

AN ABSTRACT OF THE THESIS OF

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Title: Influence of Heat Exchange on Foraging Behavior of

Zonotrichia spp.

Redacted for Privacy

Abstract approved:

Dr. John A. Wiens

The heat exchange of individuals in a foraging mixed population of Zonotrichia leucophrys and Zonotrichia atricapilla in western Oregon is analyzed with respect to the direction of stance and feeding location. Values for heat gain or loss in the field were generated from a model that estimates the equivalent black-body temperature " T_e " and from other researchers' laboratory findings for the effect of air temperature, solar radiation, and wind speed on metabolism. Observations were recorded at 1 min intervals throughout the daylight hours with samples at weekly intervals from January to March. A summation of 1,500 observations on direction of stance subjected to a χ^2 test for randomness supports the hypothesis that spatial orientation of individuals is not random. The largest percentage of time for all locations was spent facing south. All wind speeds over $1.0 \text{ m}\cdot\text{s}^{-1}$ recorded were from the south yet χ^2 analysis indicated a large difference in stance direction between sites. Also, maximum differences in T_e for different stances with respect to the wind direction were only 1°C because of the low values for incoming

short wave radiation. More important factors than heat exchange influencing the direction of stance were feeding patterns, social interactions, food availability and the location of the hedge in the area used for cover. Placing a trace line of food perpendicular to the most frequently observed direction of stance caused a significant change in percentage of time spent facing each direction for that location. Individuals were facing the same direction as the majority of their neighbors within a 2 m radius for 68% of the total number of recorded observations for a nonrandom flock orientation.

Heat production was affected by the large differences in wind speed among the microhabitats available at the site. Heavy use of an open area for feeding resulted in as much as an 8% increase in daily existence energy (DEE). The intense feeding at this site suggests that possibly the increased caloric intake per unit time at the open site compensates for the greater heat loss and increased susceptibility to predation. A second possibility relates the circadian feeding pattern to the need for a high rate of caloric intake early in the morning and late in the evening.

Influence of Heat Exchange on Foraging Behavior
of Zonotrichia spp.

by

Rob DeWoskin

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INFLUENCE OF HEAT EXCHANGE ON FORAGING BEHAVIOR OF ZONOTRICHIA SPP.

INTRODUCTION

Wintering Zonotrichia leucophrys and Zonotrichia atricapilla in Oregon have a variety of microenvironments from which to choose while foraging, from open areas with no grass to shrubs that provide protection from strong wind (see Figure 1). Whether crowned sparrows are sensitive to fluctuations in heat loss and how much effect this may have on their feeding pattern is the question this study was designed to answer. The underlying conceptual framework is represented by the first law of thermodynamics (Kleiber, 1975), which simply states that energy is conserved and that all changes in the energy of a closed system must be accounted for by whatever terms are used to describe the energy budget. For wintering Zonotrichia not reproducing, building nests, or storing energy in the form of fat, the energy budget for the steady state is:

$$M + R + C + \lambda E = 0$$

where M = metabolic rate, R = net radiation change, C = gain or loss of energy by convection, and λE = latent heat loss. To maintain a preferred temperature a sparrow can either alter its relation to the external environmental factors that influence the radiation (R) and convection (C) terms or it can undergo internal physiological responses that influence the metabolic rate (M) and latent heat loss (λE).

The external response has been quantified by Grubb (1975) for birds that changed their microenvironments as a result of excessive heat loss through convection. Mahoney (1976) has demonstrated in a

laboratory situation a preference of White-crowned Sparrows (Zonotrichia leucophrys gambelii) for radiation regimes that are close to the lower critical limit of their thermoneutral zone. But if White-crowns are unable to change their relationship to external factors, they will react with an internal response, in one case a decrease in metabolic rate with an increase in radiation (DeJong, 1976).

Measuring the internal response in the field is, of course, much more difficult than in the laboratory chamber. Gessaman (1973) reviews field techniques for estimating metabolic rate including the method of deuterium labelling and the electronic approach using telemetry. I prefer the more inclusive, heuristic methodology that has emerged from Porter and Gates' work (1969) on the thermal exchange between animals and their environments and from the construction of heat exchange models by King and his students at Washington State. The thermal dynamic method estimates metabolic rate not by measuring one variable like heart rate or carbon dioxide production, but by measuring many variables like incoming radiation, wind speed, direction of individual stance, and air temperature. These latter variables have known effects on heat exchange between White-crowned Sparrows and their environment based on many laboratory studies (King, 1964; Robinson et al., 1976; Southwick, 1971; to name just a few). The advantage to this method is that the underlying processes that influence changes in metabolic rate are explicitly known. For example, if all the environmental variables remain the same except for a change in the direction of stance with respect to the wind direction and an increase in metabolic rate results from that change, the most likely

cause for the increase would be heat loss due to convection rather than radiation loss or latent heat loss. The equation cascade (Fig. 2) illustrates how the model for heat gain and loss is constructed by relating the physiologic processes of metabolic rate (M), latent heat loss (λE) and body resistance (r_b) to the external difference in temperature between the body (T_b) and the equivalent temperature (T_e). The equivalent temperature equals T_a plus the gain or loss due to the net isothermal radiation times the body's surface layer resistance to heat flow.

This study was designed to determine quantitatively if foraging White- and Golden-crowned sparrows were oriented randomly with respect to wind direction and location and if not, what effect did nonrandom orientation have on the individual's heat exchange. Food availability and social interactions are analyzed as factors influencing orientation and, indirectly, the daily change in existence energy.

Figure 1. Study site - Finley Refuge. Located 19 Km south of Corvallis in Willamette Valley floodplain, the study site has considerable microhabitat variety. RI, R and RE are sections of the gravel road oriented due east and west. CB, FB1, FB2 and FB3 are brush areas. CBN is the northern side and CBS the southern side of the CB brush area. CB4 and FB4 are taller shrubs within the brush. M1, M2 and M3 are the open feeding area which is flat and, in part, lightly graveled. The rectangle between CBS and M1 represents the cabin from which observations were made. Dotted lines represent the distribution lines for the food experiment.

