

EFFECTS OF WIND AND ILLUMINATION ON BEHAVIOR AND METABOLIC RATE OF AMERICAN GOLDFINCHES (*CARDUELIS TRISTIS*)

GEORGE S. BAKKEN AND KIMBERLY F. LEE¹

Department of Life Sciences, Indiana State University, Terre Haute, Indiana 47809, USA

ABSTRACT.—We measured the metabolic rate of active-phase American Goldfinches (*Carduelis tristis*) with and without illumination at 10°C and four wind speeds. We observed the birds via closed-circuit television. Illumination alone increased metabolism 37%. Metabolic rate increased linearly with activity and wind speed. A decrease in activity as wind speed increased tended to counteract the increase in thermoregulatory metabolism caused by convection, and reduced the slope of metabolism-vs.-wind-speed plots. The increase of metabolism with activity was reduced by the presence of illumination, which suggests relatively more compensation for thermoregulatory metabolism by activity metabolism when illumination is present. Stepwise linear regression was used to correct for nonthermal effects of illumination and wind to improve estimates of their purely thermal effects. Received 17 December 1990, accepted 17 July 1991.

BIRDS are often fully exposed to both wind and sun while active, and may be exposed to wind when roosting. The accuracy of avian time budgets and energy budgets is significantly improved by including the effects of sun and wind on thermoregulatory metabolism (Weathers et al. 1984, Buttemer et al. 1986). A few laboratory studies of avian thermoregulatory metabolism have used wind (reviewed by Bakken 1990b), short-wave radiation heating (e.g. DeJong 1976, Hayes and Gessaman 1980), or both (e.g. Wood and Lustick 1989) as thermal variables. Wind and illumination may also affect posture and activity, and so have confounding nonthermal effects on metabolic rate that have received only scant attention (Wood and Lustick 1989, Bakken et al. 1991). The application of laboratory energetics data to free-living birds requires understanding of both the thermal and nonthermal effects of sun and wind.

Two nonthermal effects, opposite in sign, are associated with wind in the laboratory. First, fan noise and vibration increase as wind speed increases. Similar disturbances have increased corticosteroid levels, muscle tone, respiration rate, body temperature, and metabolic rate in birds (Southwick 1973, Siegel 1980, Reinertsen and Haftorn 1983). Disturbance may also increase thermal conductance as a result of increased activity and alert posture (Pohl 1969,

Wunder 1970, Pohl and West 1973). Second, wind exerts mechanical force, and birds tend to "weathercock" (i.e. face into the wind to minimize wind force). This behavior increases with wind speed, and may reduce activity and activity metabolism. Thermoregulatory metabolism may also be reduced because less activity and a less exposed posture may decrease thermal conductance. Body temperature may also decline with reduced activity.

Light also has nonthermal effects on metabolism and thermal conductance. Photoperiod entrains circadian rhythms, and metabolism, body temperature, and thermal conductance are highest during the active phase of the circadian cycle (Aschoff and Pohl 1970, Pohl and West 1973, Aschoff 1981). Illumination is also a factor. In darkness, especially with cold stress, birds place the face and beak under the scapulars to reduce heat loss. Birds orient visually and become much more active when illumination is present (Pohl 1969). The thinly insulated head is a major avenue for heat loss when the eyes and face are exposed (Hill et al. 1980). Additional processes may be involved, as metabolism increased with illumination at thermal neutral as well as cold temperatures in Chaffinches (*Fringilla coelebs*; Pohl 1969).

The net effect of wind and illumination at temperatures below the thermal neutral zone also depends on whether induced activity metabolism compensates for thermoregulatory metabolism (Pohl and West 1973, Paladino and King 1984). If complete compensation occurs,

¹ Current address: Rural Route 1, Box 57, Centerpoint, Indiana 47840, USA.

the heat produced by activity metabolism will substitute for thermoregulatory heat production; thus, increasing activity will not increase total metabolic rate. With partial or no compensation, the metabolic cost of activity will add to basal and thermoregulatory metabolism, and total metabolic rate will increase as activity increases. The extent of compensation depends on the amount of heat produced by activity and how activity affects overall thermal conductance and body temperature (Hart 1952).

