

SEASONAL DIFFERENCES IN RESTING METABOLIC RATE OF ALASKAN PTARMIGAN

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Abstract—1. The resting metabolic rates at thermal neutrality of willow ptarmigan acclimatized to summer and winter and of rock ptarmigan acclimatized to winter of 78·84, 70·50 and 70·84 kcal/bird per day respectively, are all higher than predicted by several body weight–metabolic rate equations.

2. The slope of the metabolic rate–ambient temperature line below thermal neutrality was steeper in summer than in winter in willow ptarmigan. The critical temperature of summer birds was 7·7°C and of winter birds, –6·3°C, lower than for any bird species thus far tested.

3. The slope of the metabolic rate–ambient temperature line below thermal neutrality for winter rock ptarmigan was similar to that of winter willow ptarmigan and the critical temperature was –1·3°C.

4. Alaska willow and rock ptarmigan are capable of maintaining their normal body temperature at any ambient temperature which they might encounter in arctic Alaska by a combination of excellent insulation and adequate metabolic capacity.

INTRODUCTION

THREE species of ptarmigan occur in North America, the willow (*Lagopus lagopus*), rock (*L. mutus*) and white-tailed (*L. leucurus*). All are characterized by seasonal changes in plumage color from various shades of brown to white in winter. All are exposed to cold climatic conditions and appear to be well insulated in winter by their thick feather covering which extends to the toes. Only the willow and rock ptarmigan occur in central and northern Alaska and from a metabolic point of view, present the most interesting species for study. Johnson (1968) has studied the resting metabolic rate of Colorado white-tailed ptarmigan in summer, West (1968) has traced the seasonal pattern of bioenergetics of willow ptarmigan from northern Alaska, and Moss (1972) has made some comparisons of nutrition significant to energetics of wild rock and willow ptarmigan in interior Alaska. The present study presents the seasonal changes in resting metabolic rate of captive willow and rock ptarmigan which serves as a base upon which other bioenergetic studies, such as my previous one (West, 1968), are founded.

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MATERIALS AND METHODS

Willow ptarmigan

Adult willow ptarmigan were captured by long-handled hoop nets or trap at Umiat (69°24' N lat., 152°07' W long.) and Anaktuvuk Pass (68°09' N lat., 151°46' W long.), Alaska in the summer and fall of 1964. Birds from these two areas are part of one morphologically homogeneous population (West *et al.*, 1968). Birds captured at Anaktuvuk may breed near Umiat on the Colville River and therefore the captive flock probably contained individuals from the same breeding unit. The ptarmigan were held at Umiat or Anaktuvuk until they had made the initial adjustment to captivity, then were sent by air to the Institute of Arctic Biology at College, Alaska (64°52' N lat., 147°50' W long.) where they were maintained in groups of five in raised cages throughout the year exposed to the local climate. For details on cage design see Jenkins *et al.* (1964) and West (1968). Birds gradually adapted to a diet of Purina Wild Game Bird Breeder Ration supplemented with willow branches and pigeon feed. Water or snow was always available.

Rock ptarmigan

Rock ptarmigan eggs and 1- to 5-day-old chicks were collected in the Eagle Summit area (65°29' N lat., 145°24' W long.), Alaska during June 1967 and brought to the Institute where they were hatched and/or raised to normal adult size during the summer of 1967 as part of another study. At the end of August, the birds were transferred to the same cages described above and were fed the same diet.

Metabolism tests

Oxygen consumption, and in some cases, carbon dioxide production were measured in a conventional open circuit system using a Beckman F-3 paramagnetic oxygen analyzer and a Beckman IR-215 infra red carbon dioxide analyzer (Morrison & West, 1972). All values were corrected by the appropriate formula in Depocas & Hart (1957) and to 760 mm barometric pressure and 0°C. Birds were removed from the outside pens, weighed to the nearest gram and a thermocouple of 36-gauge copper-constantan nylon coated wire was inserted under the skin in the interscapular area. The thermocouple was pushed forward about 2 cm under the skin and stitched in place. The thermocouple was then soldered to a spring coil of the same wire which led to the top of the metabolism chamber. (For details and a drawing, see Fig. 2 of West & Hart, 1966.) Body and chamber temperatures were both monitored continuously on a Leeds and Northrup 20 point recorder. Birds often managed to break one of the body temperature leads and therefore, there were unfortunately fewer body temperatures recorded at the lower chamber temperatures.