STUDY SITE FINLEY REFUGE

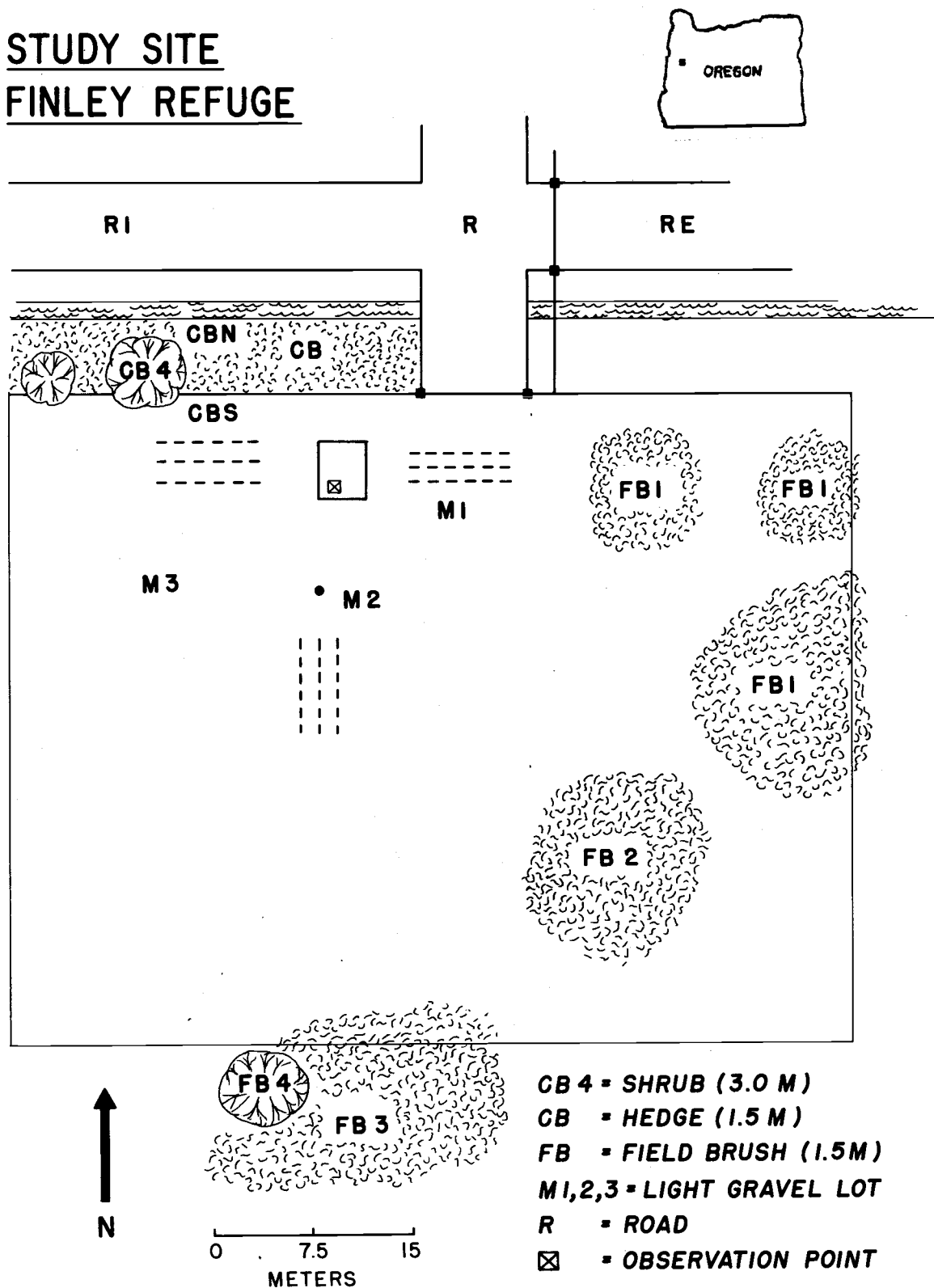


Figure 1. Study site - Finley Refuge.

Figure 2. Equation cascade. The equation cascade illustrates the way metabolic rate (M) is a function of the temperature difference between the body (T_b) and the environment (T_e) times the resistance to heat exchange. Changes in wind speed and orientation to the wind affect the value of r_a while changes in temperature and the conductance of the boundary layer of air affect the value of r_r . Net radiation exchange (R_{Ni}) is the difference between long and short wave radiation input minus long wave radiation output. Equivalent temperature (T_e) equals the ambient temperature (T_a) plus or minus any increment due to radiation times changes in resistance to heat exchange.

EQUATION CASCADE

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

$$T_e = T_a + R_{Ni} \cdot r_e / \rho c_p$$

$$R_{Ni} = R_{abs} - \epsilon \sigma T_a^4$$

$$r_e = r_a \cdot r_r / (r_a + r_r)$$

$$R_{abs} = SW_{abs} + LW_{abs}$$

$$r_r = \rho c_p / 4 \epsilon \sigma T_a^3$$

$$SW_{abs} = \alpha A_p / A_t \cdot SW_p$$

$$r_a = K (d / \mu)^{0.5}$$

TERMS

M = Metabolic Rate	μ = Wind Speed
λE = Latent Heat Loss	ρ = Air Density
T_e = Equivalent Temperature	C_p = Specific Heat of Air
R_{Ni} = Net Isothermal Radiation	σ = Stefan-Boltzman Constant
R_{abs} = Radiation Absorbed	α = Absorbtivity to Short
SW_{abs} = Short Wave Radiation Absorbed	Wave Radiation
SW_p = Direct Short Wave Radiation	A_p / A_t = Exposed Surface Ratio
LW_{abs} = Long Wave Radiation Absorbed	T_a = Ambient Temperature
r_e = Parallel Equivalent Resistance	K = Constant
r_a = Resistance to Convective Heat Flow	r_b = Body Resistance
r_r = Resistance to Radiation	ϵ = Surface Emissivity
d = Diameter Parallel to Wind Vector	T_b = Body Temperature

Figure 2. Equation cascade.

METHODS AND MATERIALS

Study Site

Crowned sparrows can be difficult to observe due to the shrub habitat where they live. I was especially fortunate to have found a site with an observation tower and an overwintering population that foraged mainly within a radius of 50 m. Located at the William L. Finley National Wildlife Refuge, 19 km south of Corvallis, Oregon, microhabitats of roadside hedge 1.5 m high, shrubs 3 m high, grass fields and a lightly graveled parking lot offered considerable variety (see Fig. 1). The site was adjacent to a crossroads in the gravel road that was oriented due east and west, serving as a good reference for taking measurements as I observed from a 5 m high vantage point. The population was accustomed to the presence of people and was generally undisturbed as I observed. The surrounding area is flood-plain.

Methods

During January, February, and March a three-probe thermograph was used to make continuous temperature recordings at the open ground site (M_3) 0.1 m above the ground level, at the top of the hedge (3CB) 1.5 m above the ground level, and within the hedge (CB) 0.1 m above the ground level. Once a week I visited the site from sunrise to sundown. Upon arriving I placed a continuous recording anemometer

0.3 m above the ground level at M_3 and a smaller hand-held anemometer at the open site M_2 , 0.1 m above the ground level. Often the sparrows would feed directly adjacent and at the same height as the smaller anemometer, so the wind measurements were good representations of the birds' experience. Radiation data were continuously recorded from the rooftop of the Oregon State University Atmospheric Science building with a pyrometer for short wave radiation. Since most days were cloudy with a thick layer of cloud, the O.S.U. readings were probably representative of those at the refuge.

Observations were recorded at 1 min intervals marked by a tone on a prerecorded tape. Measurements were made continuously through the day except for short breaks. This was possible because of the relatively comfortable observation tower where I could sit, stay warm, and see out windows on three sides. Table A lists the class divisions and assigned numbers for each variable used in the study. Initially, recorded observations were made on number of individuals feeding, frequency of pecking, activity level, location and individual orientation. As the study progressed, added variables included individual position in the flock, flock orientation, flock diameter, wind speed, and frequency of flight to the hedge from the open feeding ground.

To alter the food availability 20 g of chick scratch were distributed over three lines 7.5 m long and 1.5 m apart at a density of about $3 \text{ g} \cdot \text{m}^{-2}$ (see Fig. 1). The lines were set out upon arrival at the site for two of the sample days in February. No grain was seen by the following week.

