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TEMPERATURE REGULATION IN THE WHITE-TAILED PTARMIGAN,

Lagopus leucurus

by

RICHARD E. JOHNSON

B.S., University of California, 1958

**Presented in partial fulfillment of the requirements for the
degree of Master of Science in Zoology**

UNIVERSITY OF MONTANA

1968

Approved by:

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TABLE OF CONTENTS

	Page
INTRODUCTION	1
MATERIALS AND METHODS.	9
RESULTS.	13
Oxygen Consumption	13
Evaporative Water Loss	14
Body Temperature	16
DISCUSSION	18
Oxygen Consumption	18
Insulation	19
Evaporative Cooling.	22
Body Temperature	23
Environmental Relations.	26
SUMMARY.	28
LITERATURE CITED	29

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LIST OF TABLES

Table	Page
1. Body Temperatures at Ambient Temperatures Outside the Thermoneutral Zone	20
2. Experimental and Expected Metabolic Rates.	21
3. Body Temperatures of Ptarmigan	25

LIST OF FIGURES

Figure		Page
1.	Variation in Metabolism with Temperature for Twenty-four Fasted White-tailed Ptarmigan	12
2	Evaporative Water Loss as a Function of Ambient Temperature for Sixteen White-tailed Ptarmigan.	15
3.	Evaporative Cooling as a Function of Ambient Temperature for Sixteen White-tailed Ptarmigan.	17

INTRODUCTION

Interest in the grouse family (Tetraonidae) has resulted in numerous population and behavior studies with particular emphasis upon game management. Special importance has been placed upon factors which control population levels and fluctuations. Many authors have linked weather, and particularly ambient temperatures, with population fluctuations in these birds. Cold, late spring and summer temperatures are often correlated with low grouse populations in the fall and this is usually caused by high juvenile mortality (Blank and Ash, 1957; Myrberget; Semenov-Tain-Shansky, 1965; all in Jenkins, Watson, and Miller, 1963; Crissey in Bump, 1947; Edminster, 1947; Høglund, 1952; Moran, 1954; Larsen and Lahey, 1958; Dorney and Kabat, 1960, Ritcey and Edwards, 1963). While low air temperatures in spring can affect the young birds directly, it can also affect them indirectly by limiting their food supply (Siivonen, 1957; Jenkins, Watson, and Miller, 1963; Miller, Jenkins, and Watson, 1966; Lack, 1966).

Both high and low winter temperatures have been correlated with mortality of adult and immature birds. High winter temperatures have been correlated with low Ruffed Grouse populations in Minnesota and Wisconsin, perhaps through effects of resulting encrusted snow (Larsen and Lahey, 1958; Dorney and Kabat, 1960). However, there is considerable debate about the significance of encrusted snow (Clarke, 1936; Crissey in Bump, 1947; Edminster, 1947; Grange, 1949, Larsen and Lahey, 1958). Low winter temperatures were correlated with low spring populations of the same species in New York (Crissey in Bump, 1947).

All of these studies have related long-term weather data to population changes but no one has examined individuals of one age group at a particular season in order to determine specifically what temperature adaptations and problems do exist. The present study examines temperature regulation of breeding adult White-tailed Ptarmigan (Lagopus leucurus) in Montana.

Ptarmigan are probably basically cold-adapted birds judging from their northern distribution and arctic-alpine habitat. Three species of ptarmigan occur in Canada and Alaska, but of these only the White-tailed Ptarmigan occurs as a breeding bird in the United States. Here it is limited to the alpine zone of the Rocky Mountains and the Cascade Range. In Montana this species may encounter ambient temperatures below -45° C. in winter (U.S. Dept. of Agri., 1941). Ptarmigan use counter-current heat exchange in their legs and unlike most birds, ptarmigan have feathered feet (Irving and Krog, 1955). These two adaptations reduce heat loss considerably. Cold is also an important factor in their environment in the summer. For example, ambient temperatures frequently reach freezing and as much as two feet of snow may fall during the nesting season in Montana. Hens will remain on the nest, becoming completely buried, during such a snowfall (Nethersole-Thompson, 1939; Edwards, 1957; Choate, 1960) and eggs can withstand cooling to near freezing temperatures (Barth, 1949). In spite of these adaptations, incubation success is lowered and chick mortality is increased during heavy snowfall and hail (Choate, 1963a, b).

On the other hand, the open alpine habitat also exposes the ptarmigan to considerable radiant heating as indicated by summer ground

temperatures which may exceed air temperatures by 20° C. (Swan, 1952; Verbeek, 1965; personal obs.). High air temperatures may play a role in determining the geographic distribution and habitat selection of the White-tailed Ptarmigan during the breeding season in the United States. The excellent dorsal insulation of the ptarmigan no doubt offers considerable protection from solar radiation, but, in spite of this, birds in the sun begin to pant at relatively low air temperatures (Bradbury, 1915; Bailey and Bailey, 1918; Taylor and Shaw, 1927). In fact, these birds may pant at air temperatures as low as 21° C. (Choate, 1963a; personal obs.) which suggests that the total insulation prevents loss of body heat to this relatively cool air. On Logan Pass, Glacier National Park, Montana, where birds used in this study were obtained, air temperatures reached or exceeded 21° C. on approximately 40% of the days between mid-June and the end of August in 1960, 1961, and 1962 and reached a maximum of 32.0° C. in 1961 (Choate, 1963a). Incubating hens on exposed nests would probably experience the greatest temperature stress and setting hens have been observed panting on warm days (Choate, 1960). It is perhaps significant that Choate (1960) found that the majority of nests were at least partially protected from solar radiation by a large rock or bush.

