THERMAL EXCHANGE BETWEEN SHARP-TAILED GROUSE (*PEDIOECETES PHASIANELLUS*) AND THEIR WINTER ENVIRONMENT

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Sharp-tailed Grouse (*Pedioecetes phasianellus*) inhabit the plains and parklands of North America from Oregon to Colorado to Michigan and north to Alaska (Aldrich 1963). Winter conditions throughout their range are considered, by human standards, to be harsh. Homeotherms, including Sharp-tailed Grouse, maintain a relatively constant body temperature by physiological and behavioral thermoregulatory mechanisms. We have supplemented the information and discussion of fundamental concepts of bioenergetics found in Gates (1962), Gessaman (1973), Porter and Gates (1969), and Sturkie (1965), by investigating effects of wind on insulation properties of the feather and skin layer.

Scholander et al. (1950:246) and Bartholomew (1968a:317) described Newton's Law of Cooling in terms or equations applicable to bioenergetics of homeotherms. Kleiber (1961, 1972) and Stewart (1967:449–450) stated that Fourier's Law best describes heat flow from a homeotherm to its environment. Both laws depend on a proportionality coefficient to relate the rate of heat flow per unit of surface area to the temperature difference between core temperature and ambient temperature. This proportionality coefficient is called "thermal conductance." Thermal conductance is calculated commonly in avian energetics studies by dividing the rate of metabolism by the difference between core temperature and ambient temperature (Kendeigh 1970:63), or recording the rate of cooling in an animal's body immediately after death (Herreid and Kessel 1967). We have incorporated the information into a model that accounts for behavioral aspects of thermoregulation and predicts existence metabolism for Sharp-tailed

Grouse when subjected to different environmental conditions.

Total nonevaporative heat exchange between an animal and its environment occurs through a transition zone with a temperature gradient from deep body temperature to ambient temperature. This zone is called the thermal transfer layer. The feather layer provides the most insulation per unit of thickness, so it has the largest temperature gradient. Wind velocity, air temperature, feather orientation, net radiation flux, and physiological adjustments all influence the shape and depth of the thermal profile. An understanding of the shape of this profile under different conditions is essential for understanding total nonevaporative heat transfer.

Wind in the natural environment influences thermal exchanges between an animal and its surroundings. However, the specific effects of wind velocity on thermal conductance of birds has been little studied. Gessaman (1972), using live Snowy Owls (*Nyctea scandiaca*), found that oxygen consumption increased linearly with the square root of wind speeds up to 16 mph. Tracy (1972) and Heller and Gates (1971) briefly discussed the importance of studying the influence of wind and reported on convective coefficients for chipmunks (*Eutamias*). Most previous investigations determined thermal conductance from heat production measurements in controlled temperature metabolic chambers.

Evaporative heat loss at lower ambient temperatures is relatively constant and small. Evaporative heat loss from the Snowy Owl at $-10°$ to $-40°C$ was probably less than 3% of total heat loss (Gessaman 1972). Other investigators have reported heat loss by evaporation in birds to be less than 10% of the total at ambient temperatures below 15°C

(Bartholomew and Trost 1970:143; Mugaas and Templeton 1970:130).

MATERIALS AND METHODS

Wild adult and subadult Sharp-tailed Grouse were live-trapped by personnel of the South Dakota Department of Game, Fish, and Parks during January. Some of the grouse were held in captivity more than one year. Grouse skins were obtained from birds during January, February, and March. The operational components of the thermal conductance concept, namely, the conductive surface area, the subskin and surface temperature, the thermal transfer layer depth, and the thermal conductivity coefficients, were analyzed to determine the values needed to express nonevaporative heat flow through the thermal transfer layer. The equipment used to quantify heat flow through the skin plus feather layer included a Thermal Micro-Simulation Tunnel (TMST), infrared thermometer, and Thermal Conduction Apparatus (TCA).

THERMAL MICRO-SIMULATION TUNNEL (TMST)

Tests were conducted at the BioThermal Laboratory, Cornell University, Ithaca, New York, in the TMST to determine the effect of wind velocity, air temperature, feather orientation, and downward radiation on temperature profile characteristics through back and breast feather layers of Sharp-tailed Grouse. The TMST (fig. 1) included a test chamber approximately $15 \times 16 \times 60$ cm in size, where wind velocities from 0 to 12 mph (0–19.3 km hr^{-1}) could be controlled. The floor and ceiling of the test chamber consisted of temperature-controlled copper plates. The temperature of these plates was controlled with circulating ethylene glycol to prevent freezing when simulating winter conditions.

