences in roosting flocks studied. Estimates of our roosting flock were one-third and one-eighth the flock sizes reported by Francis (1976) and Yom-Tov et al. (1977), respectively. Metabolic heat production of large and possibly more densely roosting flocks may cause elevated air temperatures. Because ambient water vapor pressure did not differ, it apparently did not influence roosting behavior. Nocturnal roosting sites were chosen such that exposure to wind was virtually eliminated and heat loss by forced convection was thereby minimized.

To estimate the energetic advantage gained by roost site selection, we measured starlings' metabolic response to wind and temperature simultaneously. Increased wind velocity elevated metabolism at all temperatures tested. Increased metabolic heat production is required to counterbalance total heat loss that is accelerated upon subjection to wind and not sufficiently reduced by the behavioral heat-conserving mechanisms of piloerection, orientation, and beak tucking. Of total heat loss, that due to forced convection primarily causes enhanced metabolic rates. Heat loss via conduction is minimal, as only feet contacted the respiration chamber. Evaporative heat loss is a small percentage of total heat loss in birds below thermal neutrality, and radiative heat loss is constant regardless of wind velocity. At all combinations of temperature and wind velocity, except the -10.0 C and 15.1 km h^{-1} combination, metabolic rates increased linearly with the square root of wind velocity. Hence, Gessaman's (1973) equation relating metabolic rate to wind velocity is applicable and expressed as:

$$MR = f(X)^{1/2}$$

where:
MR = metabolic rate (mW g^{-1})

X = wind velocity (km h^{-1})

Synergistic effects of a 15.1 Km h^{-1} wind velocity plus a -10.0 C test temperature caused metabolic rates to increase in a non-linear way. An explanation for these markedly increased metabolic rates is that air forcibly penetrates the feather layer. Interruption of physical integrity of the feathers would increase heat loss from the bird's skin down the steep thermal gradient existing between skin surface and air temperature.

Temperature and Radiation

Calder (1974) and Southwick and Gates (1975) suggest that nest site selection by

hummingbirds reduces heat loss via thermal radiation from birds to the cold night sky. An analogous situation appears to exist concerning nocturnal roosting of starlings in dense coniferous pine plantations. By combining radiation exchange formulae with metabolic rates of starlings, the energetic advantage accruing to sheltered roost inhabitants can be estimated.

Net radiation exchange is the difference between incident radiation from the environment and outgoing radiation from bird surfaces. This has been calculated according to the following equations:

$$Hr = \varepsilon_b \sigma T_b^4 \cdot [(\varepsilon_t \sigma T_t^4)0.5 \, S.A. + (\varepsilon_t \sigma T_t^4)0.5 \, S.A.]Z +$$
$$(\varepsilon_s \sigma T_s^4)0.5 \, S.A.]1-Z]$$
$$Hr = \sigma T_b^4 \cdot [(\varepsilon_g \sigma T_g^4)0.5\,S.A. + (\varepsilon_s \sigma T_s^4)0.5\,S.A.)]$$

Where: Hr = net radiation exchange (W bird $^{-1}$)

= infrared emissivities of radiating surfaces,

Where ε_b = ε bird = 1.00 (Calder and King 1974)

εt = ε trees = .090 (Sellers 1974)

ε_g = ε ground = 0.97 (Sellers 1974)

ε_S = εsky = 0.060 (calculation based upon measured sky temperature and incident long wave radiation according to Monteith 1975)

T = temperature of radiating surfaces (K)

Where T_b = T_{bird} (it is assumed that radiation from bird surface is uniform)

T_t = T_{trees}

T_g = T_{ground}

T_s = T_{sky}

σ = Stefan-Boltzman constant (8.14 x 10^{-11} by min^{-1}K^{-4} Seller, 1974)

Z. = percentage of bird's dorsal surface exposed to trees, estimated 75%. Outside the pine woods, it is assumed that one-half of the surface is exposed to ground and one-half is exposed to sky.