In August flocking birds move to cooler locations (shade, snow) and on hot days often congregate under snowbanks. Hens with young are in moist meadows along water courses and beside snowbanks where vegetation is still green and tender and the microenvironment is cool (Choate, 1963a; personal obs.).

Thus, two behavioral patterns, movement to cool locations on hot days and selection of protected nest sites, aid them in avoiding high temperatures. Ptarmigan are found at the highest elevations in the southernmost part of their range and consequently radiant heating would be the greatest there. In these locations behavioral patterns may be exceedingly important and the lack of protected locations for nests or permanent snow providing a cooler microclimate on hot days may preclude the presence of this species especially if it is heavily insulated. Logan Pass is at the lower elevational limit of breeding birds in Glacier National Park (Parratt, 1954; personal obs.) and a large snow pack remaining from an earlier glacier and abundant shade beneath Mount Clements provide a cool microenvironment which is utilized on hot days. Glaciers and shade are available at all other locations where ptarmigan occur at similar low elevations. Ptarmigan seem to be absent from similar, apparently desirable habitats at this elevation (Aster Park, Paradise Park) that lack permanent snow or glaciers. Ptarmigan at higher elevations are not always associated with snow and ice though this association is still common. Ptarmigan occur as far south as New Mexico at much higher elevations but these areas have not been investigated.

The White-tailed Ptarmigan appears adapted to cold climate. The present study seeks to determine the role of physiological adaptation to the alpine environment and, if these adaptations exist, whether they preclude its existing elsewhere.

To accomplish this, metabolic rate and heat loss by evaporation of water were measured over a wide range of temperatures in the

laboratory on birds taken from Logan Pass. These data are compared with data from other bird species and to temperature data from Logan Pass.

Metabolism can be measured directly by measuring heat production or indirectly by measuring either oxygen consumption or carbon dioxide production. The indirect method is much simpler and is more commonly used. Precise determination of metabolic rate by the indirect method requires measurement of both oxygen and carbon dioxide as well as urinary nitrogen excretion. These data allow computation of the respiratory quotient which is necessary to determine the exact caloric equivalent of the oxygen consumed. However urinary nitrogen excretion is usually not measured since it is difficult to determine in birds and is of little significance in post-absorptive birds (King and Farner, 1961). It is now standard procedure to assume a mean caloric equivalent of 4.8 cal/cc of oxygen and thus dispense with measurements of carbon dioxide and urinary nitrogen. This latter procedure was followed in this study. For birds this usually produces excellent results but occasionally large errors have resulted. The reasons for this are unknown (King and Farner, 1961).

Standard metabolic rates are understandably greater in large animals than in small animals but this relationship is not direct. When examined on a per gram basis, however, metabolism usually increases as body size decreases. Several formulae have been proposed to describe this relationship in birds.

The Brody-Proctor equation developed in 1932 describes the relationship as nearly as it could be determined from the limited data available at that time. With increasing research, however, it became obvious

that the data from small passerine birds did not fit the equation developed for large nonpasserine birds and two equations were suggested: one for small birds and one for large birds (King and Farner, 1961). With the appearance of data from small nonpasserine birds it became clear that the difference observed earlier was really between passerine and nonpasserine birds and not simply between large and small birds. Passerine birds have a higher metabolic rate than nonpasserine birds of the same size, but the rate of increase of metabolic rate with size is the same for both groups of birds (Lasiewski and Dawson, 1967).

Scholander, et al. (1950a), and others (see review by King and Farner, 1961) have shown that over a certain range of temperatures most warm-blooded animals maintain constant metabolic rates and body temperatures. This means that heat production remains constant but heat loss is varied by physiological and physical means thereby keeping body temperature constant. Heat loss may be physiologically regulated by vasomotor control of blood distribution, evaporative cooling, and by countercurrent heat exchange in appendages (Irving and Krog, 1955; Kahl, 1963) and physically regulated by changes in feather or fur arrangement (Scholander, et al., 1950a). This ambient temperature range over which metabolism remains constant is referred to as the thermoneutral zone.

At the lower limit of the thermoneutral zone, temperatures are reached at which the animal can no longer maintain its body temperature by control of heat loss and therefore an increase in metabolism is necessary if body temperature is to remain constant. This lower limit to the thermoneutral zone is called the lower critical temperature. Below this point metabolism increases with decreasing temperature at

a constant rate and Scholander, et al. (1950a), have shown that this rate is proportional to the insulation of the animal. Thus, if metabolic rate is plotted against ambient temperature, the slope of the line at ambient temperatures below the lower critical temperature is a measure of insulation (called conductance) and can be compared with values obtained from other animals.

