STANDARD METABOLIC RATE AND LOWER CRITICAL TEMPERATURE FOR THE RUFFED GROUSE

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STUDIES on thermoregulation in the Tetraonidae (Grouse family) have not often been undertaken. *Lagopus* (ptarmigans) and *Dendragapus* (Blue Grouse) have received some detailed attention in this respect (Veghte and Herreid, 1965; West, 1968; Stiven, 1961) but there is a definite lack of information on the Ruffed Grouse (*Bonasa umbellus*). For the Ruffed Grouse we cannot, in fact, find a single documentation on the most basic aspect of thermoregulation—the standard (or basal) metabolic rate. Lack of such studies may be attributed to the difficulty of obtaining and raising grouse for experiments.

In this paper we report on body temperature, standard metabolic rate, and lower critical temperature as determined on captive Ruffed Grouse.

METHODS

Experimental birds were hatched from artificially incubated eggs collected from four nests in Hampshire County, Massachusetts, during May of 1968. They were kept in individual wire-mesh cages ($0.5 \times 0.5 \times 1$ m in size) in an open-fronted lean-to, and thus exposed to atmospheric temperature. Snow or water and turkey finisher supplemented with cracked corn and corn oil were provided ad libitum. Individuals were handled frequently and, we believe, were reasonably tractable during the experiments. Sex determination was by external criteria described by Bump et al. (1947) and Palmer (1959).

Metabolic measurements were made at night, when grouse are least active, during February and March, 1969. Oxygen consumption was determined in an open-circuit system adapted from Dawson (1958). Outdoor air flowed, in sequence, through a garden hose, a respiration chamber, then through tygon tubing to a variable speed tubing pump, a desiccant, and a flowmeter. A 200 ml-min^{-1} sample of air at the flowmeter was continuously shunted to a Beckman F3 paramagnetic oxygen analyzer. The analyzer's electrical potential, generated in proportion to the volume of oxygen in the air sample, was continuously recorded on a strip-chart potentiometer.

Air-flow through the respiration chamber varied from 1,000 to 1,300 ml-min^{-1} (not corrected to S.T.P.), but was held constant in a given experiment. Flow-rate was adjusted for each animal so that the volume percentage of oxygen in the outlet air did not fall below 19.9, the point at which oxygen-stress may begin.

The respiration chamber was a five-gallon galvanized pail with side fittings for inlet and outlet tubes. An airtight seal was assured by placing the chamber open-side downward in a saturated solution of calcium chloride. Subjects stood on 0.6 cm wire-mesh. The chamber was housed in a thermostatically-controlled cold-box.

Air-temperature in the respiration chamber was lowered in 5° steps from 20° to −40° C over a period of 4 hours. Temperature was held at each 5° step for a minimum of 20 minutes, to allow time for the subject to respond and for the oxygen-analysis system to

detect this response. Data were taken at the beginning of each step and at five-minute intervals until oxygen consumption stabilized.

Response time, which we consider that time necessary to detect a complete turnover of a volume of air in the respiration chamber, was 8 minutes at 1105.0 ml-min^{-1} (uncorrected to S.T.P.). Therefore, to avoid error due to contamination by air exhaled in the preceding temperature step, we excluded oxygen-consumption values for the first 10 minutes within a step. Consumption values, corrected to S.T.P., were calculated from the appropriate equation of Depocas and Hart (1957).

Cloacal temperature was measured with a copper-constantan thermocouple glued within a 30.5 by 0.3 cm diameter tygon tube. The tube was passed through a styrofoam block and 3 cm into the bird's cloaca; the block was then taped to the central rectrices for support.

To test the significance of the heat increment of food digestion (or specific dynamic action) in thermoregulation, birds in 12 trials were not allowed to eat for at least 5 hours before an experiment ("postabsorptive condition"), while birds in 10 trials were allowed food until a maximum of 3 hours before testing ("non-postabsorptive condition"). Work (Duke et al., 1968) done on the Ring-necked Pheasant (*Phasianus colchicus*) suggests that food will pass through a wild galliform in 1 to 8 (average 5) hours. On this basis we defined the postabsorptive condition as 5 hours without food.

Subjects were selected randomly, without regard to sex. They were allowed a minimum of 2 hours for habituation at the initial temperature. In total, seven trials were obtained from four females and 15 trials from 11 males.

RESULTS AND DISCUSSION

Effect of Experimental Conditions.—We used covariance analysis to test the effect on oxygen consumption due to absorptive condition, sex, and month. Regressions describing the relationship between a bird's oxygen consumption (ml 0_2 consumed-min^{-1}-g body wt^{-1}) and air temperature in the chamber were transformed to linearity by a logarithmic transformation of oxygen consumption. After preliminary analysis data for individuals within a subclass (e.g., postabsorptive males in February) were combined.

We concluded that all the experiments could be described by one regression, since there were no clearcut differences in oxygen consumption assignable to sex, absorptive condition, or the month in which the data were collected. If significant differences due to these variables did in fact exist, we believe they were masked by the differences between individuals within the subclasses.