T_g = T_{ground}

T_S = T_{sky}

S.A. = bird's surface area (cm^2), estimated by a cloth-covering technique (Veghte, 1975)

Z = percentage of bird's dorsal surface area exposed to the trees, where Z is estimated at 75%. Outside of the roost it is assumed that one-half of the bird's surface is exposed to the ground and one-half is exposed to the sky.

Calculated radiative heat losses from birds located outside the pine woods were greater (Kruskal-Wallace Test; P<0.001) than those calculated for birds inside the roost and ranged from 2.68 W bird $^{-1}$ at 1.0°C to 1.96 W bird $^{-1}$ at -10.0°C. For birds within the roost receiving 25% of night sky radiation upon their dorsal surfaces and the remainder from coniferous microhabitat, heat losses ranged from 1.95 W bird $^{-1}$ ± at 2.0°Cto 1.24 W bird $^{-1}$ at -10.0°C. Other heat loss values were calculated for bird roost inhabitants receiving 18 and 4% night sky radiation.

These estimates of differences between radiative losses within and outside the roost are conservative in that counter radiation to birds is based solely upon tree temperature. This is legitimate because large numbers of birds in this study did not alter air temperatures in the roost, even though bird surface temperatures slightly exceed air temperatures.

Nocturnal heat production of starlings from -10.0°C to 5.0°C is described by the following equation:

HP = 1.13 - 0.02X; r = 0.45

Where: HP = heat production (W bird $^{-1}$)

X = air temperatures (C)

From this equation, heat produced below thermal neutrality can be calculated and subsequently compared with calculated heat losses from radiation exchange formulae.

Heat loss to heat production ratios (HL/HP) analyzed by Jonckheere test revealed that those ratios of birds outside the pine woods exceed those of birds within the roost (Fig. 3). For birds outside the woods, the ratio always exceeds unity; whereas that of birds within the roost and with the most cover from sky radiation is less than one (except at the highest temperature). Birds with an estimated 82% cover from sky display H1/HP

ratios intermediate between birds of the previously described locations (75% and 96% cover).

As seen (Fig. 3), HL/HP ratios gradually decrease from highest to lowest air temperatures. This seemingly paradoxical result can be reconciled. First, at lower temperatures heat production is greater. Second, because the difference between birds' surface temperatures and air temperatures is greater at higher temperatures, a greater temperature gradient exists between birds and other environmental surfaces. This would result in a greater net radiative efflux from birds at warmer temperatures.

The discussion to this point has dealt with radiation exchange between birds and clear night skies. Cloud cover alters heat flow interactions. For example, at -3.0°C, calculated heat losses from birds located outside the pine woods and exposed to clear skies (mean temperature = -28.0°C) averaged 1.83 W bird [-1], whereas that for birds exposed to cloudy skies (mean temperature = 3.0°C) was 0.165 W bird [-1]. Cloud induced changes in heat-flow interactions correlate with alterations in roost site selection, as birds roosted nearer the canopy on cloudy, windless nights and away from the canopy on cold, clear, and/or windy nights.

From the preceding discussion, the primary microclimatological determinants of starlings' roost site selection at a particular temperature appear to be a reduction in radiative and forced convective heat losses.

With the results from our wind and radiation studies, it is possible to estimate the energy savings derived from reduced radiative and convective heat losses afforded to starlings roosting in the sheltered pine plantation, At the -10.0°C test temperature, subjecting the birds to wind velocities from 0.0 to 15.1 Km hr^{-1} caused the metabolic heat production to increase from 1.35 to 3.63 W bird[-1]; whereas, the heat production required to counterbalance the radiative heat loss at -10.0°C is 1.24 and 1.96 W bird[-1], within and outside of the roost respectively. Together the resting metabolic rate of -10.0°C must be increased 4.27 times in order *to* maintain thermal homeostasis, if the birds are exposed to the described convective and radiative heat losses outside of the roost. This value approaches the limit of the ability of winter acclimatized starlings to increase their metabolic rate, which has been reported by Lustick and Adams (1977) to be 5.14 W bird[-1]. If, as in the previous example, the resting metabolic rate at -10.0°C has to be increased by 4.27 times, the metabolic heat production would be 5.76 W bird[-1]. It is apparent, then, that the total physiologic thermogenic potential of birds of this species would be inadequate to maintain thermal homeostasis when confronted with the high rate of convective and radiative heat losses present outside of the roost. It appears therefore, that precise roost site selection in this species is a requisite component of its thermoregulatory ability and is equally as important as the physiological and insulative mechanisms governing thermal homeostasis. We should point out that the maximum wind speed tested was 15.1 Km hr^{-1}, and this is a low wind speed compared to the wind speeds measured outside the roost.