Another measure of insulation often used is insulative value. This is computed by dividing the temperature difference between the body temperature and the lower critical temperature (this difference is called the critical thermal gradient) by the standard metabolic rate (Morrison and Tietz, 1957; Misch, 1960). Both insulative value and conductance are computed for the ptarmigan in order to compare with data available for other species. Insulation can also be measured directly by heat transfer studies through skins of dead animals (Scholander, et al. 1950b) but these skins may not have the same properties as those possessed by living animals.

If ambient temperatures are lowered still further a temperature will eventually be reached beyond which the animal can no longer raise its metabolism and thereby its heat production to offset heat loss. At this point body temperature will decrease causing metabolism to decrease and death soon results. This point is termed the lower lethal temperature. Variations in this temperature are probably of adaptive significance, but few data are available in the literature probably because sacrifice of the experimental animals is required.

As ambient temperatures reach the upper end of the thermoneutral zone, a point is reached at which ambient temperature equals body

temperature. Since heat loss is proportional to the temperature gradient, any increase in ambient temperature above body temperature will result in heat gain by the animal. Passive forms of heat loss (compression of feathers or fur, peripheral vasodilation) which were effective below this temperature are not longer useful. Active heat dissipation utilizing evaporative cooling (panting, sweating) is then necessary if the animal is to maintain a constant body temperature in spite of the rising ambient temperature. Such active heat loss requires energy and results in an increase in metabolic rate and therefore in the metabolic heat to be dissipated. Both active heat loss and increased metabolic rate begin at an ambient temperature somewhat below the body temperature, which probably reflects the degree to which insulation, even when decreased to a minimum, impedes heat loss. The temperature above which metabolism increases is called the upper critical temperature. While it may seem reasonable that a high value would reflect adaptations to a warm environment in different species, this relationship is not clear since upper critical temperatures so far measured do not appreciably differ in species from thermally different habitats.

Perhaps the best measures of Physiological adaptation to heat are evaporative efficiency and ability to tolerate hyperthermia. In the present study evaporative efficiency was determined for comparison with other species. The parameters of hyperthermia were not measured because such a study would have required sacrifice of many birds which was not permitted by the Park authorities.

MATERIALS AND METHODS

White-tailed Ptarmigan were obtained with a hand net on the meadows of Logan Pass at 6,800 to 7,400 feet in Glacier National Park, Montana in June through August, 1965. Captives were transported 18 miles to St. Mary (4,500 feet) where they were maintained indoors at approximately 21° C. in cages measuring 51 x 61 x 76 cm. They were supplied with grit, water for drinking, and food.

Ptarmigan did not adapt readily to captivity and some individuals required force-feeding before accepting the new diet and conditions. A wide variety of natural foods, commercial grains, and market fruits and vegetables were tried prior to initiating the study. Meal worms (Tenebrio larvae), apple slices, and lettuce were the most readily accepted, and most individuals gained weight on this diet. Twenty-four healthy adult birds averaging 326 grams in weight (range 275-374 g.) were studied. Birds were weighed before and after each experiment. Birds were held captive from five to ten days and then returned to Logan Pass.

Oxygen consumption of resting birds that were fasted for at least 16 hours was measured at various constant ambient temperatures using a Beckman G-2 paramagnetic oxygen analyzer connected to a Brown recording potentiometer. The air passed at low pressure through an open circuit system via tygon tubing from an air pump through an equalizing chamber, a Drierite (anhydrous CaSO_4) drying train, a metabolic chamber, a silica gel drying train, an Ascarite (sodium hydrate asbestos absorbent) train, a flowmeter, and the oxygen analyzer.

Metabolic chambers were constructed from rectangular five gallon (18.9 liter) cans fitted with a wire screen floor (1/2 x 1 inch mesh) set 3-5 cm above the bottom. Mineral oil (2 cm) placed under the wire screen covered feces voided during the experiment precluding contribution of fecal water to the chamber air. Data were discarded in those cases where feces lodged on the screen.

In the type of metabolic apparatus described above the relative humidity varies with the evaporative water loss of the bird and with the ambient temperature. Since the evaporative efficiency of an animal is affected by the humidity, a rapid air flow of 1600 cc per minute was chosen which maintained a low and a fairly constant humidity (1.4 to 7.3%). The relative humidity was computed by the formula given by Lasiewski (1964) and Lasiewski, et al. (1966a).

$$\text{Relative Humidity} = 100 \left[\frac{\text{MRT}}{\text{V} (0.621) e_s} \right] \quad (1)$$

where

M = mass of water vapor (gm/min)

R = gas constant (2.87×10^6 erg/°K)

T = ambient temperature (°K)

V = cm³ air/min.

0.621 = constant

$e_s = 1,333 \text{ dynes/cm}^2 \times \text{saturated vapor pressure}$

This flow rate was sufficient to maintain the oxygen level above 20% and the CO₂ level below one percent.