The birds were placed in metabolism chambers which consisted of either rectangular or cylindrical metal containers with sealed lids and fitted with an inlet at the top, an outlet at the bottom of the chamber and a hole in the top which received a rubber stopper containing the two thermocouple leads. The metabolism chambers were then placed either in a large walk-in cold room or a smaller Missimers test chamber and left for 1 hr before taking the first measurements. After obtaining a constant metabolic rate for about 5 min on each bird being tested at the same time, the temperature was lowered and another hour was allowed for the birds to adjust to the new condition after the temperature in the birds' metabolism chamber had reached the desired level. Temperatures were always lowered for successive tests and never raised as this results in a difference in the temperature-metabolism slope (Pohl, 1969). Usually values at three and sometimes four test temperatures were obtained on the same date. The same test individuals were not utilized in tests again for 4-5 days.

All tests were run in the dark. The summer willow ptarmigan were measured at night within the times of 1800 and 0400 hr while both the winter willow and rock ptarmigan were tested during the day from about 0900 to 1700 hr.

RESULTS

Dates of summer tests span 9 July to 17 August 1965, while winter tests ran from 20 to 30 December 1965, 3 to 9 January 1966 and 24 January to 14 March 1967 for willow ptarmigan and on 13 and 14 March 1968 for rock ptarmigan. The March dates may seem late in winter but at College, temperatures average -11.4°C in March with a minimum of -40°C recorded. Average winter temperatures (October through March) in the natural habitat of the willow ptarmigan range from -24.4°C at Umiat, -22.3°C at Anaktuvuk Pass to -19.0°C at Bettles, while those birds living in College experienced acclimatization temperatures of -19.6°C , just within the range of temperatures normally encountered by female willow ptarmigan which winter furthest south (Irving *et al.*, 1967). Summer temperatures (June through August) on the breeding range near Umiat average 9.6°C while the experimental flock experienced a warmer (13.2°C) summer. (For a month-by-month comparison of temperatures in the various locations just mentioned see Table 2 of West, 1968.) Temperatures in the rock ptarmigan's habitat in the Tanana-Yukon Uplands east of Fairbanks are essentially the same as those recorded at Fairbanks (Haugen & Brown, 1970).

Only adult willow ptarmigan were used in the metabolism tests but all of the rock ptarmigan were 9 months old. The rock ptarmigan had attained adult weight and I have no reason to believe that they responded differently from adults under the same test conditions. It is unfortunate that we were unable to hold over a sufficiently large population of rock ptarmigan in order to obtain metabolic information for summer birds.

Body weights of male willow ptarmigan are heavier than those of females in almost all cases and the weights change with season (West & Meng, 1968). The average weight of the two males used in the summer tests was 592 g and of the seven females, 520 g. In winter, body weights averaged 674 g for the five males and 505 g for the five females used in the tests. Rock ptarmigan are smaller birds and the average weight of the two males used in the tests was 490 g and of the three females, 393 g.

Metabolism

There were no significant differences in metabolic rate between males and females in any of the tests in spite of the difference in body weight. Therefore the data are treated together.

The resting metabolic rate of willow ptarmigan acclimatized to summer, measured at night in the dark was 699 cc O_2 /bird per hr at thermal neutrality (Fig. 1). At lower temperatures, the metabolic rate increased linearly according to the formula:

$$y = 862.12 - 22.444T (^{\circ}\text{C})$$

where y is cc O_2 /bird per hr. The critical temperature was 7.7°C and the temperature-metabolism slope extrapolated to 40.6°C which is 1 degree above the average

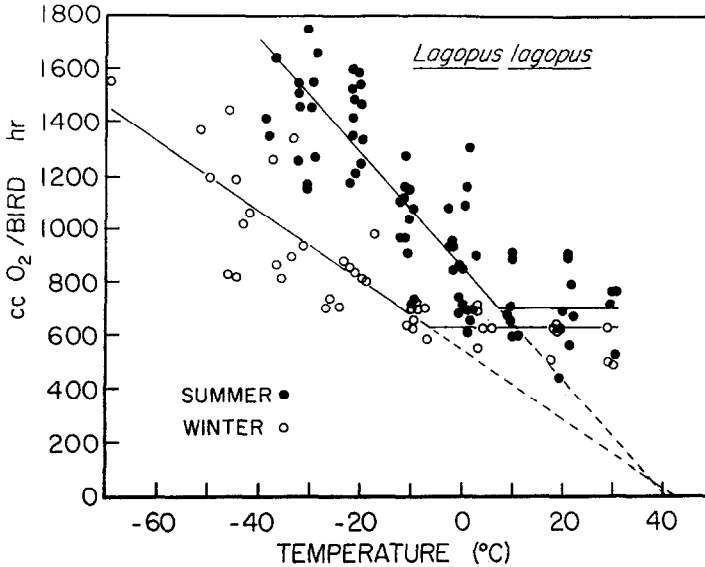


FIG. 1. Metabolic rate of willow ptarmigan acclimatized to summer (●) and to winter (○) measured at a series of ambient temperatures. Linear regression lines fitted by least squares.