We used active-phase American Goldfinches (*Carduelis tristis*) to measure the nature and significance of some of these nonthermal effects of wind and illumination for thermoregulatory studies. Goldfinches are tractable experimental subjects, and an extensive literature on their thermoregulatory physiology is available for comparison (e.g. Dawson and Carey 1976, Bakken et al. 1981, Buttemer 1981, Lustick et al. 1982). We measured diurnal oxygen consumption, evaporative water loss, and carbon-dioxide production at 10°C and four wind speeds both with and without thermally insignificant illumination. We observed activity with closed-circuit television during the measurements to allow examination of the relations among illumination, activity, wind speed and metabolic rate.

MATERIALS AND METHODS

Animals.—We captured five goldfinches in mist nets at a feeding station 7 km north-northeast of the campus of Indiana State University. We transported the birds to the laboratory and held them individually in box cages 43 × 31 × 34 cm (length × width × height). To approximate natural conditions, birds were exposed to a constant 15°C air temperature and a 12:12 l:d photoperiod. Water and thistle seed were provided *ad libitum*. One failed to maintain stable weight and was released. The remaining four (three males and one female) remained in good health except for an outbreak of coccidiosis (treated successfully with sulfadimethoxine) and were released at the end of the study. There was no evidence of molt during the period of activity. All procedures were approved by the University's Animal Care and Use Committee. Birds were taken and held under Federal permit PRT-705956 and Indiana permit 272.

Gas exchange.—We conducted gas exchange in two chambers of a controlled-environment metabolism system from 20 March to 14 April 1989. The design of the chambers is described by Bakken et al. (1989). General operating procedures and calibration were as described by Bakken et al. (1991). Temperature was

regulated at $T_a = 10^\circ \pm 0.5^\circ\text{C}$, and wind speeds (u) of 0.1, 0.64, 1.96, and 3.3 m/s (± 0.05 m/s) were generated by a centrifugal blower. The RMS turbulence level was $\Delta u/u = \pm 2\%$, and wind velocity varied $\pm 5\%$ or less across the test section. We measured wind speed with a Thermo-systems Inc. model 1053B hot-wire anemometer and 1330-18-20 hot-film sensor calibrated against a Prandtl-design Pitot tube and electronic hook gauge. Blockage ratios were less than 0.09, and, therefore, blockage should not affect heat transfer significantly (Bakken 1990a).

For respiratory-gas analysis, we measured oxygen with a Beckman F3M3 Paramagnetic Oxygen Analyzer, carbon dioxide with a Beckman 865 Infrared Gas Analyzer, and water vapor with EG&G models 880 and 911 Dewpoint Hygrometers. The open-circuit flow rate was about 1.3 L/m. We used a Z-transform analysis (modified from Bartholomew et al. 1981) to compute gas exchange for each 1.67-min sampling interval. We withheld food for 2-3 h prior to metabolic measurements. An oil-filled pan under the birds trapped droppings to prevent evaporation. All measurements were conducted between 1100 and 1700 during the active phase of the circadian cycle.

The study was designed as a series of 4×4 Latin squares. Each square used one light level, with wind speeds distributed for individuals as columns, and order of exposure as rows. On any given day, two birds were measured simultaneously in two chambers, and so only half of each square was done each day. Some data were lost to various equipment failures, and so the design was not followed rigorously. Respiratory gas exchange was measured for 30 min at each wind speed with an intervening adjustment period. The series of four wind speeds required 3 to 4 h. Illumination was held constant during the measurement period at either near darkness (<0.2 lux) or ambient laboratory illumination (ca. 500 lux). We measured illumination with a Gossen Luna-Pro light meter (minimum detectable light level 0.2 lux).