Oxygen consumption was computed using the following formula given by Depocas and Hart (1957) for open-circuit systems.

$$VO = VE \left[\frac{PIO_2 - PEO_2}{PB - PIO_2} \right] \quad (2)$$

where

VO_2 = oxygen consumption of the animal per minute

VE = volume of air flowing out of the cage per minute

PIO_2 = partial pressure of oxygen flowing into the cage

PEO_2 = partial pressure of oxygen flowing out of the cage

PB = atmospheric pressure

Gas volumes were corrected to STP. A constant ambient temperature ($\pm 0.3^\circ\text{C}.$) was maintained in the metabolic chamber by placing it within a temperature control chamber. Metabolic chamber temperatures were measured using a sensitive thermister bridge and thermister probes covered with teflon. Birds were left in the chambers for at least two hours prior to collecting data and by this time fluctuations in oxygen consumption were usually not detectable. Recordings were always continued until variation in oxygen reading for one hour was $\pm 0.04\%$ and an average rate was computed from rates at ten equally spaced points on the tracing.

Evaporative water loss was determined from the weight gain of the silica gel drying train during each experiment. Two drying tubes were used for temperatures below $25^\circ\text{C}.$ and three were used above that temperature. Additional tubes downstream in each case were shown not to trap additional water.

Evaporative water loss and oxygen consumption were measured simultaneously in order to determine the percentage of metabolic heat dissipated by evaporative cooling at each ambient temperature. Heat

Fig. 1. Variation in metabolism with temperature for twenty-four fasted White-tailed Ptarmigan.

gain and loss was calculated from oxygen consumption and evaporative water loss by assuming a caloric equivalent for oxygen of 4.8 cal/cc consumed and a latent heat of vaporisation of water of 0.58 cal/mg evaporated.

Cloacal temperatures were taken with a small quick registering thermometer placed well into the cloaca immediately after the birds were removed from the chamber.

RESULTS

Oxygen Consumption

The relation of oxygen consumption to ambient temperature in the White-tailed Ptarmigan during summer is shown in Fig. 1. The metabolic rate between ambient temperatures of 4° and 36° C. appears to be constant and has been taken as the standard metabolic rate which equals 1.30 cc O₂/gm x hr ($\sigma = 0.24$). Other ambient temperature ranges using various lower limits between 3° and 12° yield nearly identical mean metabolic rates (1.27 - 1.31).

A regression line (cc O₂/gm x hr = 1.6 - 0.047t, where t is temperature in degrees Centigrade) fitted to the points between 2° and -18° C. extrapolates to 34° C. which is below the lower limit of normal body temperature. Points below an ambient temperature of -18° C. were not used because there is evidence that these birds had lowered body temperatures (see Body Temperature). Points below -16° C. describe a slightly steeper curve and possibly resulted from undetected activity. Birds tended to be more active at these very low ambient temperatures.

If the four points between -16°C. and -18°C. are also excluded, the regression line becomes $1.7-0.036t$ which extrapolates to 47.5°C.

The point at which the first regression line intersected the basal line, 6.5°C. was taken as the lower critical temperature. A lower critical temperature of 11.5°C. is obtained using the second regression line. Both points are above the apparent visual lower critical temperature (4°C.) used in computing the standard metabolic rate (see above).

The upper critical temperature of 38°C. was determined by the intersection of the basal line and a visually fitted line through points in the upper temperature range.

All birds exposed to an ambient temperature of 39°C. or less for four hours maintained constant metabolic rates and none died. At an ambient of 40°C. and above, metabolic rates of four birds remained level or gradually increased for one half to one hour and then suddenly rose precipitously. All birds were removed at this point and those measured had elevated body temperatures. One bird at an ambient temperature of 40°C. maintained a constant metabolic rate for five hours.

Metabolic rates obtained at night (1900-2300 hours) did not differ from those obtained in the day (1000-1800 hours).

Evaporative Water Loss

Evaporative water loss increases very slowly with ambient temperature from 0° to 27°C. and more rapidly above 27° (Fig. 2). However, the onset of panting remains unknown since the curve appears to be a

Fig. 2. Evaporative water loss as a function of ambient temperature for sixteen White-tailed Ptarmigan.

continuous function and panting could not be observed within the metabolic chamber. At high ambient temperatures White-tailed Ptarmigan lose no more than 90% (one individual) of their metabolic heat by evaporative cooling (Fig. 3).

Body Temperature

Thirty-one body temperatures of nine individuals were recorded between August 10 and 25. The body temperatures of seven resting birds in cages at an ambient temperature of 22° C. averaged 39.9° and ranged between 38.6° and 40.3° C. during the day and averaged 39.3° and ranged between 38.0° and 40.2° at 8:00 AM when the lights were turned on in the morning. Body temperatures of seven resting birds within the metabolic chamber at ambient temperatures between 6° and 38° C. (thermoneutral zone) were within the day range. However one bird at an ambient temperature of 7.5° had a body temperature of 36.4° C. This bird maintained a constant metabolic rate for four hours and appeared to be healthy at the end of the experiment.

The one body temperature (39.0°) measured within the ambient temperature range between 6.5° and -17° C. was similar to those measured within the thermoneutral zone (Table 1). All birds whose metabolic rates were measured (48 measurements) in this ambient temperature range maintained a constant elevated metabolic level for four or more hours.