Differences in wind speed between the microhabitats were measured with the hand-held anemometer and the average of five 1-min readings were taken. These measurements were made for three different days with wind greater than $0.5 \text{ m}\cdot\text{s}^{-1}$.

The study ended 19 March when no crowned sparrows were seen feeding at the open area M_2 during the morning hours.

CLASSES FOR EACH VARIABLE
TABLE A

FEEDING INTENSITY:

- 1 - Occasional peck
- 2 - Search and peck, with pauses
- 3 - Continuous search and peck
- 4 - Continuous pecking

FEEDING ACTIVITY LEVEL:

- 1 - Still
- 2 - Hopping only
- 3 - Hopping with short runs
- 4 - Hopping, short runs and short flights

LOCATION:

- 1 - Ground level
- 2 - Middle of brush
- 3 - Top of brush
- 4 - Top of nearby scrub tree

INDIVIDUAL LOCATION IN FLOCK:

- 1 - Outside, periphery
- 2 - Intermediate
- 3 - Inside middle of flock

FLOCK ORIENTATION

- 1,2,3,4,5,6,7,8 - If direction of over 50% of neighbors within a 2 m radius around individual is the same

- 0 - If random

DIRECTION OF STANCE:

- 1 - N
- 2 - NE
- 3 - E
- 4 - SE
- 5 - S
- 6 - SW
- 7 - W
- 8 - NW

RESULTS

Spatial Orientation

Over 2,500 observations were recorded during this study; 1,500 included data on spatial orientation. The percentage of time spent facing each direction is illustrated in Fig. 3 for all locations combined. Individual orientation was definitely nonrandom ($\chi^2 = 240$, $P < .001$). More time was spent facing south than any other direction. For the 12 days of continuous recorded wind measurements, all wind speeds greater than $1.0 \text{ m} \cdot \text{s}^{-1}$ were from the south. These two results might lead to the conclusion that individual birds were orienting parallel to the direction of the wind. If this were the case, I would expect a similar partitioning of time spent in each direction for all the microhabitats exposed to strong wind. The test for similarity of orientation between areas M_1 , M_2 , M_3 and CBS, however, yielded a high χ^2 value ($\chi^2 = 152$, $P < .001$). When occupying the CBS area individuals spent the largest part of their time (46%) facing south and very little time (6%) facing west, but when in the M_2 area individuals spent the largest part of their time (20%) facing west.

Temperature equivalent values were generated for the difference between a perpendicular and a parallel orientation with respect to the wind to determine the effect on heat exchange. It is the r_a component in the equation for T_e (see Fig. 2) that is affected by a change in "d", the bird's diameter parallel to the wind vector. The importance of a change in the value of r_a on the value of T_e is also a function of the net isothermal radiation R_{Ni} . As R_{Ni} approaches zero

from either a negative or positive direction the effects of a change in r_a no matter how great will not make a large change in the value of T_e . These relationships are illustrated in Fig. 4 for four different wind speeds, two different temperatures and three different radiation regimes. The values for R_{Ni} of $-40 \text{ W}\cdot\text{m}^{-2}$ and $150 \text{ W}\cdot\text{m}^{-2}$ were typical values recorded by Mahoney (1976) for a White-crowned Sparrow in the shade and in the sun, respectively. The value for R_{Ni} of $-90 \text{ W}\cdot\text{m}^{-2}$ I calculated as follows:

$$R_{Ni} = (\alpha \cdot A_p / A_t) (SW_p) + (\alpha \cdot \frac{A_s}{A_t}) (LW_s) + (\alpha \cdot \frac{A_g}{A_t}) (LW_g) - \epsilon \sigma T_a^4$$

$$R_{Ni} = 0.16 \cdot 200 \text{ W}\cdot\text{m}^{-2} + 0.49 \cdot 180 \text{ W}\cdot\text{m}^{-2} + 0.49 \cdot 230 \text{ W}\cdot\text{m}^{-2} - 320 \text{ W}\cdot\text{m}^{-2}$$

$$= -90 \text{ W}\cdot\text{m}^{-2}$$

where the $(\alpha \cdot \frac{A_i}{A_j})$ terms represent the crowned sparrow's absorbtivity and exposure, SW_p is direct short wave radiation, LW_s is long wave radiation in from the sky, LW_g is long wave radiation in from the ground and $\epsilon \sigma T_a^4$ is long wave radiation out from the bird at 6°C . The values for LW_g , LW_s , $\epsilon \sigma T_a^4$ and the coefficients were obtained from the tables in Mahoney's thesis. The value for SW_p is a high estimate from the radiation data taken at the O.S.U. site. Values for short wave scattered and reflected radiation are as low as 100 and $25 \text{ W}\cdot\text{m}^{-2}$, respectively, on clear days. Since they are directly related to the direct short wave radiation, which on a clear day averages $1,050 \text{ W}\cdot\text{m}^{-2}$, on the cloudy days of this study ($SW_p = 200 \text{ W}\cdot\text{m}^{-2}$) they were probably close to zero. The estimates I have used are all conservative. If they are in error the R_{Ni} term would only be closer to zero and thus the difference in T_e would be reduced even more.

The values for ΔT_e in Fig. 4 are the differences in the value of T_e due to a rotation from a perpendicular to a parallel orientation and are quite small ($<1^\circ\text{C}$) for wind speeds greater than $0.1 \text{ m}\cdot\text{s}^{-1}$. As the wind speed increases the difference in heat exchange between stances is even less. At the low ambient temperatures encountered during these months (see Fig. 6 and 7), the T_e differences for stance would amount to less than a 5% change in the metabolic rate (using estimates from Mahoney, 1976).

The above analysis supports the hypothesis that the stance direction differences will have little effect on heat exchange at any particular location. But the effects of occupying different locations on heat exchange is important because of the differences in values for wind speed and radiation. The values in parentheses in Fig. 4 are the average T_e values for each group of environmental variables. Note how a difference in wind speed between $0.1 \text{ m}\cdot\text{s}^{-1}$ and $2.0 \text{ m}\cdot\text{s}^{-1}$ causes a corresponding change in the T_e of 5.7°C ($-8.6 \rightarrow -2.9^\circ$), again using the tables from Mahoney's thesis relating T_e to standard metabolism. This difference would cause a greater than 15% increase in the standard metabolism.

Since the proportion of time the individual bird spent facing each direction in each location does reflect its direction of motion, two other factors that influence orientation were studied and their indirect effects on heat exchange analyzed.

Food Availability and Social Interactions

Throughout the study a common feeding pattern for the flock

would result in a flow from CB to M_1 to M_2 and then a flight back to CB. These patterns are reflected by the different proportions of time spent facing each direction for each site illustrated in Fig. 3. The food lines (Fig. 1) were purposely placed in an area where the individuals were most often seen facing south (i.e., facing M_2 from M_1) and placed perpendicular to the flock motion. Crowned sparrows were observed to begin to move south from the gate to M_1 in their usual pattern, reach the line and promptly rotate 90^0 and start heading eastward. They would continue to rotate as they hopped about during feeding, but be damped by the food line and maintain a path perpendicular to the rest of the flock. A few sparrows continued to feed on the lines as the rest moved southward. As the distance between the sparrows that were feeding on the lines and the rest of the flock that moved to M_2 increased to greater than 5 m most of the food line sparrows rotated south and joined the flock. Figure 5 illustrates the large change in proportion of time spent in each direction between M_1 and the M_1 food line.