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266

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TABLE 1. A comparison of micrometeorological characteristics inside and outside of an active nocturnal communal roosting site of starlings during winter, wind velocity tests (X± S.E.).

Microclimatic Factor	Height of Recording (m)	n	Inside Roost	n	Outside Roost
Air Temperature (C)	0.5	25	-3.3± 0.6		
	2.2	25	-3.6+ 0.9	25	-3.5± 1.0
	3.7	25	-3.5± 0.9		---
	4.9	25	-3.5± 0.9		---
	5.1	25	-4.1± 0.4		---
Wind Velocity (km h⁻¹)	0.0	5	0.5± 0.3		...a
	1.5	8	0.0± 0.0		...a
	2.2	28	0.0± 0.0	25	8.8± 1.1
	3.1	5	0.0± 0.0		...a
	4.7	8	5.0± 1.4		a
	6.1	8	9.8/± 1.6		...a
	7.5	8	15.10± 2.5		...a
Ambient Water Vapor Pressure (mm Hg)	2.2	22	3.0± 0.2	22	2.9± 0.2

a wind velocity recorded at 2.2 m ranged from 10.0 to 22.0 km hr⁻¹

TABLE 2. A comparison of microclimatological characteristics and starling cloacall temperatures recorded inside and outside a starling communal roosting site during winter radiation exchange tests. (X± S.E.).

Microclimatic Factor	Inside Roost (recording height 1.8 m)	n	Outside Roost (recording height 0.0m)	n
Air Temperature (C)	-2.4± 1.0	10	-3.4± 0.9	9
Wind Velocity (km h⁻¹)	0.0± 0.0	5	0.2± 0.1	8
Ambient Water Vapor Pressure (mm Hg)	1.9± 0.3	8	2.0± 0.3	8
Ground Surface Temperature (C)	-1.7± 0.8	10	-2.8± 1.2	9
Sky Temperature (C	-24.4± 2.5	10	-24.3± 2.7	9
Tree Surface Temperature (C)	-2.4± 1.0	10	---	
Cloacal Temperature (C)	38.3± 0.5	10	38.1= 0.3	8

TABLE 3. Laboratory metabolic rate (MR in mW g^{-1}), body temperature (T_b in C), and heat transfer coefficients (h in mW g^{-1}C^{-1}) of 30 starlings at various ambient temperatures (T_a in C) and four different wind speeds (X± S.E.).