None of the nine birds studied at ambient temperatures between -18° C. and -31° C. could maintain an elevated metabolic rate for over two hours and four died after removal from the chamber. The body temperatures of two of these four upon removal from the chamber were

Fig. 3. Evaporative cooling as a function of ambient temperature for sixteen White-tailed Ptarmigan.

approximately 32°. One remained alive for three hours and the other for 20 hours. The other two birds lived for 45 minutes and eight hours but their body temperatures were not measured. Body temperatures of the five birds which lived were not taken.

Body temperatures increased as ambient temperature rose above 38° C., the upper critical temperature (Table 1). One individual at an ambient temperature of 39° C. had a body temperature of 41.1° C. and its metabolism remained constant, but high, throughout the experiment (four hours). Three birds at an ambient temperature of 40° for 20 to 30 minutes each had a body temperature of between 43.4° and 44.4° C. when removed from the metabolic chamber. The metabolism of each bird had begun to increase rapidly just prior to removal. One bird at an ambient temperature of 40° maintained a constant metabolic rate for five hours but its body temperature was not measured. This is the same individual which achieved 90% evaporative efficiency (see Evaporative Water Loss). Body temperatures were not taken of the three birds at ambient temperatures above 40° C. (40.5°, 41°, 43°), but these birds also showed the rapid increase in metabolic rates noted above. The birds at ambient temperatures of 41° and 43° C. died after one hour of exposure. All birds exposed to ambient temperatures of 40° or higher were panting very rapidly immediately after removal from the chamber. The neck of each bird was bent backward so that its head rested upon its back and the bill faced directly upward. Birds in this condition were barely able to maintain their balance. Panting and posture of this sort was never observed in the field.

DISCUSSION

Oxygen Consumption

The standard metabolic rate of $1.30 \text{ cc O}_2/\text{g} \times \text{hr}$ (or $48.8 \text{ Kcal}/24 \text{ hr}$) is slightly higher than values predicted from the Brody-Proctor, King-Farner and Lasiewski-Dawson equations (Table 2). Ptarmigan rely heavily upon camouflage for protection and selection seems to have favored a nearly continuous molt during the breeding season (Salomonsen, 1939; Johnson, 1939 in Host, 1942; personal obs.) enabling the ptarmigan to match their changing habitat rather closely. The high metabolic rate obtained in this study may reflect the energy expenditure associated with this molt. Such a correlation is well known in many other species though the exact reason for this remains uncertain (King and Farner, 1961).

Insulation

The lower critical temperature of 6.5° to 11.5° C. for the ptarmigan in this study is quite low compared to most birds and only two records have been published of lower values for birds in summer plumage, 6° C. for the Black Brant (Branta bernicla) and -7° C. for the Northwest Crow (Corvus caurinus) (Irving, et al., 1955). The low value for the ptarmigan may be partly related to its high metabolic rate, but it appears mainly to be due to its low conductance (0.036 to $0.047 \text{ cc O}_2/\text{gm hr } ^\circ\text{C.}$; this study) which is among the lowest measured for birds (Herreid & Kessel, 1967). Herreid and Kessel (1967) obtained a similar value ($0.044 \text{ cc O}_2/\text{gm hr } ^\circ\text{C.}$) for a Rock Ptarmigan of similar weight in summer plumage.

Table 1

**Body Temperatures at Ambient
Temperatures Outside the Thermoneutral Zone**

	<u>Ambient Temp. °C.</u>	<u>Body Temp. °C.</u>	<u>Time of Exposure Hours</u>
Ambient temperatures above the upper critical temperature	+40	44.4	1.2
	+40	44.1	1.5
	+40	43.4	1.3
	+39	41.4	4.0
Ambient temperatures below the lower critical temperature	-17	39.0	4.0
	-20	32.0	1.8
	-28	32.2	1.5

*N = 1 for each body temperature given.

Table 2

Experimental and Expected Metabolic Rates

	<u>Weight kg</u>	<u>Kcal/24 hr.</u>
<u>Lagopus leucurus</u>	.326	48.8
Expected Metabolism		
Brody Equation ¹ (all birds)	.326	43.4
King-Farner Equation ¹ (all birds)	.326	38.3
King-Farner Equation ¹ (birds over 0.1 kg)	.326	32.3
Lasiewski-Dawson Equation ² (nonpasserine birds)	.326	34.8

¹Equation from King & Farner (1961).

²Equation from Lasiewski & Dawson (1967).

This conductance value, though quite low for summer birds, would not be adequate to maintain normal body temperatures in winter (ambient temperature reaches $-45^{\circ}\text{C}.$) without a considerable rise (350%) in metabolic rate (Fig. 1). Greater insulation in winter would therefore seem advantageous. The consideration that feathers serve primarily for flight and do not adapt either to season or to longitudinal cline (Irving, et al., 1955; Hart, 1962) loses cogency in view of the sedentary nature of the White-tailed Ptarmigan which makes its short altitudinal migrations on foot and frequently runs from danger rather than taking flight.