The influence of flock orientation upon individual orientation is further analyzed in Table 1. Individual orientations are the same as flock orientation 68% of the recorded observations for a nonrandom flock orientation (note the large values on the diagonal). The flock was randomly oriented 38% of the time.

With these two factors in mind, a dominant individual that is seeking food and has its orientation affected by food location could in turn affect the orientation, location, and therefore the heat exchange of other subordinate members of the flock.

Location and Metabolic Rate

Ambient temperature (T_a) differences between the open ground (M_3) and the brush (CB) represent the extremes within the site. The difference in T_a is increased by increased radiation (see Table 2, noon) and decreased by increased wind. Even though SW_p was $252 \text{ w}\cdot\text{m}^{-2}$ on 17 January 1978 because of the high wind, ΔT_a was less (1.1°C) than on 29 December 1977 with a lower incoming short wave radiation but no wind. No data were available for wind speed on 26 January 1978, but the high ΔT_a indicates there was little if any wind that day. Figures 6 and 7 are graphs for total variation in the main environmental variables throughout the study. The peak values of the day for radiation and temperature most often occurred around 1230 and are shown both for magnitude deviations (vertical line) and for time of day deviations (horizontal lines) along with the highest and lowest magnitude values recorded. Note how the temperature peak and radiation peak occur at close to the same time of day. These peak value times correspond with the largest difference ΔT_a between sites.

Figure 8 illustrates the difference in metabolic rate of a crowned sparrow occupying different habitats based only upon the differences in wind speed (from results of Robinson, (1976)). Differences would be affected by differences in the direct short wave radiation but these measurements were not made at the site. For example, at mid-day the increased radiation received at the open sites compared to the hedge would lessen the difference in the amount of heat loss due to wind. The heat production at site M_2 is also increased as a result of flights to and from the hedge. Each flight to the brush took about 2s.

These flights occurred at an average of eight times per hour when feeding in the open M areas.

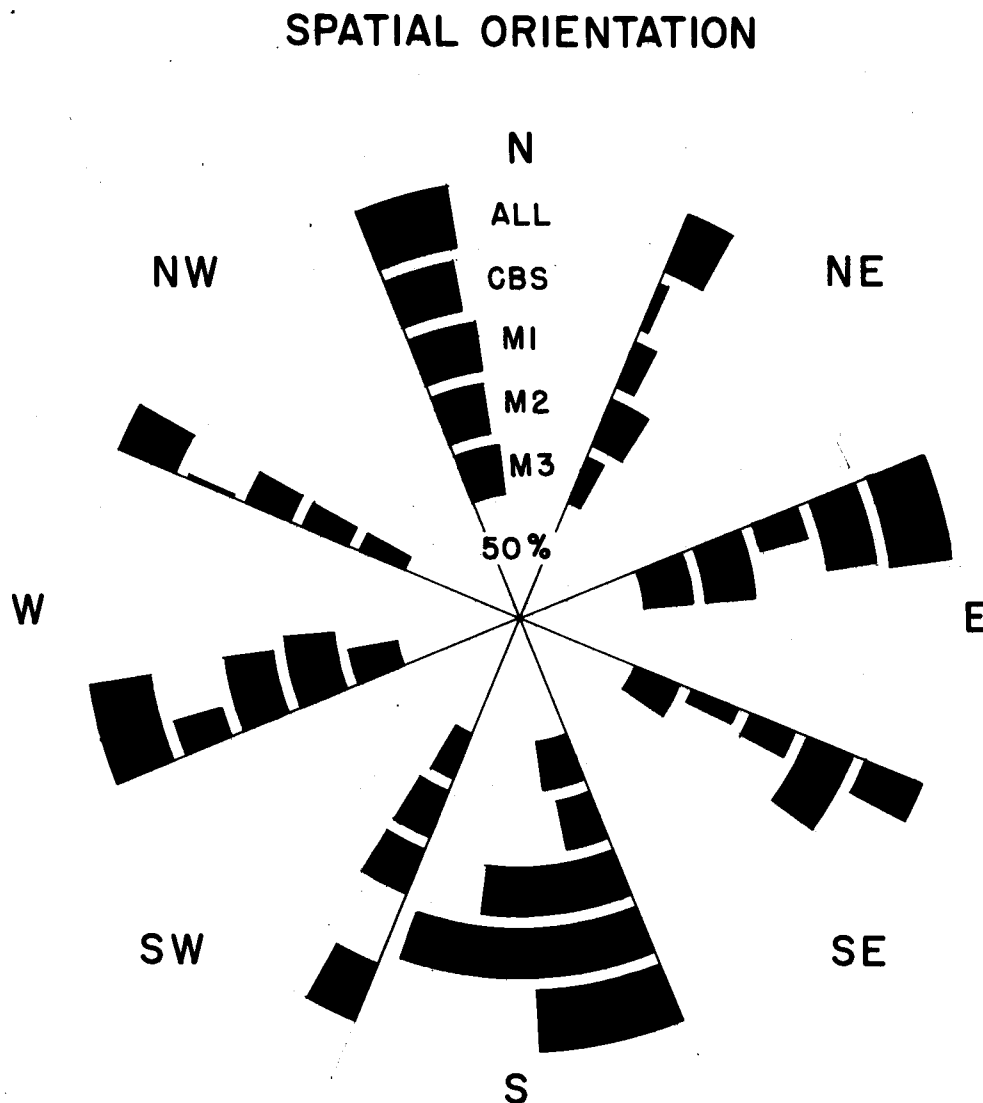
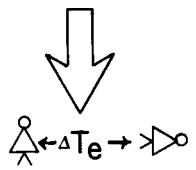


Figure 3. Spatial orientation. Each dark block represents the proportion of time spent facing the direction. No proportions higher than 50% were recorded for any one direction, but the southern component of site CBS comes close (46%). Note how the percentages significantly change ($\chi^2=152$, $P<<.001$) between sites. These values reflect the motion of individuals from one location to another (i.e. south from CBS to M3). For all locations combined, orientation is nonrandom ($\chi^2=239.5$, $P<<.001$).

ΔT_e - DIRECTION



		THICK CLOUD LAYER		SHADE		SUN	
		$R_{Ni} = -90 \text{ Wm}^{-2}$		$R_{Ni} = -40 \text{ Wm}^{-2}$		$R_{Ni} = +150 \text{ Wm}^{-2}$	
WIND SPEED $\text{m} \cdot \text{s}^{-1}$	T $^{\circ}\text{C}$	ΔT_e $^{\circ}\text{C}$	(\bar{T}_e)	$\Delta \bar{T}_e$ $^{\circ}\text{C}$	(\bar{T}_e)	ΔT_e $^{\circ}\text{C}$	(\bar{T}_e)
.1	0	1.1	(-8.6)	-.49	(-3.8)	1.8	(14.4)
	10	1.0	(1.7)	-.45	(6.3)	1.7	(23.8)
.5	0	-.85	(-5.1)	-.38	(-2.3)	1.7	(9.2)
	10	-.81	(5.0)	-.36	(7.8)	1.4	(18.3)
2.0	0	-.56	(-2.9)	-.25	(-1.3)	1.1	(4.9)
	10	-.55	(7.1)	-.24	(8.7)	.9	(14.8)
10.0	0	-.31	(-1.4)	-.14	(-0.64)	.52	(2.4)
	10	-.30	(8.6)	-.13	(9.3)	.50	(12.4)

$$T_e = T_a + R_{Ni} \cdot r_e / \rho c p$$

Figure 4. Effects of orientation on T_e . Differences in T_e (ΔT_e) between a stance parallel to the wind and one perpendicular to the wind is listed for four different wind speeds, two different temperatures and three different radiation regimes. Note how small ($<1^{\circ}\text{C}$) the change in T_e is for low R_{Ni} and wind speeds greater than $0.1 \text{ m} \cdot \text{s}^{-1}$. R_{Ni} estimates for shade and sun are from Mahoney (1976). I calculated the R_{Ni} value for an average thick cloud layer day of this study.