of all body temperatures recorded during the summer tests (39-67°C). Body temperatures did not change significantly with test temperature (Fig. 2).

Willow ptarmigan acclimatized to winter and tested during the day but in the dark had a lower resting rate at thermal neutrality (625 cc O₂/bird per hr) and a flatter temperature-metabolism slope:

$$y = 544.96 - 13.544T (^{\circ}\text{C}).$$

The critical temperature was -6.3°C and the slope extrapolated to 42.5°C, 2.3°C above the average of all body temperatures recorded during the winter tests (40-21°C). Body temperatures declined significantly with decreasing temperature, but at a very low rate:

$$T_b = 40.424 - 0.0181T_a$$

(T_b = body temperature, T_a = ambient temperature) partly due to the high values at high test temperatures (Fig. 2).

The resting metabolic rate of winter acclimatized rock ptarmigan at thermal neutrality was 628 cc O₂/bird per hr, almost the same as that of the larger winter willow ptarmigan. The temperature metabolism line fitted to the measured data was:

$$y = 684.28 - 12.964T (^{\circ}\text{C}),$$

which extrapolated to 55.75°C, far above the body temperature which averaged 40-68°C (Fig. 3). The critical temperature was 4.5°C. It may be more accurate

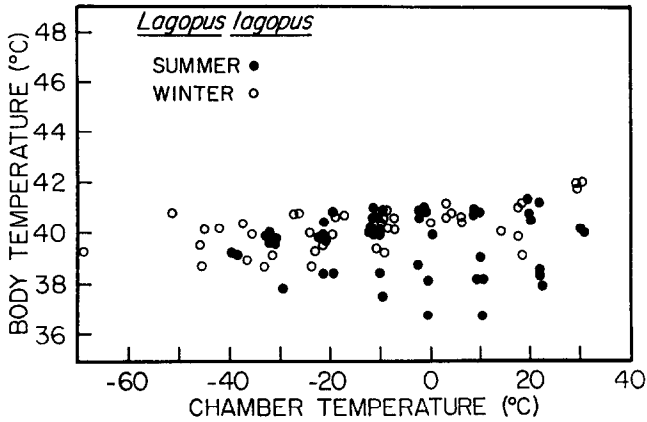


FIG. 2. Body temperatures of willow ptarmigan acclimatized to summer (●) and to winter (○) measured by indwelling thermocouples at a series of ambient temperatures.

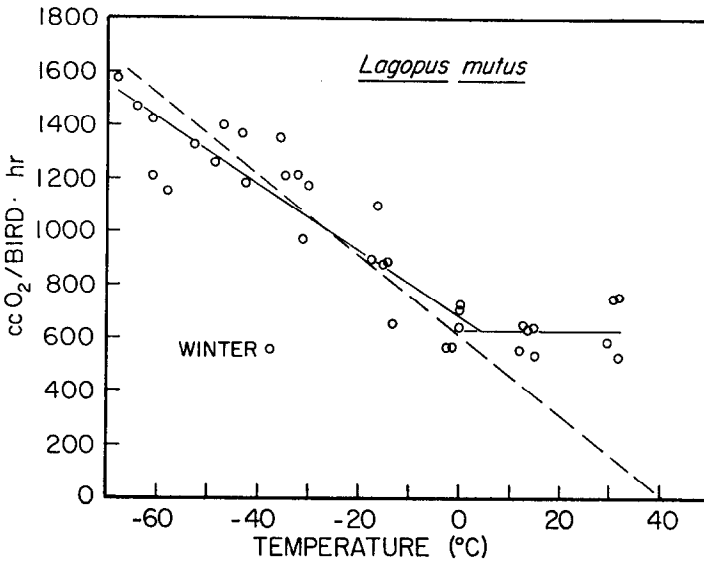


FIG. 3. Metabolic rate of rock ptarmigan acclimatized to winter and measured at a series of ambient temperatures. Solid linear regression line fitted by least squares. Dashed line is a least squares fit of the same points but forced through body temperature.