The feather layer, including intact skin, was placed on the bottom temperature-controlled plate. Subskin temperature on the flat simulator was controlled at approximately 41.5°C. Deep body temperature of Sharp-tailed Grouse was not measured, but was estimated at 41.5°C. Rasmussen and Brander (1973) found cloacal temperatures of 63 Ruffed Grouse (*Bonasa umbellus*) under a wide range of environmental temperatures to be 41.5°C. This value is in agreement with temperature data on other species of galliform birds (Sturkie 1965:194; McNab 1966:50). West (1962:294) reported that subskin temperature is within 0.5°C to 1.0°C of core temperature.

The temperature profile was determined with an array of copper-constantan thermocouples spaced at 0.25-cm intervals, mounted on a wooden dowel inserted through and perpendicular to the feather layer. Preliminary data indicated that wind would influence heat flow rates much more at lower velocities than at higher velocities (10–12 mph). Therefore, the effects of wind velocities of 0, 1, 2, 4, 6, and 10 mph and air temperatures ranging from −18°C to 24°C on the temperature profile were investigated. Wind velocity, reported in mph throughout this article, can be converted to km hr^{-1} by multiplying by 1.61.

The techniques used were slightly modified from those used by Stevens and Moen (1970) and Stevens (1972) in a larger wind tunnel called the Thermal Environment Simulation Tunnel (TEST) at the Bio-Thermal Laboratory.
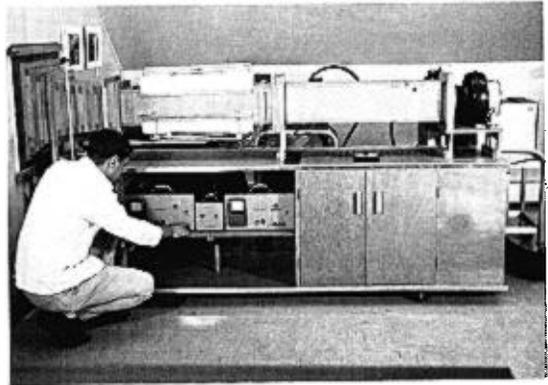
FIGURE 1. The Thermal Micro-Simulation Tunnel (TMST) was used for investigating the effect of wind velocity, air temperature, feather orientation, and radiation on the thermal properties of the feather layer. (Photo by D. M. Payne)

INFRARED THERMOMETER

A noncontact (infrared) thermometer was used for live animal and simulator surface temperature measurements. The infrared thermometer integrates the vertical and horizontal temperature over the entire target area. The infrared thermometer used has a view of 3° and was held at a distance of 12–14 inches (30–35 cm) from the live bird or the simulator feather layer. The accuracy of surface temperature measurements with conventional thermometers or thermocouples on living animals is limited by subjective placement of the sensing device in the outer layer of an irregular surface such as feathers. Live animal measurements were taken on captive Sharp-tailed Grouse at the Ithaca Game Farm, Ithaca, New York. Radiant surface temperature measurements were taken on all parts of the grouse body on calm nights when wind and solar radiation effects were minimal. The bird remained perched on a roost during measurements; a moderate degree of feather fluffing was evident. Simultaneous air temperatures were recorded by connecting a copper-constantan thermocouple and the infrared thermometer to a dual pen chart recorder.

THERMAL CONDUCTION APPARATUS (TCA)

A Thermal Conduction Apparatus (TCA) was designed and constructed to investigate the conductive properties of the feather layer. The TCA consisted of two temperature-controlled copper plates and a heat flow disk. The 7.9-cm diameter plates were surrounded with styrofoam and mounted in a wooden frame so that the distance between the plates could be accurately controlled. Heat flow between the plates was measured with a soil heat flux recording system. This system consists of a heat flow disk and a microvolt recorder. The 2.5-cm diameter heat flow disk was embedded in the bottom plate of the TCA. Styrofoam and glass wool with known conductivity values were used to calibrate the apparatus.