Seasonal changes in insulation were not measured in this study but Coates (1874) and Grinnell (1900) have made observations suggesting such a change. The insulative value ($0.84^{\circ}\text{C/Kcal/m}^2\text{ hr}$) obtained by Scholander, et al. (1950c, in Misch, 1960), for a winter ptarmigan is slightly higher than that obtained in this study based upon summer birds ($0.71^{\circ}\text{C/Kcal m}^2\text{ hr}$) but he did not specify which species he used. Herreid & Kessel (1967) found that conductance decreased (insulation increased) slightly in the Rock Ptarmigan (Lagopus mutus) between July and November but only one individual was measured in each case. Data are available for turkeys, pigeons, and several species of passerines indicating seasonal insulation change (Kendeigh, 1934; Wetmore, 1936; Hart, 1957, 1962; Dawson, 1958; West, 1960; Veghte, 1964).

Evaporative Cooling

Until recently only desert birds were thought to be able to evaporate more than 100% of their metabolic heat, but Lasiewski, et al.

(1966a) have supplied evidence indicating that nearly all birds have the capacity for such evaporative cooling at low relative humidities. The White-tailed Ptarmigan has the lowest efficiency of the species measured even though the humidity used was considerably lower than that for all other birds. Differences in efficiency in evaporative cooling may be adaptive, since the highest efficiencies are found in desert species and the lowest in an alpine species.

Body Temperature

The body temperatures obtained in this study were somewhat lower than those obtained by other workers (Table 3). The cause of this difference is not clear but it could be due to seasonal changes since all the previous data were collected in winter. Irving and Krog (1954) estimated the body temperature of resting winter ptarmigan of all three species to be 41.0° to 41.5° C.

Summer White-tailed Ptarmigan appear to maintain a uniform body temperature near 39.5° C. over the ambient temperature range from 38° to -18° C. Below -17° the ptarmigan cannot maintain normal body temperature. Veghte and Herreid (1965) found that White-tailed Ptarmigan could maintain a normal body temperature at an ambient temperature of -34° C. in winter.

The lethal body temperature cannot be determined from the present data. Ptarmigan can withstand a body temperature of 43° - 44° C. for at least a few minutes but it is not known for how long nor how much higher the body temperature could go without resulting in permanent damage.

Birds resting in the dark for one hour or less at an ambient temperature of 41° C. showed a precipitous increase in metabolic rate and then died. Since three of our birds at an ambient temperature of 40° C. for 30 minutes or less underwent a similar increase in metabolic rate, it seems likely that they would also have died within one hour if they had not been removed from the chamber sooner. It therefore appears that 40° C. for one hour or less is the lethal ambient temperature for most ptarmigan resting in the dark.

Table 3

Body Temperatures of Ptarmigan

	Air Temp. C.	N	Body Temp. C.	Reference
<u>Lagopus lagopus</u>	-37 to -15	30	41.3 (41.0-41.5)a	Irving & Krog, 1954
" "	-19	2	41.0 (41.0-41.0)c	" "
" "	-16 to -4	23	42.0 (41.0-43.0)b	" "
<u>Lagopus mutus</u>	-10	2	42.3 (41.8-42.8)c	" "
<u>Lagopus leucurus</u>	-10 to -8	13	41.5 (40.5-42.8)c	" "
" "	-8	1	40.3 c	Veghte & Herreid, 1965
" "	-18	1	40.4 c	" "
" "	-29	1	40.7 c	" "
" "	-34	1	40.8 c	" "
" "	+22	7	39.3 (38.0-40.2)d	This study
" "	+22	7	39.9 (38.6-40.3)e	This study

a shot, winter.

b shot in flight, winter

c captive birds, winter

d captive birds, summer, upon arousal at 8 AM

e captive birds, summer, day

ENVIRONMENTAL RELATIONS

Cold is an important factor in the environment of the White-tailed Ptarmigan in both summer and winter. Results of the present study suggest that this species is well adapted to these low temperatures, since the lower critical temperature is quite low and the insulative value is exceptionally high. In addition ptarmigan use counter-current heat exchange in their legs and have feathered feet and both of these adaptations reduce heat loss considerably (Irving and Krogh, 1955).

On the other hand ptarmigan may not be as well adapted to high ambient temperatures. The evaporative efficiency (90%) is the lowest value obtained for any bird measured at a low vapor pressure (2.2 mm Hg or a relative humidity of 4% at 40° C.). However, on Logan Pass the relative humidity never drops below 26% even when ambient temperatures between 20° and 32° C. are reached (Choate, 1963a); this corresponds to vapor pressures between 4.5 and 9.2 mm Hg. Since evaporative cooling in birds is dependent upon the water vapor pressure gradient between the respiratory surface and that of the environment (Lasiewski, et al., 1966), the evaporative efficiency of a ptarmigan on Logan Pass on a hot day would be less than the maximum value observed in the laboratory.