Behavioral observations.—We observed the birds with a closed-circuit black-and-white television (Sony Videocam model AVC 3260 with $f/1.8$ zoom lens) placed directly above the chamber. For illumination, a very small incandescent lamp (14V, 1W, 3.5 mm diameter) operated at 12V, 0.6W) was placed on a support in the center of the camera lens. The bulb was shielded so that the lens received only reflected light. The bottom of the oil pan under the birds was covered with reflecting tape, which directed most of the incident light directly back to the lens. Thus, the silhouette of the bird could be seen with less ambient illumination than that provided by a full moon (0.2 lux).

For consistency, one of us (KFL) scored all behavior during the experiment. Activity codes for a bird refer to the entire 30-min run, and were: (0) inactive; (1) shifted occasionally on perch; (2) reversed position on perch periodically; (3) occasionally left perch and

moved wings; (4) frequently on and off perch using wings. In principle, the head position could be determined by visualizing the silhouette of the beak. However, the beak was frequently invisible due to extreme ptilioerection. Our general impression was that the face and eyes were usually exposed when the cage was illuminated, or when activity scored 3 or 4 without illumination. Otherwise, the face and eyes were covered by the scapulars.

Data analysis.—We used routines from the SYSTAT and SYGRAPH packages for statistical and graphical analysis (Wilkinson 1988a, b). The specific tests, sample sizes (n), standard errors (SE), and probability of type I error (P) are indicated in the text. A two-tailed probability value is given, except as indicated. Because only four birds were used, it is unknown as to whether our findings can be generalized to a larger population, such as the goldfinches of Indiana.

RESULTS

Activity.—We examined each bird's activity level in relation to wind speed, illumination, and wind speed \times illumination interaction. Because there was no significant tendency for particular birds to be more active than others (contingency chi-square, $df = 3$, $P = 0.22$), all data were combined. There were too few data ($n = 66$) to test the full design (i.e. two light levels by four wind speeds by five activity levels). Thus, we condensed the table to low (0.1 and 0.64 m/s) and high (1.96 and 3.3 m/s) wind speeds, and quiet (code 0 or 1) and active (code 2-4) behavior.

We found a significant decrease in activity at high wind speed by using the Mantel-Haenszel chi-squared test to control for illumination levels ($P = 0.04$, $n = 66$). Although there were too few data for an adequate test of individual illumination treatments, the decrease in activity at high wind speed appeared more marked when illumination was absent (illuminated, $P = 0.48$, $n = 30$; none, $P = 0.06$, $n = 36$). Because birds are highly visual animals, we expected activity to increase when illumination was present. Combining wind speeds, we found the data to be suggestive, albeit statistically nonsignificant, of increased activity by illuminated birds (Mantel-Haenszel chi-squared test to control for wind speed, one-tailed, $P = 0.066$, $n = 66$).

Metabolic rate.—The respiratory quotient (RQ) was approximately 0.71 (SE = 0.012, $n = 47$), as estimated by averaging the respiratory exchange ratios for all data. Thus, we assumed a thermal equivalence of 19.6 joules/ml oxygen consumed (Bartholomew 1977).

We then fitted a stepwise-multiple-regression model to the data for metabolic rate (M). Predictor variables were wind speed (u , m/s), activity code ($A = 0$ to 4), illumination ($I = 0$ if absent, $I = 1$ if present), and body mass at the beginning of the experiment (m , grams), as well as interaction terms ($u \cdot I$, $u \cdot A$, and $A \cdot I$), $m^{2/3}$, $m^{3/4}$, and \sqrt{u} . Individuals were included as a categorical variable to account for repeated measures. This model found that there was a significant mass effect that was best predicted by $m^{1.0}$. Wind effects were best predicted by $u^{1.0}$. Individual code did not enter the model.