Cloacal Temperature.—Cloacal temperature was used as an approximation of deep-body temperature during the experiments. For the nine birds from which readings were obtained, temperatures remained fairly constant at exposures from 20° to −40° C. Mean temperature in 63 determinations was 41.5° C (standard error 0.19, range 40.4° to 42.6° C). This is slightly lower than 42.5° C reported by Bernard et al. (1944) for a single Ruffed Grouse.

Standard Metabolic Rate.—King and Farner (1961) define standard meta-

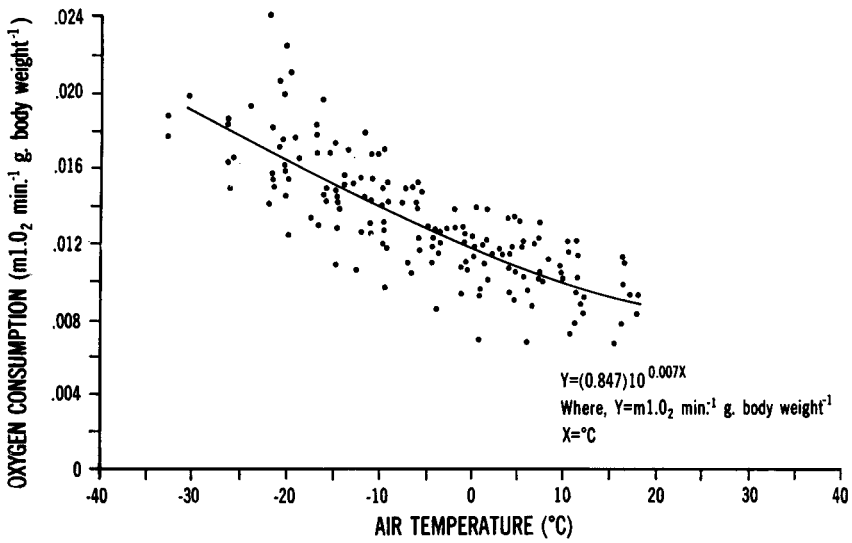

FIG. 1. Regression of oxygen consumption on air temperature, all grouse. Each datum represents the average of 3 to 4 readings. Line fitted by method of least-squares.

bolic rate (SMR) as the heat production per unit time when the homeotherm is in a postabsorptive condition (i.e., not digesting or absorbing food), in thermoneutral surroundings, and as completely as possible at muscular and psychical rest.

The standard metabolic rate was determined by averaging the oxygen consumption values above the lower critical temperature. In a few cases where the oxygen consumption vs. temperature graph was hyperbolic the minimum point on the curve was taken as the standard metabolic rate.

Average values for smallest subclasses, were lumped according to sex, month, and absorptive condition and subjected to paired t-tests. There were no statistically significant differences ($P < 0.05$). The standard metabolic rate for grouped data was 0.61 ml 0_2 consumed-min^{-1}-g body weight^{-1}. Variance in terms of mean standard deviation (n = 14) was 0.09.

We assumed the test subjects maintained a respiratory quotient of 0.8 and, therefore, were generating 4.8 kcal for each liter of oxygen consumed during standard metabolism. A grouse at mean weight (644 g) would then produce 46.1 ± 1.8 kcal-day^{-1}. The variance indicated is one standard error of the estimate, S_{yx}. Comparative analysis with published predictors (King and Farner, 1961; Lasiewski and Dawson, 1967; Zar, 1968*a*, 1968*b*) is most valid in the case of Zar's (1968*a*) equation for Galliformes:

$$M = 72.6W^{0.698} \pm 15.3$$

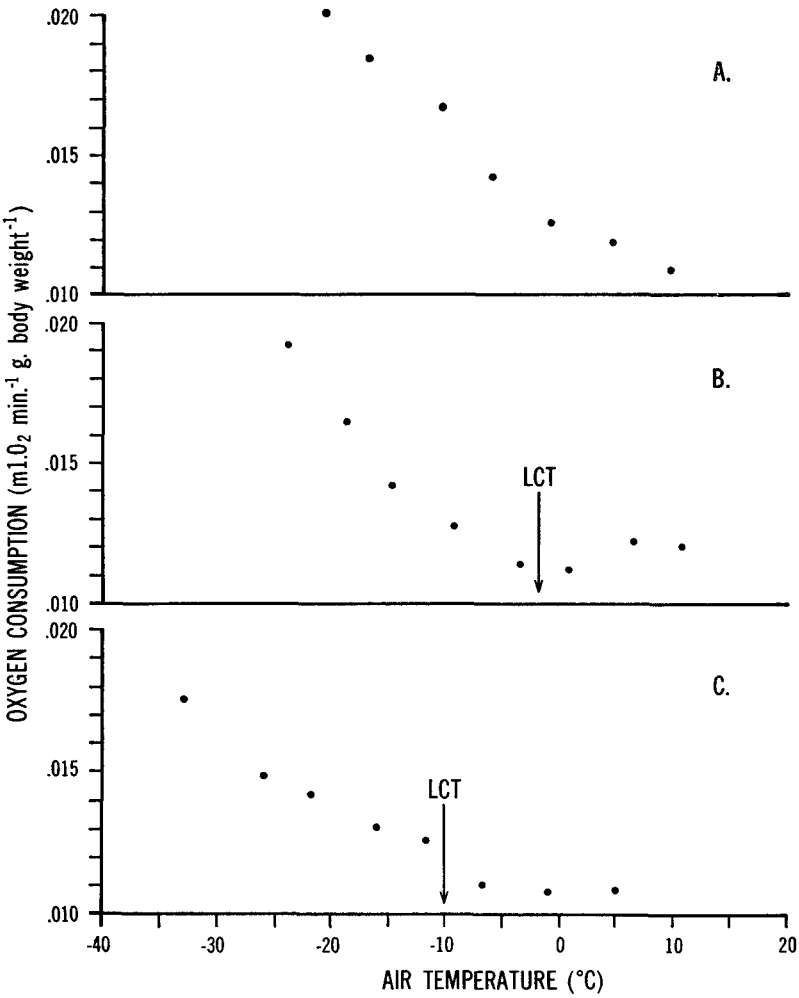

FIG. 2. Selecting the point of lower critical temperature (LCT), actual data on 3 individuals. (A) Linearity, LCT not apparent. (B) Hyperbolic metabolic response; LCT = -2.0° C. (C) Classic, discontinuous response; LCT = -10.0° C.

where M = kcal bird-day^{-1}, W = body weight in kg, and the variance is the standard error of estimate. Zar (1968*a*) used data from Lasiewski and Dawson (op. cit.) which involved 13 determinations of metabolic rates from eight species of Galliformes. While our determination (46.1) is 14 percent lower than 53.4 kcal-day^{-1} for a 644 g bird as predicted by the equation, there is marked overlap when our upper confidence limit (mean plus two

standard errors), 49.7, is compared with 22.8, the lower limit ($\bar{x} - 2s_{\bar{x}}$) of Zar's prediction. The statistical picture is not entirely clear (Zar, 1968*b*), but this degree of overlap strongly suggests that our estimate for the Ruffed Grouse fits predictions from regressions concerning the relationship between metabolic rate and body weight in birds in general.

Lower Critical Temperature.—Lower critical temperature (LCT) is defined as the temperature below which a resting animal must increase its metabolic rate from the basal level (i.e., the SMR) to meet environmental demands for heat. In classic theory metabolic activity increases quite abruptly as environmental temperature shifts into the zone below thermoneutrality and the transition can be identified by graphical procedures. Data from Scholander et al. (1950), Steen (1958), Dawson and Tordoff (1959), King (1964), Veghte (1964), and West and Hart (1966) confirm this view.

But our data more closely agree with those of West (1962) in that the transition from constant to increasing metabolism occurred over an extended range of temperature. While we did not test our animals at temperatures above 20° C, we suspect that the extended shape of the metabolic response is hyperbolic (Fig. 2b) and not discontinuous as classic theory holds (Fig. 2c).

Therefore, we chose Barott and Pringle's (1946) visual method of describing the lower critical temperature, rather than the Scholander method (Scholander et al., op. cit.) of extrapolating a tangent along the ascending oxygen-consumption curve to body temperature. The method of our choice, in its adapted form, is a visual estimation of the midpoint of the curve connecting the values for oxygen consumption in the zone of relative constancy with the portion of the graph with an increasing and constant slope. Three representative sets of data illustrate the method (Fig. 2).

Even by this method we could not assign values for the lower critical temperature in eight of the 22 trials (Fig. 2a). In those eight cases there was no apparent zone of constant oxygen-consumption and the graphs were essentially linear with no transformation of data. We believe that initial experimental temperature was, in these cases, at or below the critical temperature.

We did assign values for the lower critical temperature to 14 of 22 grouse. Average values for the smallest subclasses were lumped according to sex, month, and absorptive condition. *T*-tests ($P < 0.05$) did not indicate statistically significant differences attributable to sex or absorptive condition.

The LCT for all grouse combined was -0.3° C. The linear equation describing oxygen consumption *below* this point is

$$Y = 0.011 - 0.0002X$$

where Y = ml O_2-min^{-1}-g body weight^{-1}, and X = °C.

SUMMARY

Cloacal temperature, standard metabolic rate, and lower critical temperature were determined for 16 Ruffed Grouse in February and March. Oxygen consumption values were determined over a temperature range of 20° C to −40° C. Differences were not statistically significant when results were arranged by sex, month, and absorptive condition. A regression describing the relationship of oxygen consumption to air temperature was derived for the combined results of all grouse.

Standard metabolic rate for a grouse of average body weight (644g) was 0.01 ml O_2 consumed-min^{-1}-g body $weight^{-1}$. There was a small change in the lower critical temperature from February (−6.0° C) to March (0.3° C); the LCT for all subclassifications combined was −0.3° C.

Cloacal temperature averaged 41.5° C in 63 determinations on nine grouse.

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IMPORTANT ANNOUNCEMENT

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