THERMAL CONDUCTIVITY OF FEATHERS

The thermal conductivity coefficient (k) of the feather layer of the Sharp-tailed Grouse was determined in two ways. The first method was by placing a heat-flow disk between the skin and bottom plate of the TMST flat plate simulator. The coefficient was determined

using *thermal* depth. Thermal depth is defined as the distance (cm) between the skin and the point within the feather layer where the radiant surface temperature (determined with an infrared thermometer) equals the temperature of the thermal profile (determined with an array of thermocouples). Thermal depth proved to be a better parameter than physical depth for heat transfer determinations through irregular biological materials. Thermal depth is less than physical depth of the feather layer and is influenced strongly by wind velocity. In the second method, thermal conductivity was determined in the TCA and expressed as Kcal m^{-2} hr^{-1} $°C^{-1}$ cm of *physical* depth. The values are different because, under similar conditions, the heat flow will be the same but the thermal depth will be less than physical depth.

RESULTS AND DISCUSSION

Nonevaporative heat dissipated by the body is transferred through the skin and feather layer by conduction. Under winter conditions, energy reaching the surface of the feathers is dissipated primarily by radiation and convection. Conduction through the thermal transfer layer (skin + feathers) is expressed as follows (modified from Weast and Selby 1967: F-65):

$$Q_k = A_k t k (T_b - T_s)/d$$

where: Q_k = Heat exchange by conduction (Kcal)
   A_k = Conductive surface area (m^2)
   t = Time (hr)
   k = Thermal conductivity coefficient (Kcal m^{-2} hr^{-1} $°C^{-1}$ cm)
   T_b = Subskin temperature (C)
   T_s = Surface temperature (C)
   d = Thermal transfer layer depth (cm)

Each factor in the above formula was evaluated for the feather layer of Sharp-tailed Grouse. Many of these factors are variables when applied to a living system in a thermally dynamic environment. The results of the investigation on each factor follow.

SURFACE AREA (A_k)

Surface areas were calculated from 16 freshly killed grouse during late fall hunting seasons in South Dakota. The grouse body was approximated with geometrical shapes to permit surface area calculations. Included in the sample were six young and two old males, and five young and three old females. A surface area:body weight relationship was calculated using linear regression with a log-log transformation of data. The prediction equation is as follows:

$$A_k = (7.46 W^{0.65}) \times 10^{-4}$$

where: A_k = Surface area (m^2)
   W = Body weight (g)

Surface area data indicate that the head and neck, when fully extended, can comprise 20% of the total surface area. Thermoregulatory behavior involves pulling the head in, thus reducing the proportion of surface area with the high thermal conductance value and the total effective surface area. The surface area of the head can be reduced to approximately 5% of the total (maximum) surface area.

The surface area:weight relationship on the 16 grouse measured was somewhat variable ($r = 0.65$), but did conform very closely to the two-thirds power relationship reported by other authors (Brody 1945:360; Bartholomew 1968b:60; Guyton 1971). Other authors have used similar formulas for calculating surface area. Kendeigh (1970:63) used 10 $W^{0.667}$ for all birds and Mitchell (1930:447) used 8.19 $W^{0.705}$ for White Leghorn Chickens. The values predicted and used here for Sharp-tailed Grouse are conservative estimations of surface area compared to the other two equations.

THERMAL CONDUCTIVITY OF FEATHERS (k)

The average conductivity coefficient (k) of grouse feather layer for 70 replications in the TMST was 1.77 Kcal m^{-2} hr^{-1} $°C^{-1}$ for each centimeter of thermal depth. The standard error was 0.087, and the 95% confidence interval using a "t" statistic was 1.60–1.94. There was no difference between back and breast feathers or according to feather orientation.

The value of 1.77 is lower than the reported conductivity coefficients for commercial insulative materials. Styrofoam has a k value of 2.85 and glass wool, a value of 3.00, using physical depth (Weast and Selby 1967:E-5). The thermal conductivity from TCA measurements for grouse feathers was 3.54 Kcal m^{-2} hr^{-1} $°C^{-1}$ cm, with an average physical depth of 1.48 cm for breast and back feather layers. The thermal conductivity of the neck and head feathers is not significantly different from breast and back feathers. The physical depth of head and neck feather layers is 0.48 cm, which is approximately 33% of the physical depth of the breast and back feathers.

Although the two conductivity values appear quite different, total heat flow through the breast or back feather layer is similar if calculated on either a thermal depth or physical depth basis. TCA values are comparable to TMST values at wind speeds above 10 mph because (1) thermal transfer layer depths decrease with increased wind speed, and (2) the TCA essentially reduces the thermal transfer layer to the physical depth of the feather layer. The similarity of heat-flow rates calcu-

TABLE 1. Formulas for predicting feather surface temperatures (Y) °C of back and breast feather tracts from air temperature (X) °C at various wind velocities (TMST flat plate simulator).