EFFECTS OF FOOD LINE

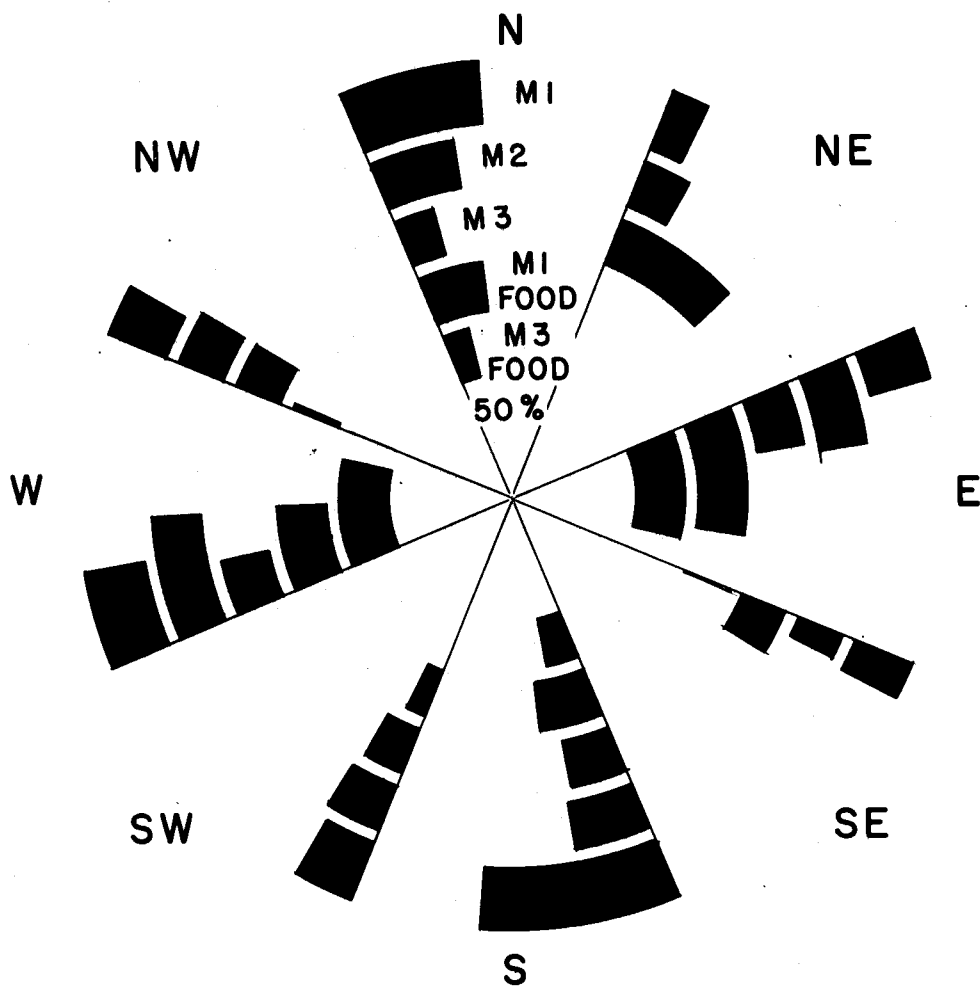
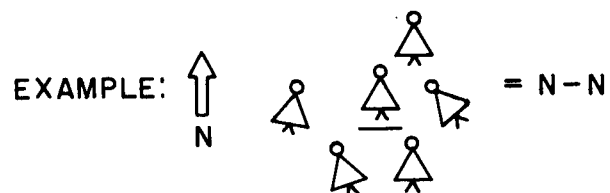


Figure 5. Food line experiment. A light trace of chicken scratch was distributed in lines as shown on Fig. 1 for two of the sample days. The effect of food distribution is to significantly ($P < 0.001$) change for site M1 the proportion of time spent facing each direction. Note the large east and west components of M1 food.

SOCIAL INTERACTIONS: INDIVIDUAL → FLOCK

TABLE I

IND.	FLOCK								
	N	NE	E	SE	S	SW	W	NW	
N	85	0	8	0	24	5	9	2	59
NE	2	36	0	0	3	4	0	4	40
E	5	1	91	0	17	0	18	0	87
SE	1	1	0	15	2	3	2	3	45
S	17	1	11	2	165	3	10	0	74
SW	2	6	3	4	7	55	7	1	36
W	7	1	12	0	16	3	69	12	100
NW	3	3	2	0	4	2	3	27	<u>44</u>
SUB-TOTAL = 799;									485
TOTAL =									1284



Note how large the values on the diagonal are representing the individual orientation which coincides with the flock orientation, when present, 68% of the time.

AMBIENT TEMPERATURE DIFFERENCE BETWEEN M3 & CB

TABLE 2

DATE	TIME	ΔT_{M3-CB} (°C)	SW_p ($W \cdot m^{-2}$)	WIND SPEED $m \cdot s^{-1}$
12-29-77	8:00	0	0	0
	12:00	2.3	104	0
	16:00	0.6	35	1.789
	18:00	0.6	14	0.894
1-17-78	8:00	0	0	.223
	12:00	1.1	252	2.235
	16:00	0.0	70	.894
	18:00	-1.1	14	.224
1-26-78	8:00	0.0	0	NA
	12:00	6.2	378	NA
	16:00	1.1	140	NA
	18:00	-2.2	7	NA

Ambient temperature T_a is affected by incoming short wave radiation and wind. Note how for 26 January 1978 when radiation is high the difference between the open area and the brush is greater than either 29 December 1977 with no wind or 17 January 1978 with high SW_p but also high winds. NA = Data not available.

Figure 6. Variability in environment. Graphs for SW and T are based upon continuous recordings, while the wind speed is the sum of 12 days of recordings at 1 week intervals. The dots are the mean (M) values with standard deviation (SD) extending on either side. Highs and lows are designated by a single bar. For SW and T, the middle vertical line represents the M and SD for the peak value of the day. The horizontal lines represent the M and SD for the time of the peak value.