To simplify subsequent models, we adjusted all data to M_{13} , the metabolic rate of a "standard" 13-g goldfinch (slightly larger than the 12.6-g mean mass of the birds at the time of each experiment). The defining relation was

$$M_{13} = M - 0.062(m - 13). \quad (1)$$

The M_{13} data were plotted as a function of u (Fig. 1) with separate linear regressions for data taken with and without illumination. Birds with illumination had a higher metabolic rate and stronger dependence on wind speed than birds without illumination. However, the slope for data taken with illumination is not significantly greater than that for data taken without illumination (one-tailed, $P = 0.10$).

We then removed the mass variables from the list of predictor variables and fitted a stepwise multiple regression to the M_{13} data ($n = 66$, adjusted $r^2 = 0.510$, $P < 0.00001$):

$$M_{13} = 0.471 + 0.069u + 0.175I + 0.089A - 0.055A \cdot I. \quad (2)$$

Parameters were significant (u and a , $P < 0.00001$; I , $P = 0.00007$; $A \cdot I$, $P = 0.02$). The model parameters were chosen so that the constant is the metabolic rate of a quiet ($A = 0$) 13-g bird in the dark ($I = 0$) with no wind ($u = 0$). Illumination is a categorical variable with two levels. Thus, the regression coefficient for I gives the change in M_{13} due to presence/absence of illumination. None of the other predictor variables entered the regression.

To verify that a linear model was appropriate for the arbitrary activity score, we visualized the form of the dependence of M_{13} on the activity code A by setting the A coefficient in equation 2 equal to zero and using the residuals in a Tukey box plot. The relation between M_{13} and A was essentially linear (Fig. 2).

The effects of A , I , and $A \cdot I$ can be removed

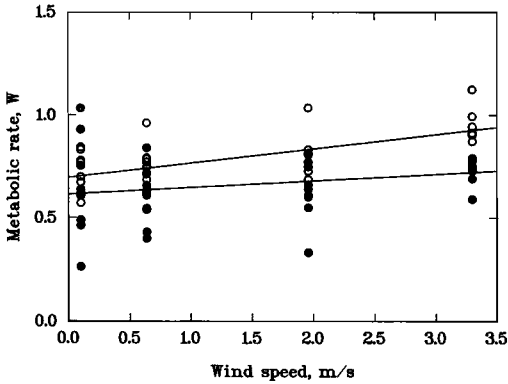


Fig. 1. Metabolic rate adjusted to a standard 13-g mass as a function of wind speed for active-phase American Goldfinches with (open circles) and without (filled circles) illumination. Upper line is linear regression for data taken with illumination, and lower line for data taken without illumination. Slope of upper regression is significant ($P = 0.001$), but slope of lower regression is not ($P = 0.18$).

similarly to give the underlying response of M_{13} to u by setting the constant and coefficient for u equal to zero, and plotting the residuals of this modified model (Fig. 3).

The effect of the $A \cdot I$ term in the model (which indicated a behavioral response to light that altered metabolic rate) can be clarified by fitting separate models to data taken with and without illumination. With illumination ($n = 30$, adjusted $r^2 = 0.445$, $P = 0.0002$),

$$M_{13} = 0.637 + 0.074u + 0.034A. \quad (3)$$

Without illumination ($n = 36$, adjusted $r^2 = 0.377$, $P = 0.0002$),

$$M_{13} = 0.480 + 0.063u + 0.087A. \quad (4)$$

Comparison of the A -coefficients shows that the effect of A on M_{13} is 2.56 times as great in the dark as it is in the light.

Evaporative water loss and thermal conductance.—The ratio of evaporative cooling E (i.e. W/animal) to metabolic heat production E/M averaged 0.16 (SE = 0.016). No valid multiple-regression model for E/M was found using any combination of illumination, wind, activity, mass, or interaction terms among these variables as predictors (all $P > 0.12$). Thus, net heat production (metabolism less evaporative cooling) is approximately $0.84M$.