The low evaporative efficiency suggests that the ptarmigan is poorly adapted physiologically to air temperatures above that of its body and although the insulation on the dorsum shields solar radiation, the insulation on the rest of his body including the legs prevents rapid dissipation of body heat. While at rest in the metabolic chamber, the

bird withstood ambient temperatures as high as 38° C. without utilizing appreciable, if any, energy for evaporative cooling. One can project that while at rest in the alpine at these ambient temperatures the bird would remain comfortable. But if they became active in the midday sun (e.g., foraging) they would have to frequent shade and cool areas intermittently to dissipate the heat collected during this activity. Panting may occur at this time. The relatively heavy summer insulation is apparently selected for to withstand the rather frequent summer cold periods, such as snow storms, at the expense of limiting their tolerance to the intermittent warm periods.

Ptarmigan, therefore, appear to be adapted to cold environments both in winter and summer, primarily because of their heavy insulation. The presence of shade and cool areas in certain alpine areas allow the ptarmigan to escape the intense solar radiation and the high ambient temperatures resulting from this radiant heat. The cool microenvironment provided by snow and shelter appears essential to ptarmigan and adds further meaning to three of the four factors (i.e., vegetation type, rock size, and snow) suggested as important in habitat selection by Weeden (in Choate, 1963a). It also appears that cool ambient temperatures should be included as a fifth factor in habitat selection, since habitats apparently lacking only this one factor are also lacking ptarmigan.

SUMMARY

1. The temperature regulation of adult White-tailed Ptarmigan (Lagopus leucurus) was studied in June through August, 1965.
2. Birds were captured on Logan Pass at 6,800 to 7,400 feet in Glacier National Park, Montana, and transported 18 miles to St. Mary (4,500 feet) where all experimental work was done.
3. Oxygen consumption, evaporative water loss, and body temperature were measured over a wide range of ambient temperatures.
4. The standard metabolic rate of 48.8 Kcal/24 hr. for the ptarmigan is slightly higher than expected and may be associated with the continuous molt in this species.
5. The lower critical temperature (6.5° to 11.5° C.) is one of the lowest values recorded for birds and reflects the ptarmigan's excellent insulation.
6. The ptarmigan has the lowest evaporative efficiency recorded in birds. Differences in efficiency of evaporative cooling may be adaptive, since they are correlated with habitat.
7. Ambient temperature may be an important factor in habitat selection in some cases.

LITERATURE CITED

- Bailey, V., and F. M. Bailey. 1918. Wild Animals of Glacier National Park. National Park Service, Washington, D.C.
- Barth, E. K. 1949. Redetemperatuer og rugevaner. *Naturen* 73, 81-95.
- Bradbury, W. C. 1915. Notes on the nesting of white-tailed ptarmigan in Colorado. *Condor* 17, 214-222.
- Bump, G., R. W. Darrow, F. C. Edminster, and W. F. Crissey. 1947. The ruffed grouse - life history-propagation - management. New York Const. Dept., Albany. 915 pp.
- Choate, T. S. 1960. Observations on the reproductive activities of white-tailed ptarmigan (Lagopus leucurus) in Glacier Park, Montana. Master's thesis, University of Montana, Missoula.
- _____. 1963a. Ecology and population dynamics of white-tailed ptarmigan (Lagopus leucurus) in Glacier National Park, Montana. Doctoral dissertation, University of Montana, Missoula.
- _____. 1963b. Habitat and population dynamics of white-tailed ptarmigan in Montana. *J. Wildl. Mgmt.* 27, 684-699.
- Clarke, C. H. D. 1936. Fluctuations in numbers of ruffed grouse Bonasa umbellus (Linne), with special reference to Ontario. *Univ. Toronto Studies, Biol. Series, Bull.* 41. 118 pp.
- Coues, E. 1874. Birds of the Northwest. U. S. Geological Survey, Washington, D.C.
- Dawson, W. R. 1958. Relation of oxygen consumption and evaporative water loss to temperature in the cardinal. *Physiol. Zool.* 31, 37-48.
- Depocas, F. and J. S. Hart. 1957. Use of the Pauling oxygen analyzer for measurement of oxygen consumption of animals in open-circuit systems and in a short-lag closed-circuit apparatus. *J. Appl. Physiol.* 10, 388-392.
- Dorney, R. S. and C. Kabat. 1960. Relation of weather, parasitic disease and hunting to Wisconsin ruffed grouse populations. *Wisconsin Conserv. Dept. Tech. Bull.* 20.
- Edminster, F. C. 1947. The ruffed grouse. The MacMillan Co., N. Y. 385 pp.
- Edwards, J. G. 1957. The ptarmigan of Glacier National Park. *Audubon Mag.* 59, 252-255.