Wind velocity mph	Formula	Correlation coefficient	Sample size
0	$Y = 5.978 + 0.855X$	0.99	34
1	$Y = 9.256 + 0.776X$	0.99	34
2	$Y = 9.726 + 0.765X$	0.99	30
4	$Y = 7.707 + 0.814X$	0.97	29
6	$Y = 7.472 + 0.819X$	0.99	27
10	$Y = 7.113 + 0.828X$	0.99	41

lated by both methods can be illustrated by reducing to a common unity those values in the conductivity equation that do not change between methods as shown below:

TCA value (Kcal m^{-2} hr^{-1} °C^{-1})

$$Q_k = \frac{A_k t k (T_b - T_s)}{\text{physical depth}} = \frac{(1)(1)(3.54)(1)}{1.48}$$

$$= 2.39$$

TMST value at 10 mph wind speed (Kcal m^{-2} hr^{-1} °C^{-1})

$$Q_k = \frac{A_k t k (T_b - T_s)}{\text{thermal depth}} = \frac{(1)(1)(1.77)(1)}{0.72}$$

$$= 2.46$$

RADIANT SURFACE TEMPERATURE

A noncontact infrared thermometer was used to measure radiant surface temperature of various body regions on captive Sharp-tailed Grouse. The head differed in surface temperature from the rest of the body. A linear relation existed between air temperature and radiant surface temperature over the temperature range investigated. The formula for predicting feather surface temperature (C) from ambient temperature (C) is as follows:

Head: $Y = 19.05 + 0.54X$
$r = 0.98; N = 66$

Body: $Y = 5.25 + 0.87X$
$r = 0.99; N = 222$

where: Y = Feather Surface Temperature (C)

X = Ambient Temperature (C)

Moen (1968:340) likewise observed a linear relationship between air temperature and radiant surface temperature of deer.

The infrared thermometer was used to measure the radiant surface temperature of the feather tracts used on the flat simulator in the TMST. Radiant surface temperatures did not
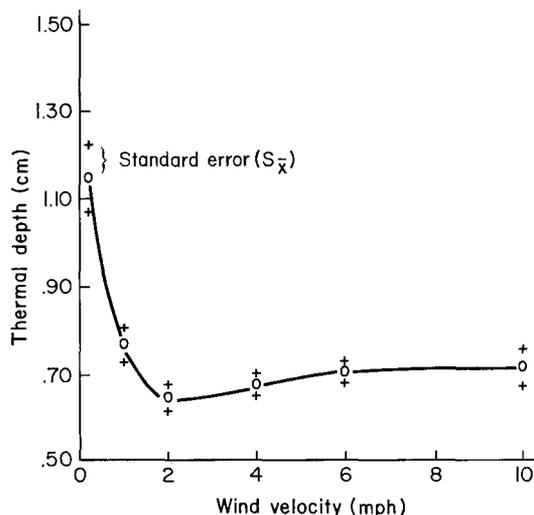
FIGURE 2. Effect of wind velocity on thermal depth of breast and back feather tracts of Sharp-tailed Grouse.

vary between breast feathers and back feathers or between orientation with or against the wind. Linear regression formulas were developed to predict feather surface temperatures from air temperatures and wind speeds (table 1).

The feather surface temperature was lowest at 0 mph wind velocity. The surface temperature rose as wind velocity was increased to 2 mph then fell as wind speeds (over 2 mph) increased convective heat loss. The two main purposes of measuring the radiant surface temperature on the live bird were: (1) to determine the areas on the grouse body where significant differences occurred; and (2) to provide a check on the flat plate simulator used in the TMST. The predictive formulas for 0 mph wind velocity are very similar on both the live bird and on the feather plus skin plate simulator.