VARIABILITY IN ENVIRONMENT

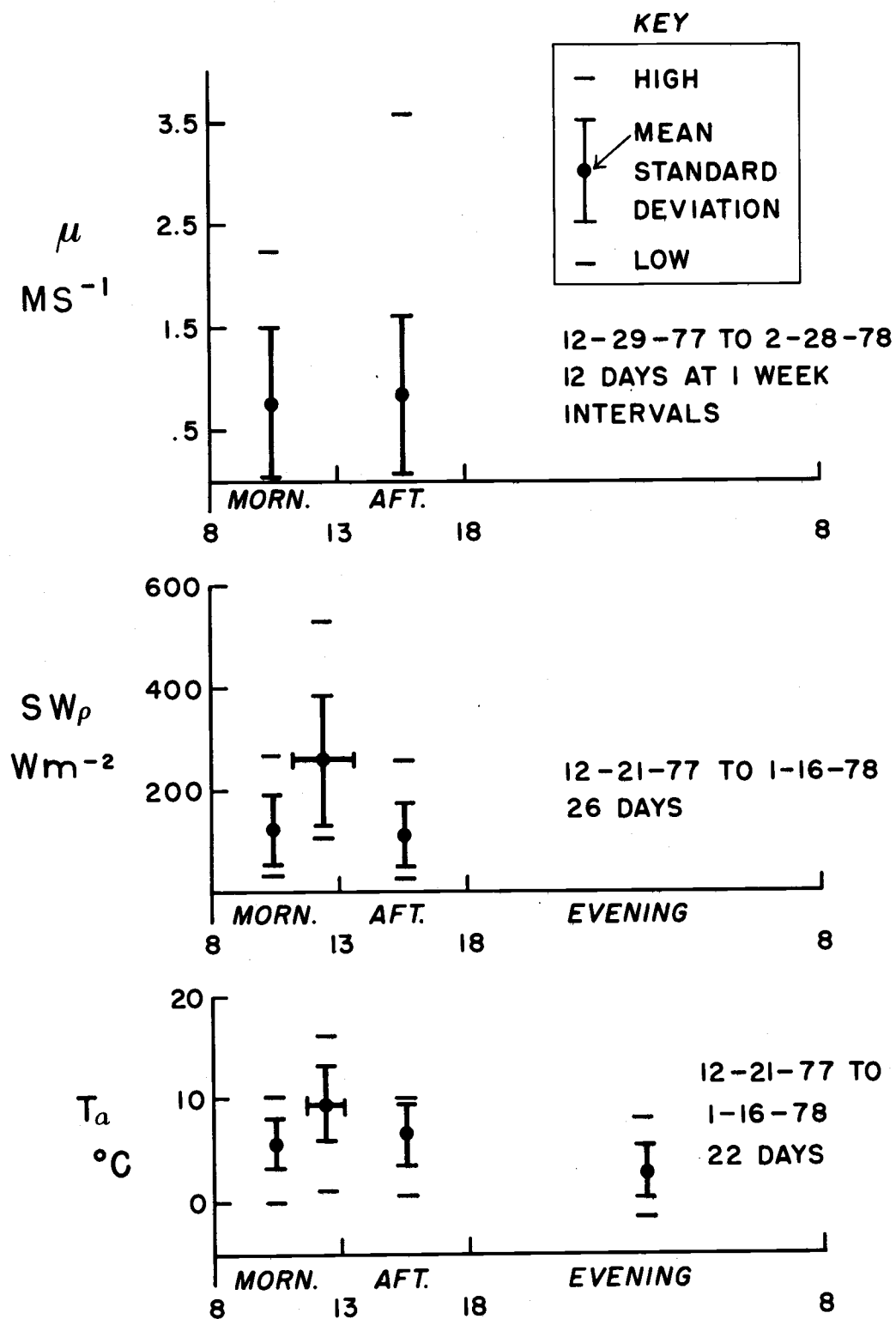


Figure 6. Variability in environment.

VARIABILITY IN ENVIRONMENT

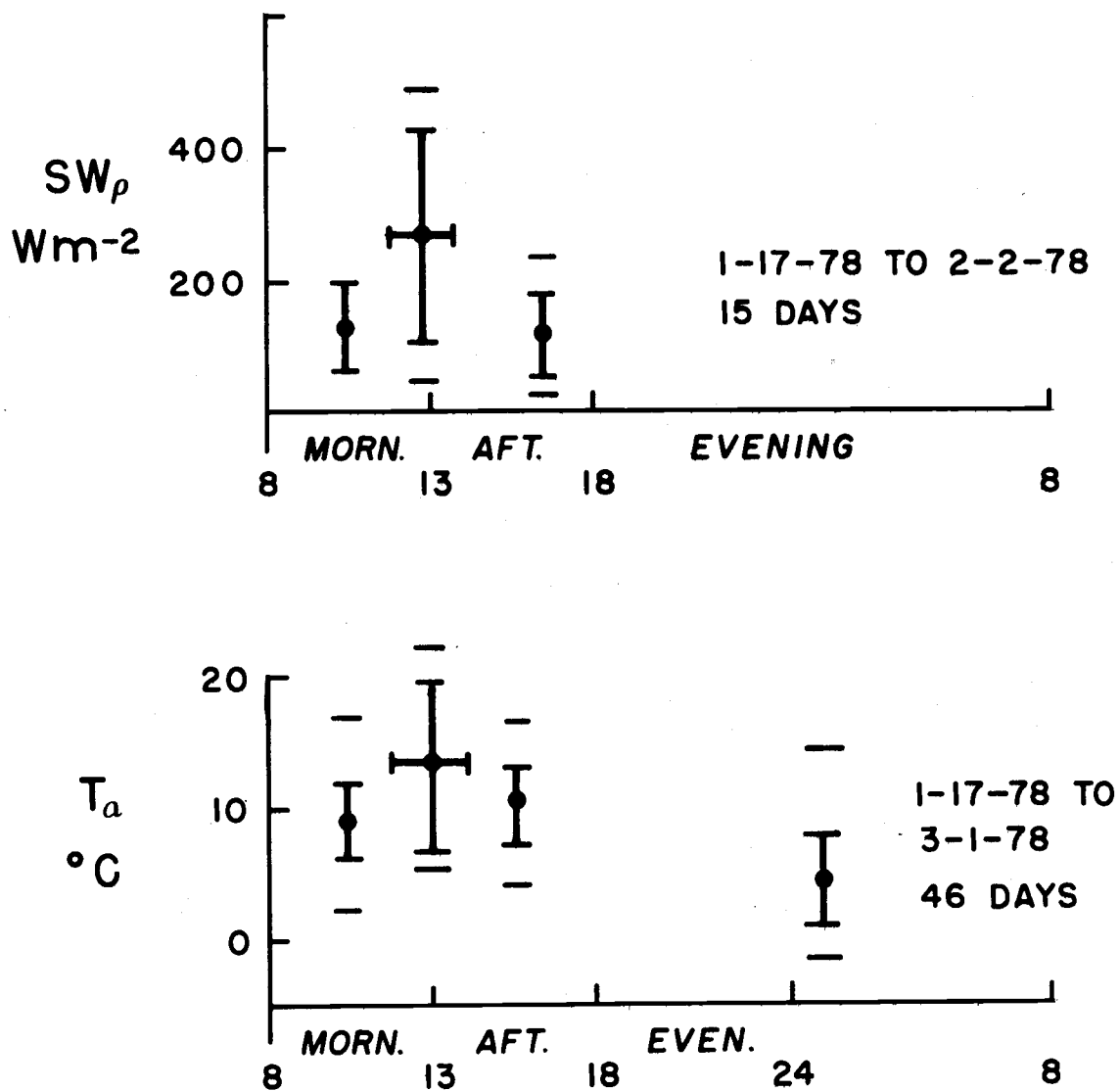


Figure 7. Format is the same as Fig. 6. These graphs show the slight rise in T_a for the latter half of the study, but the relative constancy of the direct short wave radiation SW_p .