- Grange, W. B. 1949. The way to game abundance. Charles Scribner's Sons, N. Y.
- Grinnell, J. P. 1900. Birds of the Kotzebue Sound region, Alaska. Pacific Cst. Avifauna 1, 1-80.
- Hart, J. S. 1957. Climatic and temperature-induced changes in the energetics of homeotherms. Rev. Can. Biol. 16, 133-174.
- _____. 1962. Seasonal acclimatization in four species of small wild birds. Physiol. Zool. 35, 224-236.
- Herreid, C. P. and B. Kessel. 1967. Thermal conductance in birds and mammals. Comp. Biochem. Physiol. 21, 405-414.
- Höglund, N. 1952. Capercaillie reproduction and climate. Finnish Game Foundation, Helsinki (Riis tatieteellisä Julkaisuja). Papers on Game Research 8.
- Host, P. 1942. Effect of light on the molts and sequences of plumage in the willow ptarmigan. Auk 59, 388-403.
- Irving, L. and J. Krog. 1954. Body temperatures of Arctic and sub-Arctic birds and mammals. J. Appl. Physiol. 6, 667-680.
- _____. and _____. 1955. Temperature of skin in the Arctic as a regulator of heat. J. Appl. Physiol. 7, 355-364.
- _____. H. Krog, and M. Monson. 1955. The metabolism of some Alaskan animals in winter and summer. Physiol. Zool. 28, 173-185.
- Jenkins, D., A. Watson, and G. R. Miller. 1963. Population studies on red grouse, Lagopus lagopus scoticus (Lath.) in North-East Scotland. J. Animal Ecol. 32 (3), 317-376.
- Kahl, Jr., M. P. 1963. Thermoregulation in the Wood Stork, with special reference to the role of the legs. Physiol. Zool., 36, 141-155.
- Kendeigh, S. C. 1934. The role of environment in the life of birds. Ecol. Monogr. 4, 299-417.
- King, J. R. and D. S. Farner. 1961. Energy metabolism, thermoregulation and body temperature. In Biology and Comparative Physiology of Birds (Edited by Marshall, A. J.), Vol. 2, pp. 215-288. Academic Press, London.
- Lack, D. 1966. Population studies of birds. Clarendon Press, Oxford. 341 pp.

- Larsen, J. A. and J. F. Lahey. 1958. Influence of weather upon a ruffed grouse population. *J. Wildl. Mgmt.* 22, 63-70.
- Lasiewski, R. C. 1964. Body temperature, heart and breathing rate, and evaporative water loss in hummingbirds. *Physiol. Zool.* 37, 212-223.
- _____, A. L. Acosta, and M. H. Bernstein. 1966. Evaporative water loss in birds--I. Characteristics of the open flow method of determination, and their relation to estimates of thermoregulatory ability. *Comp. Biochem. Physiol.* 19, 445-457.
- _____, and W. R. Dawson. 1967. A re-examination of the relation between standard metabolic rate and body weight in birds. *Condor* 69, 13-23.
- Miller, G. R., D. Jenkins, and A. Watson. 1966. Heather performance and red grouse populations. *J. Appl. Ecol.*, 3, 313-326.
- Misch, M. S. 1960. Heat regulation in the northern bluejay, Cyanocitta cristata bromia. *Physiol. Zool.* 33, 252-259.
- Moran, P. A. P. 1954. The statistical analysis of game bird records, II. *J. Animal Ecol.*, 23, 35-37.
- Morrison, P. R. and W. J. Tiets. 1957. Cooling and thermal conductivity in three Alaskan mammals. *J. Mammal.*, 38, 78-86.
- Nethersole-Thompson, C. and D. Nethersole-Thompson. 1939. Some observations on the sexual life, display and breeding of the red grouse. *Br. Birds* 32, 247, 254.
- Parratt, L. P. 1964. Birds of Glacier National Park. Glacier Natural History Association, West Glacier, Montana.
- Ritecy, R. W. and R. Y. Edwards. 1963. Grouse abundance and June temperatures in Wells Gray Park, British Columbia. *J. Wildl. Mgmt.* 27, 604-606.
- Salomonsen, P. 1939. Moults and Sequences of Plumages in the Rock Ptarmigan (Lagopus mutus (Montin)). Haase, Copenhagen.
- Scholander, P. F., R. Hock, V. Walters, F. Johnson, and L. Irving. 1950a. Heat regulation in some arctic and tropical mammals and birds. *Biol. Bull.*, 99, 237-259.
- _____, V. Walters, R. Hock, and L. Irving. 1950b. Body insulation of some arctic and tropical mammals and birds. *Biol. Bull.*, 99, 225-236.

- Siivonen, L. 1957. The problem of the short-term fluctuations in numbers of tetraonids in Europe. Papers on Game Research 19. Finnish Game Foundation, Helsinki. 44 pp.
- Svan, L. W. 1952. Some environmental conditions influencing life at high altitudes. Ecology 33, 109-111.
- Taylor, W. P. and W. T. Shaw. 1927. Mammals and Birds of Mt. Rainier National Park. National Park Service Washington, D.C.
- U. S. Department of Agriculture. 1941. Yearbook of Agriculture. U. S. Govt. Printing Office, Washington, D.C.
- Veghte, J. H. 1964. Thermal and metabolic response of the gray jay to cold stress. Physiol. Zool., 37, 316-328.
- _____ and C. F. Herreid. 1965. Radiometric determination of feather insulation and metabolism of Arctic birds. Physiol. Zool., 38, 267-275.
- Verbeek, N. A. M. 1965. Breeding biology, behavior and ecology of the water pipit (Anthus spinoletta), Master's Thesis, University of Montana, Missoula.
- West, G. C. 1960. Seasonal variation in the energy balance of the tree sparrow in relation to migration. Auk 77, 306-329.
- Wetmore, A. 1936. The number of contour feathers in passeriform and related birds. Auk 53, 159-169.