in this case to force the linear regression through body temperature (dashed line in Fig. 3) in which case the formula for the line becomes:

$$y = 609.35 - 15.817T (^{\circ}\text{C}),$$

and the critical temperature drops to -1.3°C . With the few data points and the two low values around -60°C , the latter line may be more realistic. Body temperatures of rock ptarmigan also declined significantly with decreasing chamber temperature:

$$T_b = 40.844 - 0.0142T_a,$$

because like the winter willow ptarmigan, birds tested near 30°C showed a tendency towards an elevated body temperature (Fig. 4).

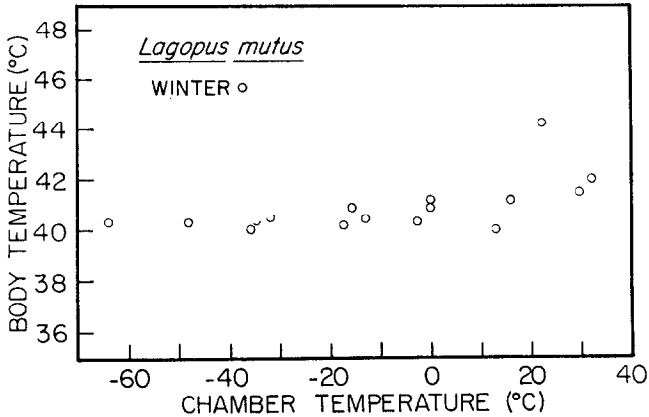


FIG. 4. Body temperatures of rock ptarmigan acclimatized to winter and measured by indwelling thermocouples at a series of ambient temperatures.

The R.Q. ($\text{cc CO}_2/\text{cc O}_2$) for winter acclimatized rock ptarmigan did not change with temperature and averaged 0.7086 ± 0.0089 ($n = 35$) which indicates that the birds were in a post-absorptive state. Therefore, 4.7 kcal/l. of oxygen was used to convert oxygen consumption values to their caloric equivalents.

DISCUSSION

The average resting metabolic rate of the summer acclimatized willow ptarmigan at thermal neutrality ($699 \text{ cc CO}_2/\text{hr}$) was not significantly higher than that of winter acclimatized birds ($625 \text{ cc O}_2/\text{hr}$) nor was there a significant difference between the values for winter acclimatized willow and winter acclimatized rock ptarmigan ($628 \text{ cc O}_2/\text{hr}$).

The resting metabolic rates of either rock or willow ptarmigan measured in the dark at thermal neutrality were higher than those predicted by either Lasiewski & Dawson (1967) or Aschoff & Pohl (1970), or than the existence rates predicted by Kendeigh (1970) for non-passerine birds (Table 1). The rock ptarmigan in winter is 44 per cent higher than predicted for a resting bird in the dark during its normal active time by Aschoff & Pohl (1970), while the willow ptarmigan in winter is only 14 per cent higher. Although the summer willow ptarmigan were

TABLE 1—MEASURED AND PREDICTED RATES OF METABOLISM OF WILLOW AND ROCK PTARMIGAN AT THERMAL NEUTRALITY (kcal/bird per 24 hr)

Species and season	Average body wt. (g)	This study	Lasiewski & Dawson (1967)*	Aschoff & Pohl (1970)†	Kendeigh (1970)‡
Willow ptarmigan (summer)	539	78.84	50.08	57.99	62.18
Willow ptarmigan (winter)	590	70.50	53.47	61.94	66.58
Rock ptarmigan (winter)	432	70.84	42.61	49.27	52.53

$$* \log M = \log 78.3 + 0.723 \log W.$$

$$\dagger \log M = \log 91.0 + 0.729 \log W.$$

$$\ddagger \log M = -0.2673 + 0.7545 \log W.$$

M = kcal/bird per 24 hr. W = body wt. in kg.

tested at night, and could be thought to be in their normal rest time, previous observation has shown that they are normally active for the full 24 hr during summer (West, 1968). Therefore, the prediction of Aschoff & Pohl for the normal active time was used in Table 1. Nevertheless, the measured value was 36 per cent higher than that predicted.