Computation of thermal conductance requires knowledge of the bird's body temperature. However, passerine body temperature ris-

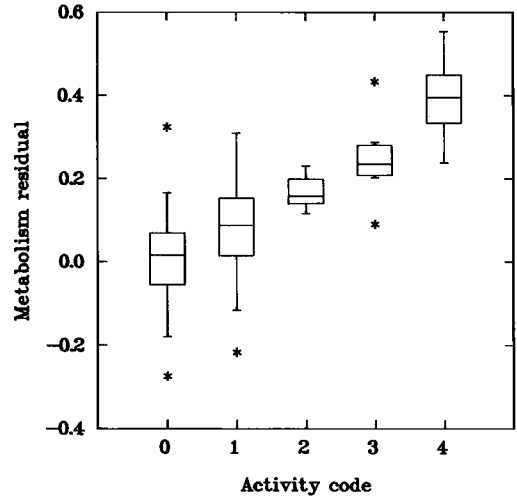


Fig. 2. Effect of activity (see text for code interpretation) on metabolic rate (controlled for effects of wind) and illumination using equation 2. Data displayed as Tukey box plots. Horizontal line inside box denotes mean, and asterisk (*) indicates extreme values. Increase of metabolic rate is linear function of activity score, even though activity scale is arbitrary.

es rapidly when the animal is disturbed (Southwick 1973), and we were not able to remove the chamber hatch quickly enough to obtain reliable values. Lustick et al. (1982) found that the body temperature (T_b) of illuminated, active-phase American Goldfinches held in captivity for some time averaged 38°C at an air temperature of 10°C , and did not vary with wind speeds up to 2.8 m/s. This T_b is somewhat lower than the $39\text{--}40^\circ\text{C}$ body temperature of freshly caught birds in their rest phase (Dawson and Carey 1976). Assuming that $T_b = 38^\circ\text{C}$ is most likely to be representative of our captive birds, the approximate overall thermal conductance (K_c) at 10°C is:

$$K_c = (M - E)/(T_b - T_a) = 0.030M_{13}. \quad (5)$$

where M_{13} is computed using equation 2. Other values of T_b may be substituted, if desired.

DISCUSSION

Activity, illumination, and metabolic rate.—Metabolic rate is most strongly affected by activity, and increased as much as 75% as A increased from 0 to 4 (equation 2). Thus, activity metabolism does not fully compensate for thermoregulatory metabolism at 10°C . This is consistent with results for locomotion in White-

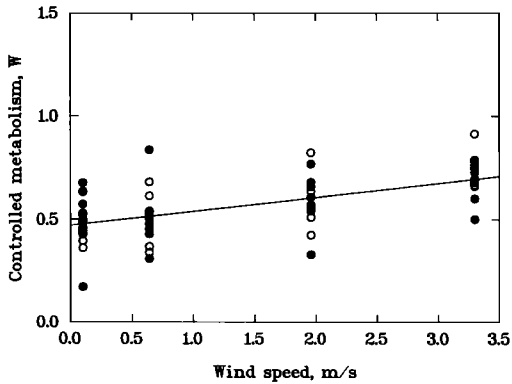


Fig. 3. Metabolic rate of active-phase American Goldfinches (adjusted to 13-g mass). Equation 2 used to remove nonthermal effects of light, activity, and light \times activity interaction to give response of a quiet animal in darkened enclosure. Symbols as in Figure 1. All data described by common regression line. Compared to uncontrolled data taken without illumination (Fig. 1), mean metabolic rate is reduced and effect of wind speed increased.

crowned Sparrows (*Zonotrichia leucophrys*), where activity metabolism did not compensate at 12°C, although it did at -10°C (Paladino and King 1984).