Figure 8. Heat production - Watts·meter⁻². Values at each site are the heat production in W·m⁻² based upon Robinson, Campbell and King's (1976) results. Ambient temperature is 6°C and wind speed measurements for each site are given below. Note the high value at CB4 and the low at the northern edge of the roadside brush, CBN. The wind was from the south.

HEAT PRODUCTION WATTS · METER⁻²

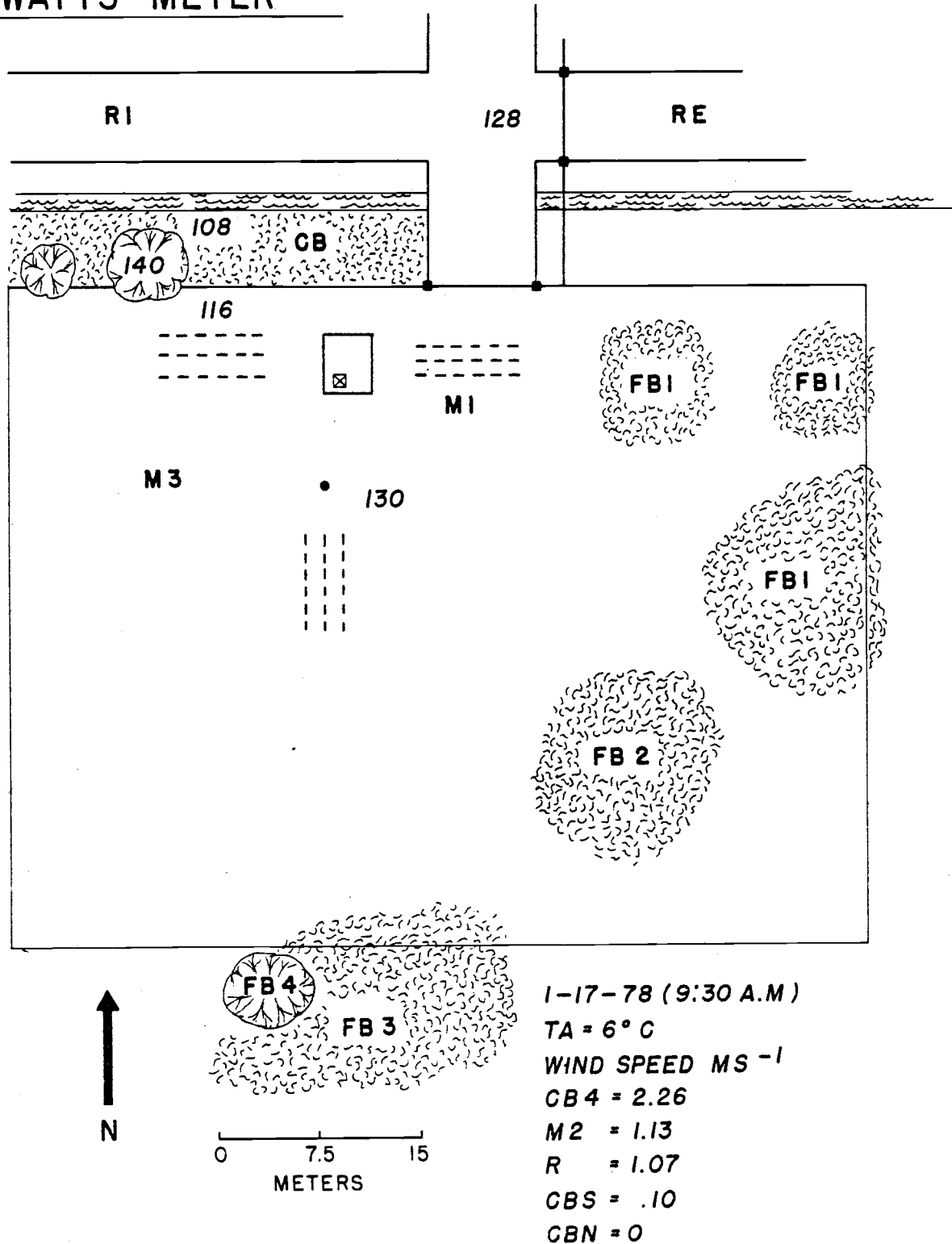


Figure 8. Heat production - Watts · meter⁻².

DISCUSSION

For the site occupied in this study and for the environmental conditions illustrated in Fig. 6 and 7, the results indicate that the direction of stance for Golden- and White-crowned Sparrows is not randomly distributed. The distributions for time spent facing each direction are also significantly different between locations. The direct effect on the individual's heat exchange because of a change in the direction faced is small. T_e values change by less than 1°C for all wind speeds greater than $0.5 \text{ m}\cdot\text{s}^{-1}$. This difference decreases as the wind increases and as net radiation gain approaches zero. The percent of time an individual spent facing a particular direction often reflects the direction it was moving. For example, the flock would move from CBS south to M_3 (see Fig. 1) while feeding and this motion is reflected in a large percentage of time spent facing south. Factors that affect orientation then in turn may be affecting the individual's direction of motion from one location to another and thus indirectly affecting its heat exchange. The food line experiment is a good example of this phenomena. White-crowned Sparrows changed the direction of their hopping at M_1 as they followed the food eastward towards a new location rather than towards M_2 . This change in feeding pattern is quantified as a change in the percentage of time spent in the east-west directions (see Fig. 5). If the food line extended into the tall grass where the wind speed is considerably reduced this would result in a reduction in the individual's metabolic rate compared to remaining in the open M_2 area. A second factor

indirectly influencing an individual's heat exchange by influencing its movement from location to location is the orientation of the flock. Individuals faced the same direction as those within a 2 m radius 68% of the time for recorded observation where the flock was nonrandomly oriented. In the food line experiment, the majority of the flock at one point crossed over the lines, heading from M_1 to M_2 . As a result all but one of the individuals facing east and west on the lines rotated south and joined the flock at M_2 . A change in location because of social interactions will change an individual's heat exchange depending upon the difference in the wind and radiation between each location.

Robinson et al. (1976) performed laboratory studies on White-crowned Sparrows (Zonotrichia leucophrys gambelii) to determine the effects of wind on heat production. Their results are used for the estimates in Table 3. Wind speed varied from zero at ground level in the brush to as much as $1.13 \text{ m}\cdot\text{s}^{-1}$ in the open area, M_2 . Wind speed differences that were greater ($\mu = 2.23 \text{ m}\cdot\text{s}^{-1}$ at M_2) have been recorded but $1.13 \text{ m}\cdot\text{s}^{-1}$ is closer to the average (Fig. 6) and is used here for estimates of heat production. Figure 8 illustrates heat production as a function of wind speed for four areas: M_2 , 4CB, CBS, and CBN. The grass at CBS and the protection of the brush at CBN caused dramatic reductions in the wind speed and consequently lowered heat production.