THERMAL DEPTH

Thermal depth is the distance from the skin to the point within the feather layer where the radiant surface temperature equals the temperature on the thermal gradient. The average physical depth of the back or breast feather layer of the Sharp-tailed Grouse was 1.48 cm; the thermal depth was less than the physical depth. The thermal depth decreased from 1.15 cm at zero mph to 0.77 cm at 1 mph and an average of 0.69 cm at wind velocities of 2 or more (fig. 2). Ambient temperature did not influence thermal depth. Temperature profile characteristics did not vary significantly between breast feather and back feather models or with feather orientation.
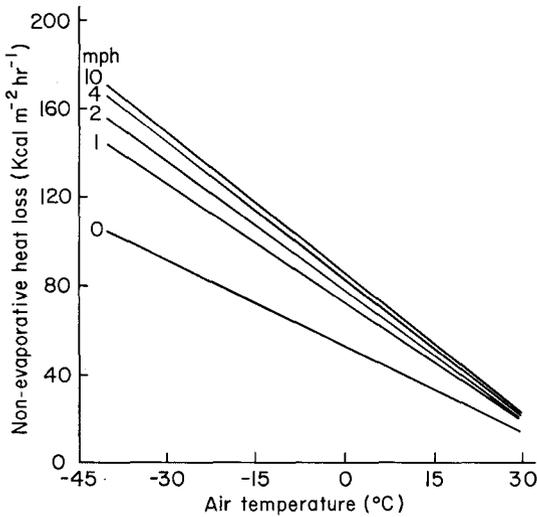
FIGURE 3. Effect of air temperature and wind speed on nonevaporative heat flow through the breast or back feather layer.

FIGURE 4. Effect of wind velocity on the thermal conductance of a body of a Sharp-tailed Grouse.

THERMAL EXCHANGE BETWEEN BIRD AND ENVIRONMENT

Heat exchange properties are expressed in terms of conductive heat transfer. Conductive heat transfer through the feather layer is greatly influenced by ambient temperature and wind velocity. A nonlinear relationship existed between wind velocity and thermal depth, and between wind velocity and radiant surface temperature (fig. 2). A linear relationship existed between ambient temperature and radiant surface temperature. Feather orientation, feather tract (back or breast), and increasing net radiation loss did not influence total heat flow. The insulating properties of the feather layer inhibit heat absorption as well as protect the birds from excessive heat loss. Although direct solar radiation supplies energy (heat) to the feather surface, much of this heat is dissipated to the winter environment by convection and radiation rather than absorbed into the body of a bird. Porter and Gates (1969:233) discussed some general aspects of solar radiation on bioenergetics.

Predicted nonevaporative heat flow through the back or breast feather layer at an air temperature of -40°C varied from 107 Kcal m^{-2} hr^{-1} at zero mph wind velocity to 172 Kcal m^{-2} hr^{-1} at 10 mph wind velocity (data from table 1 and fig. 2 with $K = 1.77$). The relationship between heat loss and wind velocity is nonlinear, with the greatest wind effect at the lower wind velocities (fig. 3). Stevens and Moen (1970:111) reported a similar relationship with thermal exchanges through deer hair.

Thermal conductance values for the body,

excluding the head, were determined for 0, 1, 2, 4, 6, and 10 mph wind velocities by dividing the nonevaporative heat loss (Kcal m^{-2} hr^{-1}) in figure 3 by the difference between body temperature (41.5°C) and ambient temperature.

Thermal conductance values were 1.32 (Kcal m^{-2} hr^{-1} °C^{-1}) at zero mph, 1.79 at 1 mph, 1.96 at 2 mph, 2.09 at 4 mph, 2.10 at 6 mph, and 2.12 at 10 mph wind velocity (fig. 4). A modified formula for a parabolic arc offered a nearly perfect fit of the data points.

Thermal conductivity and physical depth of the head and neck feathers were determined with the TCA. Thermal conductivity of head and neck feathers was the same as for body feathers (3.54 Kcal m^{-2} hr^{-1} °C^{-1} cm). The physical depth was 0.48 cm, which is approximately 33% of the physical depth of the body feathers (1.48 cm). The effects of wind on thermal properties of the head and neck feathers were not measured in the TMST test chamber due to small size of the feather tracts covering the head and upper neck. Data from the TCA corresponded to values determined at 10 mph in the TMST on body feather layers. Nonevaporative heat flow from the head and neck was determined for 10 mph by assuming that the same relationship would exist with head and neck feathers as existed with the body feather tracts. For the first approximation of heat loss from the head, the same equation for the effect of wind velocity on heat loss from the body was used by multiplying the 10 mph value by approximately 3 to compensate for the reduction in depth of head and neck feathers. The conductance equation for the head is as follows:

$$K_h = 6.50 - [(2.84 - \sqrt{U_w})^2/10]$$

where: K_h = Thermal conductance of the head (Kcal m^{-2} hr^{-1} °C^{-1})

U_w = Wind velocity (mph)

The relatively shallow depth of the feathers on the head allows heat to dissipate at a higher rate per unit area than the thicker body covering. Our data indicate that the head loses three times more heat per unit area at 10 mph wind velocity than the body. The first approximation used here predicts that the head dissipates over four times more heat per unit area at zero mph wind velocity than the body. The amount of heat lost from the head is an important relationship in avian energetics which warrants further investigation. We found no data in the literature on the relative heat loss from the head as compared with the rest of the body. Veghte and Herreid (1965) discussed the increased surface temperature of the head and mentioned behavioral thermoregulation of smaller birds by tucking the head under a wing. They omitted head temperatures from their predicted values for existence metabolic rate.