Illumination alone produced a 37% increase in metabolic rate (equation 2). This is greater than the 20% increase of metabolic rate during active phase typical of birds of similar mass (Aschoff and Pohl 1970). Illumination also substantially reduced the relative effect of A on M_{13} (equations 2-4). As we made all measurements in the active phase, the observed response of M_{13} probably resulted from the interacting effects of illumination and activity on thermal conductance (Pohl and West 1973, Pauls 1981). The argument is as follows.

When illuminated, our birds maintained visual contact with their surroundings. Higher levels of activity (codes 2-4) also required visual contact with the surroundings and reduced ptioerection. Wing use exposed the poorly insulated axilla. These effects all increase thermal conductance and metabolic rate. Active birds may have had a higher M_{13} in order to maintain muscle tone and a higher T_b than quiet birds. In darkness (equation 3), the conductance of a resting bird attained minimal values. Disruption of insulation by activity probably increases conductance. For our birds, the extra heat produced by activity metabolism did not fully compensate for the increased conductance; M_{13} was

sensitive to A (Hart 1952). With illumination (equation 4), the conductance of inactive birds did not reach the minimal values observed in darkness, because the face was exposed to maintain visual contact. As a result, illumination alone elevated M_{13} in resting birds, and further disruption of insulation by activity had relatively less effect on heat loss. Thus, more of the heat produced by activity metabolism substituted for thermoregulatory metabolism when the animal was illuminated than when the animal was in the dark, which resulted in reduced dependence of M_{13} on A . Because we used only one temperature, we can only make statements about the relative degree of substitution of heat produced by activity for thermoregulatory heat production with and without illumination.

Metabolism and wind.—The metabolic rate of our captive, active-phase goldfinches at 10°C, corrected for illumination and activity and extrapolated to $u = 0$ (i.e. the constant in equation 2), was 0.471 W. This value is close to that of freshly captured, rest-phase goldfinches determined by a similar extrapolation of data taken at several wind speeds to $u = 0$ (0.474 W; Buttemer 1981), and is 6% greater than that of captive rest-phase goldfinches measured at 10°C in free convection (0.444 W, Dawson and Carey 1976; 0.442 W, Lustick et al. 1982). The regression models of Aschoff and Pohl (1970) predict active-phase resting metabolism 16% greater than that in rest-phase for a 13-g bird. This discrepancy may suggest that the disruption of insulation by activity and by exposing the face to maintain the visual contact are major factors in the increase of active-phase metabolism relative to rest-phase metabolism, and that the data used by Aschoff and Pohl (1970) may not have been fully corrected for activity and posture. Alternatively, we may have overcorrected; however, this is unlikely, as the regression line of M_{13} on u for birds in the dark with activity codes of 0 and 1 ($n = 21$) nearly overlies the regression of controlled M_{13} on u in Figure 3.

The principal nonthermal effect of wind was to decrease activity, although the effect was less marked with illumination than in the dark. Thus, wind decreased activity metabolism at the same time as convection increased heat loss. Data uncorrected for activity may underestimate the increase in thermoregulatory metabolism caused by wind (Figs. 1 and 2), unless there is full compensation of activity metabolism for thermoregulatory metabolism (Hart

1952). A similar effect of wind on activity (but more marked in light than dark) was observed in the Tufted Titmouse (*Parus bicolor*), but not the Carolina Chickadee (*Parus carolinensis*; Wood and Lustick 1989).

Bakken (1990b) reviewed studies of the effect of wind on avian metabolic rate. He noted, that when a linear regression of the form $M = a + b\sqrt{u}$ was fitted to metabolism or thermal conductance data, the ratio b/a was approximately 0.26 for all passerine species studied. Our data are broadly consistent. The ratio of b/a was 0.33 when the effects of A , I , and $A \cdot I$ were removed (found by fitting a model similar to equation 2, but using \sqrt{u} in place of u , and then taking the ratio of the coefficient for \sqrt{u} to the constant). This value is slightly larger than the value for mostly quiet rest-phase goldfinches at the same temperature ($b/a = 0.30$; Bakken et al. 1981). Without activity correction, the interaction of wind and activity results in $b/a = 0.21$ with illumination, and $b/a = 0.11$ without illumination.