Johnson (1968) in measuring the resting metabolic rate of summer acclimatized white-tailed ptarmigan also found that at thermal neutrality his values were higher than predicted. Using Aschoff and Pohl's active-time formula, the white-tailed ptarmigan values are 21 per cent higher than predicted. I have no explanation for the difference between the measured and the predicted values. Observation of ptarmigan indicates that they are not hyperactive birds but just the contrary. Johnson's (1968) hypothesis that the increase is associated with summer molt does not explain the higher rates of winter birds.

Although there is a significant change in body temperature from high to low temperatures for winter ptarmigan of both species, the changes are so small as to have little biological significance. Ptarmigan are well insulated in winter and the significant slope may reflect an inability to unload heat at the high ambient test temperatures which were 25–30°C above any experienced in nature at that time of year.

Average heat loss coefficients for all temperatures below thermal neutrality are well within the range predicted by Herreid & Kessel (1967). Summer willow ptarmigan had a heat loss coefficient of 0.20 cal/g per hr per °C, higher than the predicted value of 0.16. On the other hand, winter willow ptarmigan had a lower coefficient than that predicted: 0.12 vs. 0.15 cal/g per hr per °C. The predicted value and the measured coefficient for winter rock ptarmigan were identical, 0.18 cal/g per hr per °C. The values measured here are three to four times those measured by Gessaman (1972) for the snowy owl (*Nyctea scandiaca*) which occupies the same region in winter.

The slope of Johnson's (1968) regression line for summer white-tailed ptarmigan ($-15.323 \text{ cc O}_2/\text{bird per hr per } ^\circ\text{C}$) is similar to that for the winter willow and rock ptarmigan but lower than that for the summer willow ptarmigan. This may indicate that white-tails in summer are better insulated than willow ptarmigan in summer. Johnson notes that none of his birds measured between -18 and -31°C could maintain an elevated metabolic rate for over 2 hr and four of the nine birds used died subsequent to the experiments. In contrast, summer acclimatized willow ptarmigan were tested between -18 and -38°C on the same night and therefore were in the metabolism chambers for a minimum of 3 hr. They did not show any significant drop in body temperature nor did any of the birds die as a result of the tests. Therefore, even though possibly slightly better insulated, the white-tails apparently do not have the same metabolic capacity as their northern congeners.

This paper gives resting metabolic rates for thermoregulation for willow ptarmigan upon which the seasonal pattern of other energy demanding activities are based (West, 1968). In the caged birds I studied, existence in winter required additional energy at all ambient temperatures above -35°C . Below this temperature, activity must be greatly reduced and therefore caged existence requires little additional energy above the resting energy requirement at very cold temperatures. At temperatures above -35°C in winter, however, caged birds utilized increasingly more energy above the resting level until at 0°C , the additional cost was about 30 kcal/day (West, 1968).

In summer, molting birds in cages required only about 17 kcal/day over the resting rate at 18°C , but due to increased activity, the additional cost of caged existence rose again to about 30 kcal/day near 0°C . Therefore, it appears that ptarmigan are less inclined towards added energy expenditure for activities other than thermal regulation at both the high and low ends of the annual climatic temperature gradient than they are in the middle of the range when the ambient temperatures are between 0 and 10°C . And in fact, during the breeding season when the greatest energy expenditure outside of thermal regulation in the cold is required, the ambient temperature on the breeding grounds averages $5-8^\circ\text{C}$.

The data in Fig. 1 indicate that the small seasonal change in insulation makes a large difference in the energy required for a willow ptarmigan to exist in the cold. At -40°C for example, a bird in winter plumage has only to increase his resting metabolic rate at thermal neutrality 1.7 times while the same bird in summer plumage must increase its rate 2.5 times. Similarly, a bird capable of utilizing $1800 \text{ cc O}_2/\text{hr}$ in summer, presumably can do the same in winter. The 1800 cc O_2 in summer allows the bird to maintain its body temperature while existing at -42°C while the same energy expenditure in winter would permit the bird to exist at -93°C , lower than any temperature recorded on Earth.

The excellent insulation also permits birds in summer to exist without increasing their metabolic rate down to 7.7°C , 1 degree above the average temperature in June on the breeding range. While in winter, rock ptarmigan, by gradually increasing insulation, can exist down to -1.3°C before raising their metabolic rate,

and willow ptarmigan in winter extend this ability down to -6.3°C lower than any other bird species thus far examined, except possibly the arctic gull (*Larus hyperboreus*) measured by Scholander *et al.* (1950).

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Key Word Index—Metabolic rate; winter/summer metabolism; Alaska; ptarmigan metabolism; *Lagopus lagopus*; *Lagopus mutus*; *Lagopus leucurus*.