BEHAVIORAL THERMOREGULATION

Grouse can select from several alternatives in order to conserve heat during subfreezing conditions. One effective response is the selection of a favorable habitat. Ambient temperature and wind velocity greatly influence nonevaporative heat dissipation. Grouse can reduce heat loss by adding insulation such as nocturnal roosting in the snow or dense vegetative cover. Such responses also reduce wind velocities over a bird's surface.

Another effective response is to pull in the head, reducing the effective surface area of the head and neck. Grouse can vary the effective surface area of the neck and head from 5 to 20% of the total surface area. A 1000-g grouse could maintain a nonevaporative heat dissipation rate of 1.5 times basal metabolic rate between -7°C and 12°C at zero mph wind velocity by adjusting its head exposure. A similar rate of heat dissipation could be maintained between 10°C and 20°C at 10 mph wind velocity. The nonlinear effect of reducing surface area of the head on nonevaporative heat loss illustrates that a relatively greater amount of heat is conserved with each percentage reduction in head exposure (fig. 5). This maximum "balling up" behavior has been observed under field conditions where high heat loss would be expected (K. E. Evans, unpubl. data).
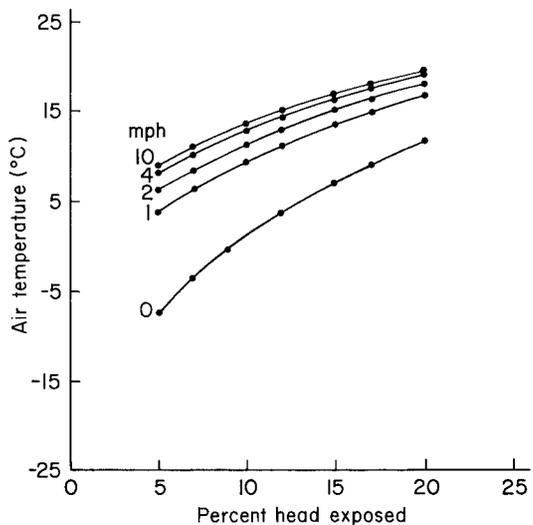
FIGURE 5. Effect of wind velocity and head extension at ambient temperatures where predicted nonevaporative heat loss by a 1000-g grouse would be 1.5 times BMR.

Behavioral thermoregulation involves the selection of habitats and postures to regulate beneficially heat loss. The available habitats contain gradients of nearly all factors that influence heat loss. The gradient of heat exposure has been discussed. Temperature gradients often exist within and between habitat types and physiographic exposures. Overhead cover reduces net radiative heat loss by protecting a bird's surface from exposure to the night sky which, when clear, is colder (Moen and Evans 1971:152). Wind velocity gradients also exist through the vertical and horizontal planes of grouse habitats. Evans (1971:93–98) has given a detailed discussion of the energetic influences of the vertical distribution of wind within a shrub canopy and in and over grass cover.

MAINTENANCE METABOLISM

Maintenance or existence metabolism values have been determined for many homeothermic species under a variety of environmental conditions. Of special interest to this investigation was the energy requirement for Willow Ptarmigan (*Lagopus lagopus*) determined by West (1968) and the review of the influence of ambient temperatures and body weight on existence metabolism (Kendeigh 1970). We developed maintenance metabolism prediction data for two additional variables, namely, wind velocity and behavioral thermoregulation. The equation representing total heat exchange between a Sharp-tailed Grouse and its environment is as follows:

$$Q = (K_h A_h + K_b A_b) \Delta T t + Q_e$$

where:

Symbol	Characteristic	Remarks
Q	= Total heat exchange (Kcal)	
K_h	= Thermal conductance of the head (Kcal m^{-2} hr^{-1} °C^{-1})	$6.50 - [(2.84 - \sqrt{U_w})^2/10]$ U_w = Wind velocity in mph
K_b	= Thermal conductance of the body (Kcal m^{-2} hr^{-1} °C^{-1})	$2.12 - [(2.84 - \sqrt{U_w})^2/10]$
A_h	= Surface area of the head (m^2)	Behavioral thermoregulation between 5 and 20% of maximum surface area: $(7.46 W_{(g)}^{0.65}) \times 10^{-4}$ $W_{(g)}$ = body weight in grams
A_b	= Surface area of the body (m^2)	80% of maximum surface area
ΔT	= Temperature (°C) gradient between deep body temperature (41.5°C) and ambient temperature	
t	= Time (hr)	
Q_e	= Respiratory heat loss (Kcal)	Less than 10% of total heat loss at ambient temperatures below 15°C (Mugaas and Templeton 1970:130; Bartholomew and Trost 1970:143).