Bakken (1990b) also suggested that the unusual sensitivity of metabolic rate to wind in some nonpasserines may have been due to exposure of the head during the study. As our birds apparently exposed the head when illuminated, the slope of a M_{13} -vs.- u scattergram should be greater for data taken with illumination. The slope was significantly different from zero when data were taken with illumination, but was not significantly different from zero for data taken without illumination (Fig. 1). This difference is as predicted, but the slope for data taken with illumination was not significantly greater than that taken in darkness (one-tailed $P = 0.10$). Further, the $u \cdot I$ interaction term did not enter the multiple-regression model (equation 2). Much of the difference in slope was removed when the activity parameter A was included in the regression (equations 3 and 4). Thus, while our results are consistent with Bakken's (1990b) hypothesis, the mechanism is complex and the hypothesis is not confirmed statistically.

The complex interactions of wind, behavior, heat loss, and metabolism present a difficult problem for estimating the net metabolic effect of wind on active-phase birds foraging in exposed habitats. The net effect is not obvious, and further study and modeling are required. Clearly, it is important either to eliminate measurements during activity or to correct for ac-

tivity when assessing the thermal effect of wind and light. The information available in a study of metabolic responses to both thermal and nonthermal effects of wind and light can be greatly increased by observing the behavior of the animals via closed-circuit television. Data may then be fitted to mechanistic or multiple-regression models to separate and quantify the various effects of wind and light on metabolism. This will allow more accurate modeling of the energetics of active, free-living animals.

ACKNOWLEDGMENTS

We thank C. Starkey and the Indiana State University Mobile TV facility for the use of two black-and-white CCTV systems. Supplies and publication costs were supported by Indiana State University. Construction of the experimental apparatus was supported by NSF grants DEB 80-21321 and BSR 83-00651. This work was part of an undergraduate research project by KFL.

LITERATURE CITED

- ASCHOFF, J. 1981. Thermal conductance in mammals and birds: Its dependence on body size and circadian phase. *Comp. Biochem. Physiol.* 69A:611-619.
- ASCHOFF, J., AND H. POHL. 1970. Rhythmic variations in energy metabolism. *Fed. Proc.* 29:1541-1552.
- BAKKEN, G. S. 1990a. Blockage errors in studies of the effect of wind on thermoregulatory responses. *J. Therm. Biol.* 15:207-210.
- BAKKEN, G. S. 1990b. Estimating the effect of wind on avian metabolic rate with standard operative temperature. *Auk* 107:587-594.
- BAKKEN, G. S., W. A. BUTTEMER, W. R. DAWSON, AND D. M. GATES. 1981. Heated taxidermic mounts: A means of measuring the standard operative temperature affecting small animals. *Ecology* 62: 311-318.
- BAKKEN, G. S., D. J. ERSKINE, AND M. T. MURPHY. 1989. A wind tunnel metabolism chamber with small volume and good air flow characteristics. *J. Physics E: Scientific Instruments* 22:1048-1050.
- BAKKEN, G. S., M. T. MURPHY, AND D. J. ERSKINE. 1991. The effect of wind and air temperature on metabolism and evaporative water loss rates of Dark-eyed Juncos, *Junco hyemalis*: A standard operative temperature scale. *Physiol. Zool.* 64:1023-1049.
- BARTHOLOMEW, G. A. 1977. Energy metabolism. Pages 57-110 in *Animal physiology: Principles and adaptations*, 3rd ed. (M. S. Gordon, Ed.). Macmillan, New York.
- BARTHOLOMEW, G. A., D. VLECK, AND C. M. VLECK. 1981. Instantaneous measurements of oxygen consumption during pre-flight warm-up and post-