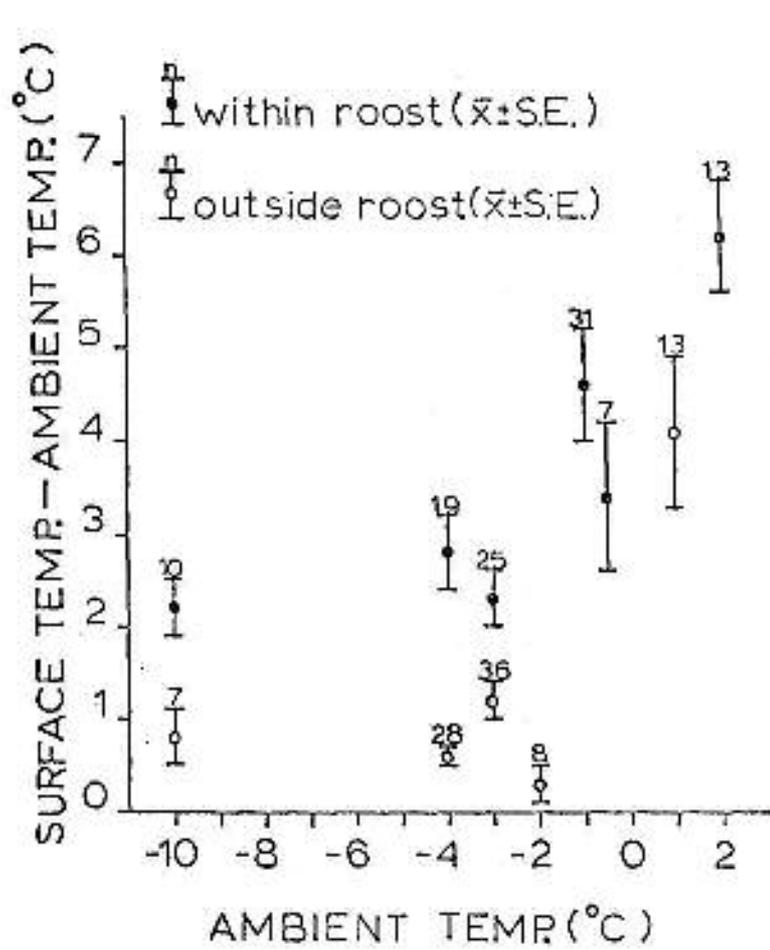|	0.0 km h^{-1}			2.93 km h^{-1}			7.30 km h^{-1}			15.10 km h^{-1}		
T_a	MR	T_b	h	MR	T_b	h	MR	T_b	h	MR	T_b	h
5.0	13.11 ± 0.96	--	--	18.30 ± 1.67	--	--	21.43 ± 2.34	--	--	23.05 ± 4.46	--	--
0.0	13.28 ± 0.73	37.4 ± 0.6	0.34 ± 0.02	20.09 ± 1.73	36.5 ± 0.3	0.58 ± 0.03	20.07 ± 1.73	35.0 ± 0.4	0.57 ± 0.05	20.48 ± 2.73	36.0 ± 0.4	0.59 ± 0.08
-10.0	16.85 ± 1.23	35.0 ± 0.4	0.35 ± 0.02	21.20 ± 1.73	35.5 ± 0.2	0.48 ± 0.03	25.28 ± 1.06	34.8 ± 0.3	0.56 ± 0.03	45.37 ± 0.73	35.5 ± 0.3	1.01 ± 0.61