Wild adult and subadult Sharp-tailed Grouse were kept in captivity and fed natural diets to determine maintenance metabolism under various winter conditions (Evans and Dietz 1974). This information provided an additional check on the values predicted by the heat transfer investigation of maintenance metabolism. The energy requirements for maintenance determined by feeding trials were compared with the predicted energy requirements determined from thermal transfer layer conductance values and measured surface areas.

Predicted requirements for food compared favorably with actual dry matter intake on 9 of the 12 experimental feeding trials where weight changes were available (data from Evans 1971:99). The three trials that did not compare favorably involved one bird which spent much time running back and forth in the pen. This bird's metabolizable energy intake was 2.5–3.5 times basal during the feeding trials. The extra activity level raised the heat production value above the homeothermic requirement and explains why the predicted feed intake values are much lower than actual dry matter intake.

SUMMARY

Winter energetics of Sharp-tailed Grouse includes both heat production and heat loss fac-

tors. This report deals with factors influencing nonevaporative heat loss by grouse during fall and winter on the northern Great Plains. Maintenance metabolic rate, weight change features, effective surface area, thermal transfer properties, thermoregulatory behavior, wind velocity, and ambient temperature were analyzed to facilitate the prediction of energy requirements for homeothermy.

The equation representing nonevaporative heat exchange between a Sharp-tailed Grouse and its environment is $Q = (K_h A_h + K_b A_b) \Delta T t$. Q is heat exchange (Kcal); K_h and K_b are thermal conductance values for the head and body, respectively; A_h and A_b are the effective surface area of the head and body, respectively; ΔT is the temperature (C) gradient between deep body temperature and ambient temperature; and t is time. Thermal conductance values change with wind velocity up to approximately 8 mph and can be predicted with the following two equations: $K_h = 6.50 - [(2.84 - \sqrt{U_w})^2/10]$ and $K_b = 2.12 - [(2.84 - \sqrt{U_w})^2/10]$, where U_w is the wind velocity in mph.

Behavioral thermoregulation involves the selection of habitats and postures to regulate heat balance. The series of habitats and postures available contains gradients of ambient temperatures and wind velocities that greatly

influence nonevaporative heat dissipation. Grouse can vary the effective surface area of the neck and head from 5 to 20% of the maximum surface area. Maximum surface area (m²) was determined to be $(7.46W_{(g)}^{0.65})$ $\times 10^{-4}$. A 1000-g grouse at an ambient temperature of $-20°C$ and an 8 mph wind velocity in exposed areas could utilize the available habitat and posture gradients to regulate nonevaporative heat loss between 142 Kcal/day (1.9 XBMR) and 319 Kcal/day (4.3 XBMR).

ACKNOWLEDGMENTS

LITERATURE CITED

ALDRICH, J. W. 1963. Geographic orientation of American Tetraonidae. J. Wildl. Mgmt. 27:529–545.

BARTHOLOMEW, G. A. 1968a. Body temperature and energy metabolism, p. 290–354. In M. S. Gordon [ed.] Animal function: principles and adaptations. Macmillan Co., New York. 560 p.

BARTHOLOMEW, G. A. 1968b. Energy metabolism, p. 48–65. In M. S. Gordon [ed.] Animal function: principles and adaptations. Macmillan Co., New York. 560 p.

BARTHOLOMEW, G. A., AND C. H. TROST. 1970. Temperature regulation in the Speckled Mousebird (Colius striatus). Condor 72:141–146.

BRODY, S. 1945. Bioenergetics and growth. Reinhold Publ. Corp., New York. 1023 p.

EVANS, K. E. 1971. Energetics of Sharp-tailed Grouse (Pedioecetes phasianellus) during winter in western South Dakota. Ph.D. Thesis. Cornell Univ., Ithaca, New York. 169 p.