- flight cooling in sphingid and saturniid moths. *J. Exp. Biol.* 90:17-32.
- BUTTEMER, W. A. 1981. The thermal significance of winter roost-site selection by American Goldfinchs (*Carduelis tristis*). Ph.D. thesis, Univ. Michigan, Ann Arbor.
- BUTTEMER, W. A., A. M. HAYWORTH, W. W. WEATHERS, AND K. A. NAGY. 1986. Time-budget estimates of avian energy expenditure: Physiological and meteorological considerations. *Physiol. Zool.* 59: 131-149.
- DAWSON, W. R., AND C. CAREY. 1976. Seasonal acclimatization to temperature in cardueline finches. I. Insulative and metabolic adjustments. *J. Comp. Physiol. B* 112:317-333.
- DEJONG, A. A. 1976. The influence of simulated solar radiation on the metabolic rate of White-crowned Sparrows. *Condor* 78:174-179.
- HART, J. S. 1952. Effects of temperature and work on metabolism, body temperature, and insulation: Results with mice. *Can. J. Zool.* 30:90-98.
- HAYES, S. R., AND J. A. GESSAMAN. 1980. The combined effects of air temperature, wind, and radiation on the resting metabolism of avian raptors. *J. Therm. Biol.* 5:119-125.
- HILL, R. W., D. L. BEAVER, AND J. H. VEGHTE. 1980. Body surface temperatures and thermoregulation in the Black-capped Chickadee (*Parus atricapillus*). *Physiol. Zool.* 53:305-321.
- LUSTICK, S., B. BATTERSBY, AND L. MAYER. 1982. Energy exchange in the winter acclimatized American Goldfinch, *Carduelis (Spinus) tristis*. *Comp. Biochem. Physiol.* 72A:715-719.
- PALADINO, F. V., AND J. R. KING. 1984. Thermoregulation and oxygen consumption during terrestrial locomotion by White-crowned Sparrows *Zonotrichia leucophrys gambelii*. *Physiol. Zool.* 57:226-236.
- PAULS, R. W. 1981. Energetics of the red squirrel: A laboratory study of the effects of temperature, seasonal acclimatization, use of the nest and exercise. *J. Therm. Biol.* 6:79-86.
- POHL, H. 1969. Some factors influencing the metabolic response to cold in birds. *Fed. Proc.* 28: 1059-1064.
- POHL, H., AND G. C. WEST. 1973. Daily and seasonal variation in metabolic response to cold during rest and forced exercise in the Common Redpoll. *Comp. Biochem. Physiol.* 45A:851-867.
- REINERTSEN, R. E., AND S. HAFTORN. 1983. Nocturnal hypothermia and metabolism in the Willow Tit *Parus montanus* at 63°N. *J. Comp. Physiol. B* 151: 109-118.
- SIEGEL, H. S. 1980. Physiological stress in birds. *BioScience* 30:529-533.
- SOUTHWICK, E. E. 1973. Remote sensing of body temperature in a captive 25-g bird. *Condor* 75:464-466.
- WEATHERS, W. W., W. A. BUTTEMER, A. M. HAYWORTH, AND K. A. NAGY. 1984. An evaluation of time-budget estimates of daily energy expenditure in birds. *Auk* 101:459-472.
- WILKINSON, L. 1988a. SYGRAPH. SYSTAT, Evanston, Illinois.
- WILKINSON, L. 1988b. SYSTAT: The system for statistics. SYSTAT, Evanston, Illinois.
- WOOD, J. T., AND S. I. LUSTICK. 1989. The effects of artificial solar radiation on wind-stressed Tufted Titmice (*Parus bicolor*) and Carolina Chickadees (*Parus carolinensis*) at low temperatures. *Comp. Biochem. Physiol.* 92A:473-477.
- WUNDER, B. A. 1970. Energetics of running activity in Merriam's chipmunk, *Eutamias merriami*. *Comp. Biochem. Physiol.* 33:821-836.