FIGURE 1. Surface temperatures of starlings within the roost and outside the roost minus ambient temperature.
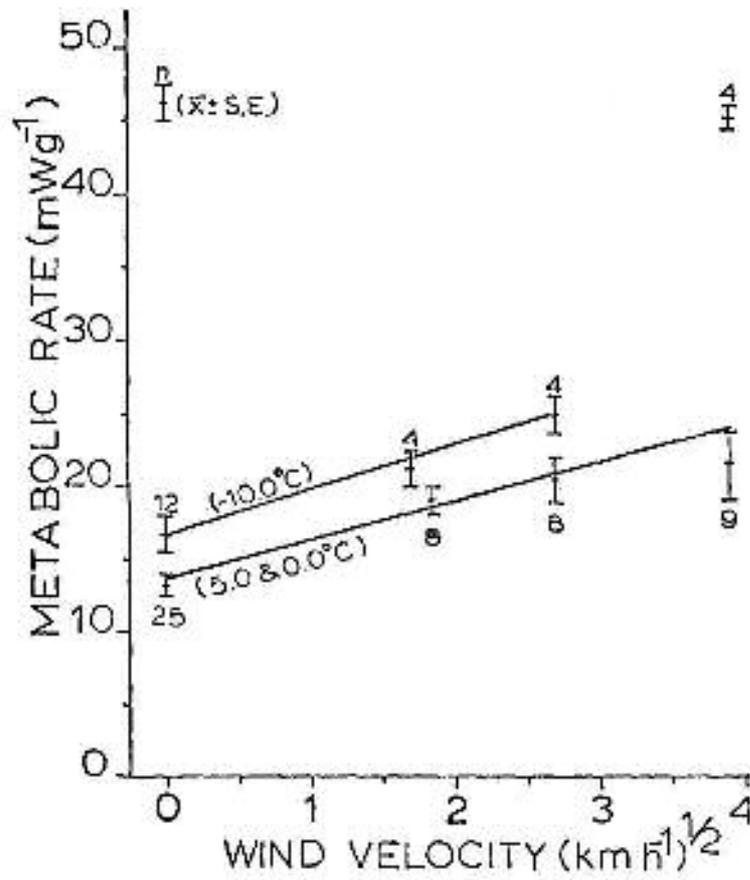
FIGURE 2. Metabolic rates of 30 starlings at three temperatures and four wind velocities. At -10.0C, the data for 1.71 km h^{-1} is shifted to left to avoid confusion.
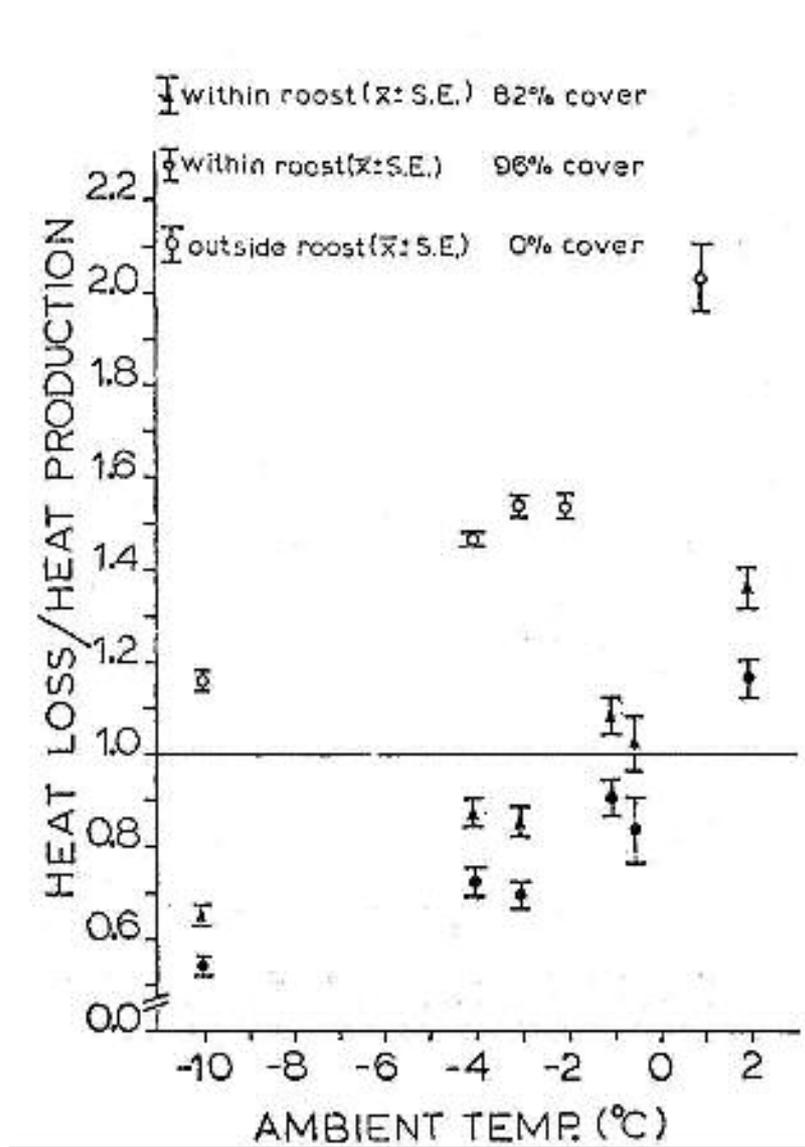
FIGURE 3. Ratios of heat loss to heat production of starlings located outside the roost and Inside the roost with different estimates of cover from the night sky. Sample sizes given in Figure 1.