The middle part of Table 3 presents Mahoney's (1976) estimates of the daily existence energy (DEE) for two temperatures, 4°C and 7.6°C . The DEE total is composed of a basal part (DEE_b), a thermoregulatory part

(DEE_{tr}), and an activity part (DEE_A). The estimate for the activity part can vary from one to two times the basal metabolic rate so the values in parentheses for the total DEE are the low estimates and the other value the high estimate. Activity is calculated for a 12-h day.

I calculated heat production in $KJ \cdot d^{-1} \cdot bird^{-1}$ by using the results of Robinson's work times the amount of time spent in each location. Errors in these estimates could result from differences in the thermoneutral zone between the field birds of this study in Oregon and the birds from Washington that Robinson measured in the laboratory. Both studies were done during winter months. The totals are slightly lower than Mahoney's, possibly because of a shorter day (10 h) for activity. The T_a for the bottom calculations was $6.2^{\circ}C$.

The emphasis here is on the relatively large changes in $W \cdot m^{-2}$ between sites. For example, by feeding at M_2 for 2 h in the morning and 2 h in the afternoon rather than remaining near or in the brush, an additional 2.5 KJ per day is expended, representing about a 4% increase in DEE. If an additional hour is spent at the top of the shrub (4CB) because of flights to the hedge, another 0.8 KJ is expended for a 5% increase in the DEE. For one of the sample days when winds were high from the south, 7 h were spent feeding at M sites and 1 h in 4CB, resulting in an 8% increase in heat production.

The differential heat loss between M areas and CB could be reduced if the sparrows were to feed at the open site during mid-day when the incoming radiation was the highest. The brush habitat at this time has a reduced short wave radiation value as reflected in

the larger T_a difference seen in Table 2. In this respect, the previous calculation for the increased cost of feeding in the open would be reduced if the flock fed at the open site during the peak value for incoming direct short wave radiation. Instead of feeding in the open area during mid-day, the flock most commonly moves into the brush, thereby spending their time at each site when the thermal environment is the least optimal.

To determine if this increased cost in heat production for feeding in the M areas is placing a stress upon the individual in the flock, consecutive daily tabulations of time spent in each area and the heat loss from the previous night would need to be known. For example, would a cold night causing a large heat loss result in less time spent feeding at M_2 ? One result that indicates the individuals are stressed in M areas is the consistently high (3-4) feeding intensity (see Table A) recorded for all observations in M_2 and M_3 areas. Possibly the crowned sparrows have adopted a strategy of an "energy maximizer" (Rapport and Turner, 1975). The rates of cost to gain for food capture may be much lower in the open, flat, two-dimensional M area than in the relatively dense and three-dimensional area of the grass and brush. This reduced ratio would compensate for the increased heat loss. Also, White-crowned Sparrows have regular feeding periods throughout the day (Morton, 1967) that are associated with other circadian rhythms (Gwinner, 1973). These physiological processes could be an important driving force requiring a minimum caloric intake to satisfy a morning break fast or to prepare for a long evening in the brush. Certainly food analysis should be a part

of any further work done in this area.

Table 3. Heat exchange at different sites based on wind speed. Heat production values are taken from Robinson, Campbell and King's work (1976) on the effects of wind speed at different temperatures on heat loss. The wind speed measurements were made with a hand-held anemometer. Mahoney's data in the middle part of table are present for comparison. Lower values in parentheses for total DEE are estimates of activity based on a factor of 1 times basal metabolic rate rather than 2. The two values in the total DEE column are considered by Mahoney to be upper and lower limits. The example calculation simply shows how the DEE can change as a result of spending time in the open areas based only on differences in wind speed. Differences in the incoming short wave radiation SW_p (see Table 2) and differences in activity would make the change in DEE greater.

HEAT EXCHANGE AT DIFFERENT SITES BASED ON WIND SPEED

TABLE 3

SITE	WIND SPEED (ms^{-1})	HEAT (Wm^{-2})	PRODUCTION $\text{KJ} \cdot \text{hr}^{-1} \cdot \text{bird}^{-1}$
M2	1.13	130	3.28
4CB	2.25	140	3.53
CBS	0.97	116	2.92
CBN	0.0	108	2.72

FROM MAHONEY (1976)

T ($^{\circ}\text{C}$)	DEE_A	DEE_{TR} ($\text{KJ} \cdot \text{day}^{-1} \cdot \text{bird}^{-1}$)	DEE_b	TOTAL
4	30.6	24.1	33.3	88.0 (72.7)
7.6	33.4	17.1	33.3	83.8 (67.1)

EXAMPLE CALCULATION

HOURS SPENT	SITE	$\text{KJ} \cdot \text{d}^{-1} \cdot \text{b}^{-1}$ TOTAL	% INCREASE
1) 24	CBN	65.28	65.28
2) 7	FEEDING M2	22.96	8% ↑
1	SCATTER 4CB	3.53	
3	CBS	8.76	
13	CBN	35.36	
		70.61	

CONCLUSION

Spatial orientation for foraging White-crowned Sparrows (Zonotrichia leucophrys) and Golden-crowned Sparrows (Zonotrichia atricapilla) is not random. Between locations at the western Oregon study site there are significant differences in the proportion of time spent facing each direction. The influence of spatial orientation on the change in heat production is quantified with a thermodynamic model that estimates the heat gradient between a crowned sparrow and its environment. The calculated changes in the value of the equivalent temperature (T_e) of 1°C for a change in direction of stance leads to the conclusion that heat exchange is not an important determinant of this variable. The direction of stance does reflect the pattern of motion of individuals from one location to another. Differences in the heat production of crowned sparrows occupying different locations is significant. In this sense, behavioral factors that influence the stance direction in turn influence the individual's choice of location and consequently its heat production. Food availability is one factor that alters the proportion of time spent facing each direction. Social interactions and the formation of a foraging flock also influenced the direction that an individual faced.

Open areas exposed to wind demand a greater heat production from crowned sparrows than do the protected areas of the hedge, yet the flock persists in feeding in the open areas at times when the thermal environment is the least conducive to energy conservation, and enters the hedge during mid-day when the thermal environment is

more favorable in the open areas. Exactly how much heat stress is placed upon an individual because of this behavior requires data for consecutive days in the field, a higher resolution for time spent per location, and an analysis of the caloric content of the food available at each site. The calculated total added heat costs of using the open areas for foraging are conservative as they do not include the added cost of the radiation differential between the open area and the hedge and the increased activity of short flights to the hedge from the open areas when predators fly overhead.

Cost to gain ratios of foraging in the open areas could be low enough to compensate for the increase in heat production. Searching for food is easier in the flat, two-dimensional, open area as opposed to the hopping over twigs and tall grass of the more three-dimensional brush areas. Feeding intensity in the open areas was high. If the crowned sparrows have a minimum requirement for rate of net caloric intake because of physiological circadian rhythms, these combined influences could result in the early and late afternoon feeding at the open areas.

The thermodynamic model that estimates the equivalent temperature T_e was not difficult to use in a field situation. In contrast to a single measurement of metabolic rate, the values generated from the model can be directly related to the most influential environmental factors. The resulting hypothesis can then be tested by designing studies with specific alterations in the study area (i.e., similar to the food line alteration). The non-interference with the population was a further advantage of the model.

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