EVANS, K. E., AND D. R. DIETZ. 1974. Nutritional energetics of Sharp-tailed Grouse during winter. J. Wildl. Mgmt. 38:622–629.

GATES, D. M. 1962. Energy exchange in the biosphere. Harper and Row Publ., New York. 151 p.

GESSAMAN, J. A. 1972. Bioenergetics of the Snowy Owl (Nyctea scandiaca). Arctic Alpine Res. 4:223–238.

GESSAMAN, J. A. 1973. Ecological energetics of homeotherms. Monograph Series, Vol. 20. Utah State Univ. Press, Logan. 155 p.

GUYTON, A. C. 1971. Medical physiology. Fourth ed. W. B. Saunders Co., Philadelphia. 1032 p.

HELLER, H. C., AND D. M. GATES. 1971. Altitudinal zonation of chipmunks (Eutamias): Energy budgets. Ecology 52:424–433.

HERREID, C. F., AND B. KESSEL. 1967. Thermal conductance in birds and mammals. Comp. Biochem. Physiol. 21:405–414.

KENDEIGH, S. C. 1970. Energy requirements for existence in relation to size of bird. Condor 72:60–65.

KLEIBER, M. 1961. The fire of life, an introduction to animal energetics. John Wiley & Sons, New York. 454 p.

KLEIBER, M. 1972. A new Newton's Law of cooling? Science 178:1283–1285.

McNAB, B. K. 1966. An analysis of the body temperature of birds. Condor 68:47–55.

MITCHELL, H. H. 1930. The surface area of Single Comb White Leghorn chickens. J. Nutr. 2:443–449.

MOEN, A. N. 1968. Surface temperatures and radiant heat loss from white-tailed deer. J. Wildl. Mgmt. 32:338–344.

MOEN, A. N., AND K. E. EVANS. 1971. The distribution of energy in relation to snow cover in wildlife habitat. In A. O. Haugen [ed.], Proceedings of the "Snow and Ice in Relation to Wildlife and Recreation" symposium. Feb. 11–12, 1971. Iowa State Univ., Ames. p. 147–162.

MUGAAS, J. N., AND J. R. TEMPLETON. 1970. Thermoregulation in the Red-breasted Nuthatch (Sitta canadensis). Condor 72:125–132.

PORTER, W. P., AND D. M. GATES. 1969. Thermodynamic equilibria of animals with environment. Ecol. Monogr. 39:227–244.

RASMUSSEN, G., AND R. BRANDER. 1973. Standard metabolic rate and lower critical temperature for the Ruffed Grouse. Wilson Bull. 85:223–229.

SCHOLANDER, P. F., R. HOCK, V. WALTERS, F. JOHNSON, AND L. IRVING. 1950. Heat regulation in some arctic and tropical mammals and birds. Biol. Bull. 99:237–258.

STEVENS, D. S. 1972. Thermal energy exchange and the maintenance of homeothermy in white-tailed deer. Ph.D. Thesis. Cornell Univ., Ithaca, New York. 231 p.

STEVENS, D. S., AND A. N. MOEN. 1970. Functional aspects of wind as an ecological and thermal force. Trans. N. Amer. Wildl. Nat. Res. Conf. 35:106–114.

STEWART, R. E. 1967. Animal thermoneutrality as a thermodynamic rate process. In S. W. Tromp and W. H. Weihe [eds.], Biometeorology, Vol. 2, part 1. Pergamon Press Ltd., London. 520 p. p. 448–451.

STURKIE, P. D. 1965. Avian physiology. Second ed. Cornell Univ. Press, Ithaca, New York. 766 p.

TRACY, C. R. 1972. Newton's Law: Its application for expressing heat losses from homeotherms. BioScience 22:656–659.

VEGHTE, J. H., AND C. F. HERREID. 1965. Radiometric determination of feather insulation and metabolism of arctic birds. Physiol. Zool. 38:267–275.

WEAST, R. C., AND S. M. SELBY [eds.]. 1967. Handbook of chemistry and physics. 48th ed. The Chemical Rubber Co., Cleveland, Ohio, variable paging.

WEST, G. C. 1962. Responses and adaptations of wild birds to environmental temperature. *In* J. P. Hannon and E. Viereck [eds.], Comparative physiology of temperature regulation. Arctic Aeromedical Lab., Ft. Wainwright, Alaska. p. 291–333.

WEST, G. C. 1968. Bioenergetics of captive willow ptarmigan under natural conditions. Ecology 49: 1035–1045.